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Comparative analysis of shell occupation by two southern populations of the hermit crab *Loxopagurus loxochelis* (Decapoda, Diogenidae)

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COMPARATIVE ANALYSIS OF SHELL OCCUPATION BY TWO SOUTHERN
POPULATIONS OF THE HERMIT CRAB *Loxopagurus loxochelis*
(DECAPODA, DIOGENIDAE)

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ABSTRACT

The present study aimed to comparatively verify the relation between the hermit crabs and the shells they use in two populations of *Loxopagurus loxochelis*. Samples were collected monthly from July 2002 to June 2003, at Caraguatatuba and Ubatuba Bay, São Paulo, Brazil. The animals sampled had their sex identified, were weighed and measured; their shells were identified, measured and weighed, and their internal volume determined. To relate the hermit crab's characteristics and the shells' variables, principal component analysis (PCA) and a regression tree were used. According to the PCA analysis, the three gastropod shells most frequently used by *L. loxochelis* varied in size. The regression tree successfully explained the relationship between the hermit crab's characteristics and the internal volume of the inhabited shell. It can be inferred that the relationship between the morphometry of an individual hermit crab and its shell is not straightforward and it is impossible to explain only on the basis of direct correlations between the body's and the shell's attributes. Several factors (such as the morphometry and the availability of the shell, environmental conditions and inter- and intraspecific competition) interact and seem to be taken into consideration by the hermit crabs when they choose a shell, resulting in the diversified pattern of shell occupancy shown here and elsewhere.

RESUMO

O presente estudo teve como objetivo verificar de forma comparativa a relação entre ermitões e conchas utilizadas por duas populações de *Loxopagurus loxochelis*. Foram realizadas coletas mensais, de julho 2002 a junho 2003, nas Enseadas de Caraguatatuba e de Ubatuba, São Paulo, Brasil. Os animais amostrados foram identificados quanto ao sexo, pesados, e mensurados; as conchas de gastrópodes foram identificadas, mensuradas, pesadas e tiveram seu volume interno determinado. Para relacionar as variáveis dos ermitões com as conchas foram utilizadas a análise de componentes principais (PCA) e a árvore de regressão. As três conchas de gastrópodes utilizadas mais intensamente diferiram em tamanho de acordo com a PCA. A árvore de regressão explicou com sucesso a relação entre características do ermitão e volume interno das conchas habitadas. Inferiu-se que a relação entre a morfometria de um ermitão e sua concha não é simples e não é possível de ser explicada com base somente em correlações diretas entre atributos do corpo e da concha. Inúmeros fatores (como morfometria e disponibilidade da concha, condições ambientais e competição inter e intra-específica) interagem e devem ser levados em consideração na escolha de uma concha pelos ermitões, resultando no diversificado padrão de ocupação de conchas demonstrado neste e em outros trabalhos correlatos.

Descriptors: Diogenidae, Shell utilization, PCA, Regression tree, Atlantic.

Descritores: Diogenidae, Utilização de conchas, PCA, Árvore de regressão, Atlântico.

INTRODUCTION

Gastropod shells constitute a vital resource for hermit crabs (CONOVER, 1978; GARCIA; MANTELATTO, 2000), providing them with many important conditions, such as protection against predators (REESE, 1969; VANCE, 1972; BERTNESS, 1982) and physical stress (BOLLAY, 1964; REESE, 1969), and granting protection to their eggs during the egg-laying period (FOTHERINGHAM, 1976). Gastropod shell availability acts as a limiting factor to these animals' populations (PROVENZANO, 1960; VANCE, 1972a; KELLOGG, 1976; SPIGHT, 1977; BARNES, 1999) and influences their growth rates (MARKHAM, 1968; CHILDRESS, 1972; VANCE, 1972; FOTHERINGHAM, 1976a; BERTNESS, 1981; HAZLETT, 1981) and egg production (BOLLAY, 1964; BERTNESS, 1981; ELWOOD et al., 1995; MANTELATTO et al., 2002).

Understanding the hermit crab's pattern of shell occupancy is not a straightforward task. Its selection of its shell takes into consideration mainly the latter's size and shape (GRANT; ULMER, 1974), but also involves specific exploratory behavior by which the shell's overall condition, weight, color and even internal volume can be assessed (MITCHELL, 1976). Moreover, the pattern of the hermit crab's shell occupancy may vary amongst populations of a given species as it is influenced both by the availability of a particular kind of shell and the environmental characteristics (MANTELATTO; GARCIA, 2000), as well as by the relative abundance of the living gastropods and their mortality rates (OHMORI et al., 1995; MANTELATTO; MEIRELES; 2004). All these factors are closely related to the biogeographical distribution of the species and the adjacent environmental conditions in those different areas (MANTELATTO et al., 2010).

Hermit crabs tend to occupy shells in better condition when inhabiting places with high shell abundance, as distinct from places with a shortage of shells (SCULLY, 1979). There is often a large overlap in the way the shells are used by coexistent species (HAZLETT, 1981). The change to a new shell may occur when the hermit crab finds an empty one or obtains it from another individual, through a ritualized behavior (HAZLETT, 1981; SATO; SENO, 2006).

The hermit crab *Loxopagurus loxochelis* (Moreira, 1901) (Diogenidae) is a monotypical hermit crab genus, endemic to the southwestern Atlantic coast, occurring in Brazil (from Bahia to Rio Grande do Sul), Uruguay, and Argentina (MELO, 1999). As a consequence of its widespread distribution in South America, knowledge of its biology has been accumulating over recent years (see AYRES-PERES;

MANTELATTO, 2008 for revision). Recollecting specific information related to shell studies in that area, we may cite the epibiont diversity and the pattern of shell occupancy (MARTINELLI; MANTELATTO, 1998 and 1999; AYRES-PERES et al., 2008; CARRANZA et al., 2008; AYRES-PERES; MANTELATTO, 2010), shell preference under laboratory conditions (BIAGI et al., 2006) and the shell's influence on fecundity (TORATI; MANTELATTO, 2008).

In the light of this scenario, this study sought to ascertain the comparative relationship between the hermit crabs and the shells they use, in two populations of *L. loxochelis*. This investigation was based on biological data obtained by continuous sampling undertaken in natural environment and compared by means of multivariate analysis.

MATERIAL AND METHODS

Sampling

Loxopagurus loxochelis was sampled monthly from July 2002 to June 2003, in two areas: Caraguatuba (23°36'09" to 23°40'12"S and 45°07'16" to 45°25'35"W) and Ubatuba (23°26'08" to 23°31'57"S and 44°55'28" to 45°03'18"W), in São Paulo State, Brazil. A boat equipped with two "double-rig" trawl nets was used to sample the hermit crabs at 5, 10, 15, 20, 25 and 30 m deep along a transect parallel to the coastline (AYRES-PERES; MANTELATTO, 2008a). After being captured, the crabs were kept frozen until further analysis in the laboratory. After defreezing, at room temperature, the crabs were removed manually from their shells. Then their characteristics were recorded as follows: sex (according to the gonopore position), fresh weight (in g), cephalothoracic shield length (CSL) and width (CSW), and left chelae length (LCL) and width (LCW). Individuals with CSL < 4.0 mm were considered juveniles, following Ayres-Peres and Mantelatto (2008, 2008a). Gastropod shells were identified according to Rios (1994), and the following characteristics of each shell were analyzed: aperture length (SAL) and width (SAW), dry weight (SDW) and internal volume (SIV). The shells' internal volume was obtained by filling them with sand ($\phi = 0.105 - 0.25$ mm), as in Bertness (1981) and Mantelatto and Garcia (2000). The shells broken during the crabs' removal were discarded for the purposes of this analysis.

Statistical Analysis

1) Shell occupation in relation to areas/depths: cluster analysis using the PVCLUST package (SUZUKI; SHIMODAIRA, 2006), available for R software (R

Core Development Team, 2010), was applied to verify whether the gastropod shells utilized by *L. loxochelis* differed across different water depths (5, 10, 15, 20, 25 and 30 m) and sampling areas (Caraguatatuba and Ubatuba regions).

2) Hermit crab and gastropod shell characteristics: the three shells that were most used by *L. loxochelis* in our samples: *Buccinanops gradatum*, *Olivancillaria urceus* and *Stramonita haemastoma* - and which corresponded to about 90% of the total individuals captured (see Results) - were chosen to relate the hermit crab's characteristics to the pattern of shell occupancy. These characteristics (width, length, internal volume and dry weight) were compared using principal component analysis (PCA). PCA was also employed to compare the hermit crab's characteristics (cephalothoracic shield length and width, chelipeds length and width, weight) as between the two study areas. The significance of the differences between these groups was tested using Analysis of Similarity (ANOSIM). A third PCA was employed to see whether the males and females of *L. loxochelis* occupied different gastropod shells according to their attributes. We employed a 2-way ANOSIM to test the differences between sexes and species. In both ANOSIM tests, the Euclidean dissimilarity measure and 10000 permutations were used. PCA and ANOSIM were run using PAST software (HAMMER et al., 2001).

3) Hermit crab *versus* shell: An attempt was made to relate the hermit crab's characteristics (sex, dry weight, cephalothoracic shield length and width, propodus length and width) as independent variables influencing the use of the shell through a regression tree analysis. Regression trees are particularly useful in ecological studies for at least two reasons: this method permits the joint use of both qualitative and quantitative variables as predictors (independent variables) and it allows the inclusion of multiple predictors irrespective of whether multicollinearity exists between them (DEATH; FABRICIUS, 2000; PRASAD et al., 2006). regression trees are, therefore, well suited to relate the hermit crab's characteristics to the shell's, because the former often include both qualitative (e.g., sex) and quantitative variables (e.g., size, weight); further, variables such as size, volume and weight are often closely correlated to each other, i.e., are collinear. Four trees were built, one for each shell's characteristics (aperture width, length, dry weight and internal volume) as the dependent variable; however, only the tree that explained a significant portion of the total variance was kept. This tree was then pruned (using the 1-SE rule; see DE'ATH, 2002) to obtain a tree with a minimum number of splits but that explained the largest portion of the variance. These procedures used the RPART package

(THERNEAU; ATKINSON, 2010) for R software (R Core Development Team, 2010).

RESULTS

In Caraguatatuba, 366 hermit crabs using 14 different kinds of gastropod shells were captured. Of this total, 53.8% of the individuals occupied the *Buccinanops gradatum* shells, 31.3% occupied the *Olivancillaria urceus* and 8.5% occupied the *Stramonita haemastoma*. In Ubatuba, *L. loxochelis* was less abundant (126 ind.) and found only in five gastropod species' shells. Sixty-three percent of these individuals were found in *O. urceus* and 30.2% in *B. gradatum* (Table 1).

The cluster analysis indicated that the gastropod community inhabited by *L. loxochelis* in the two bays was different; it also evidenced differences between depths. *Loxopagurus loxochelis* was absent at 5m deep, in Ubatuba. At the shallowest site (5m deep) of Caraguatatuba and at the deepest sites of Caraguatatuba and Ubatuba bays (30 and 25m, respectively), *L. loxochelis* used a different combination of shells from that used at intermediate depths (Fig. 1). In the shallow waters of Caraguatatuba (5m), *L. loxochelis* was found to occupy the greatest diversity of shells, comprising eight gastropod species' (*Buccinanops gradatum*, *Chicoreus tenuivaricosus*, *Dorsanum molinifera*, *Fusinus brasiliensis*, *Olivancillaria urceus*, *Phalium granulata*, *Polinices hepaticus* and *Stramonita haemastoma*), though it was most frequently found in *S. haemastoma*. On the other hand, at 30m in this same bay, the hermit crabs were distributed among four gastropod species' shells. The cluster formed in the intermediate depths of Caraguatatuba (Fig. 1) is characterized by the use of five or six species, but highly skewed towards *B. gradatum* (60% of total individuals, on average), followed by *O. urceus* (27% of total individuals, on average). The intermediate depths at Ubatuba were quite different from that cluster (Fig. 1), as fewer gastropod species were used (two to five) and the shell occupation was more evenly distributed among *B. gradatum* and *O. urceus*. The deepest site cluster at Ubatuba (25m) differed from the others mainly because the shell used by *L. loxochelis* was highly skewed towards *O. urceus* (22 out of 23 individuals).

The three gastropod shells most frequently used by *L. loxochelis* varied in size (Fig. 2). PCA axis 2 (23% of variance explained) indicates that *O. urceus* shells are heavier than those of *S. haemastoma* and *B. gradatum*, which have, on the other hand, larger aperture widths (Fig. 2). There were little differences between the species along the PCA axis 1, which was related to the shell's internal volume and aperture length (Fig. 2). ANOSIM indicated that the differences

between the species are significant (ANOSIM $r = 0.18$; $p < 0.0001$): *O. urceus* differing from *S. haemastoma* (Bonferroni-corrected $p = 0.013$) and from *B. gradatum* (Bonferroni-corrected $p < 0.0001$).

The individuals of the two *L. loxochelis* populations studied did not differ with respect to the

body characteristics measured (ANOSIM $r = 0.002$; $p = 0.45$) (Fig. 3). Despite their being different populations the geographical separation and the environmental pressures were insufficient to produce morphometric changes whether in the males or the females of the population studied.

Table 1. Gastropod species occupied by *Loxopagurus loxochelis* (Anomura, Diogenidae) in Caraguatatuba (CAR) and Ubatuba (UBA) bays, São Paulo State, Brazil, from July/2002 to June/2003.

Gastropod shells	Males		Non-ovigerous females		Ovigerous females	
	CAR	UBA	CAR	UBA	CAR	UBA
<i>Agaronia travassoi</i> (Morretes, 1938)	-	01	-	-	-	-
<i>Buccinanops deformis</i> (King & Broderip, 1832)	01	-	-	-	02	-
<i>Buccinanops gradatum</i> (Deshayes, 1844)	120	20	60	15	16	03
<i>Chicoreus tenuivaricosus</i> (Dautzenberg, 1927)	-	-	01	-	-	-
<i>Conus clerii</i> Reeve 1844	-	-	01	-	-	-
<i>Cymatium parthenopeum</i> (von Salis, 1793)	01	1	01	-	-	-
<i>Dorsanum moliniferum</i> (Valenciennes, 1834)	01	-	01	-	-	-
<i>Fusinus brasiliensis</i> (Grabau, 1904)	02	-	01	-	-	-
<i>Olivancillaria urceus</i> (Röding, 1798)	66	56	40	22	08	02
<i>Phalium granulata</i> (Born, 1778)	03	-	-	-	-	-
<i>Polinices hepaticus</i> (Röding, 1798)	03	-	-	-	02	-
<i>Polinices lacteus</i> (Guilding, 1834)	-	-	01	-	-	-
<i>Prunum martini</i> (Petit, 1853)	-	-	01	-	-	-
<i>Stramonita haemastoma</i> (Linnaeus, 1767)	23	3	06	1	02	02
<i>Tonna galea</i> (Linnaeus, 1758)	01	-	-	-	-	-
Total	221	81	113	38	30	07

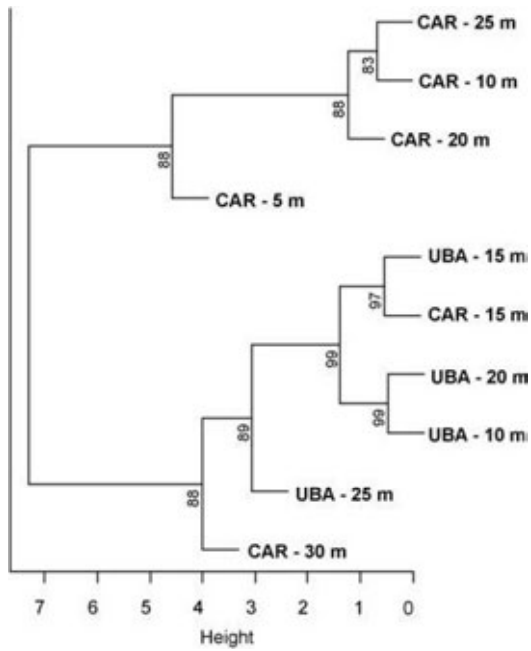


Fig. 1. Cluster analysis of the gastropod species' diversity utilized by the hermit crab *Loxopagurus loxochelis* (Diogenidae) in different depths (from 5 to 30 m) and in two areas in São Paulo, Brazil. Values near groups are AU values (approximate unbiased bootstrap). CAR = Caraguatatuba bay and UBA = Ubatuba bay

PCA axis 1 (90% of variance explained), which was related to the chela width and the

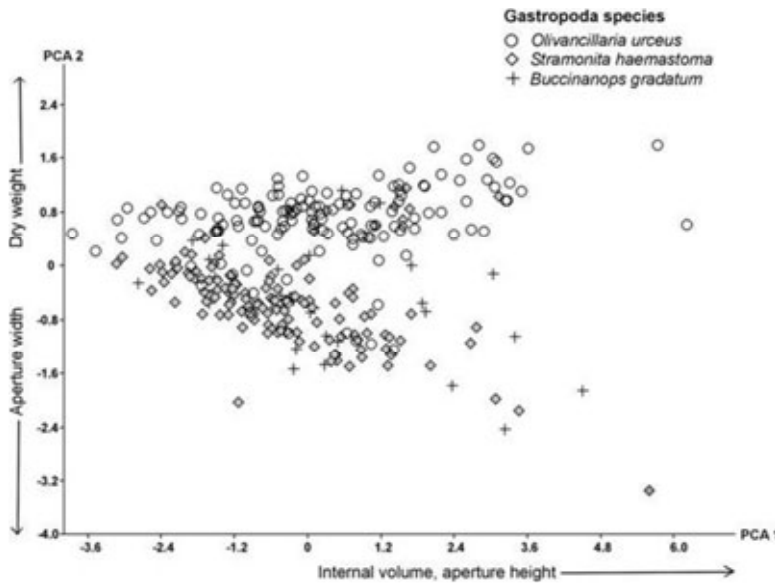


Fig. 2. Principal component analysis (PCA) of the gastropod shell's attributes occupied by the hermit crab *Loxopagurus loxochelis* (Diogenidae). The two attributes with larger scores of each PCA axis are shown next to the axes, and the setae indicate the direction of the increase. These two axes explained 90% of the total variance.

cephalothoracic shield length and width (Fig. 4), indicates differences between the sexes: the females of *L. loxochelis* were smaller than the males, irrespective of the shell utilized (Fig. 4). Axis 2 shows a tendency on the part of lighter females with larger cephalothoracic shields to occupy more *B. gradatum* than the other two gastropods and it can also be noted that small males are not found in *S. haemastoma* shells (Fig. 4). ANOSIM indicates that *L. loxochelis* male and female characteristics are significantly statistically different ($r = 0.20$; $p < 0.0001$), but differences between the gastropod species' are not ($r = 0.054$; $p = 0.006$).

When occupation was analyzed, based on hermit size-class at Caraguatatuba, it was noticed that the animals in the smaller classes (2.0 – 4.4 mm) occupied the *O. urceus* shells more frequently, and that, in the intermediate classes (4.4 – 6.8 mm), there was more frequent occupation of *B. gradatum*. In the final classes (6.8 – 8.0 mm), more diverse shell occupation was seen, and no hermit crabs were found occupying *B. gradatum* (Fig. 5). Juveniles (CSL < 4.0 mm) used nine species of gastropod shells, *O. urceus* being the predominant one. At Ubatuba, *O. urceus* species were the most used by all size classes, except by the classes 6.8 – 7.4 mm, the individuals of which occupied only *B. gradatum* (Fig. 6). Only in the intermediate classes (4.4 – 6.8 mm) did individuals of *L. loxochelis* use shells different from the two most frequently occupied ones. Juveniles used *O. urceus* shells almost exclusively (85.7% of juveniles).

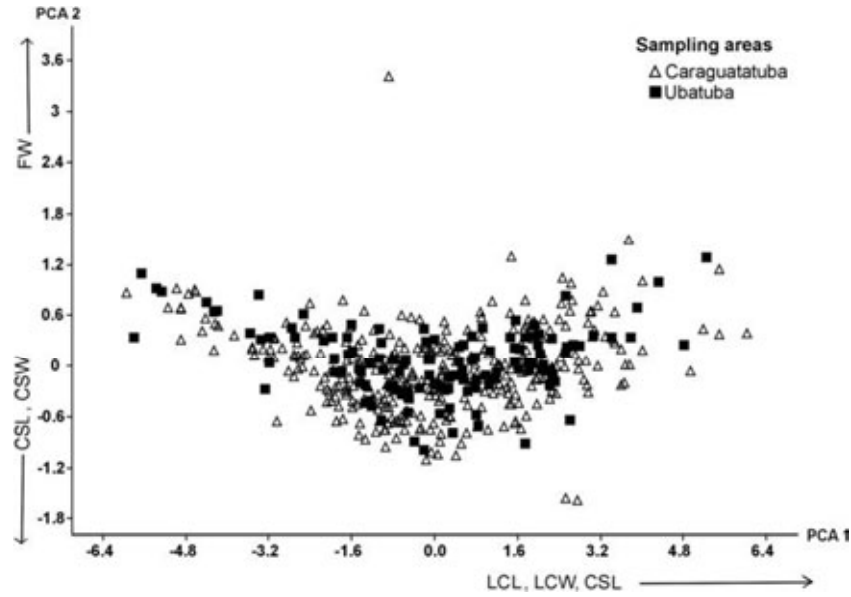


Fig. 3. Principal component analysis (PCA) of the hermit crab *Loxopagurus loxochelis*'s (Diogenidae) attributes in two sampling areas in São Paulo, Brazil. The three attributes with larger scores of each PCA axis are shown next to the axes, and the setae indicate the direction of the increase. LCL = left chela length; LCW = left chela width; CSL = cephalothoracic shield length; CSW = cephalothoracic shield width. These two axes explained 95% of the total variance.

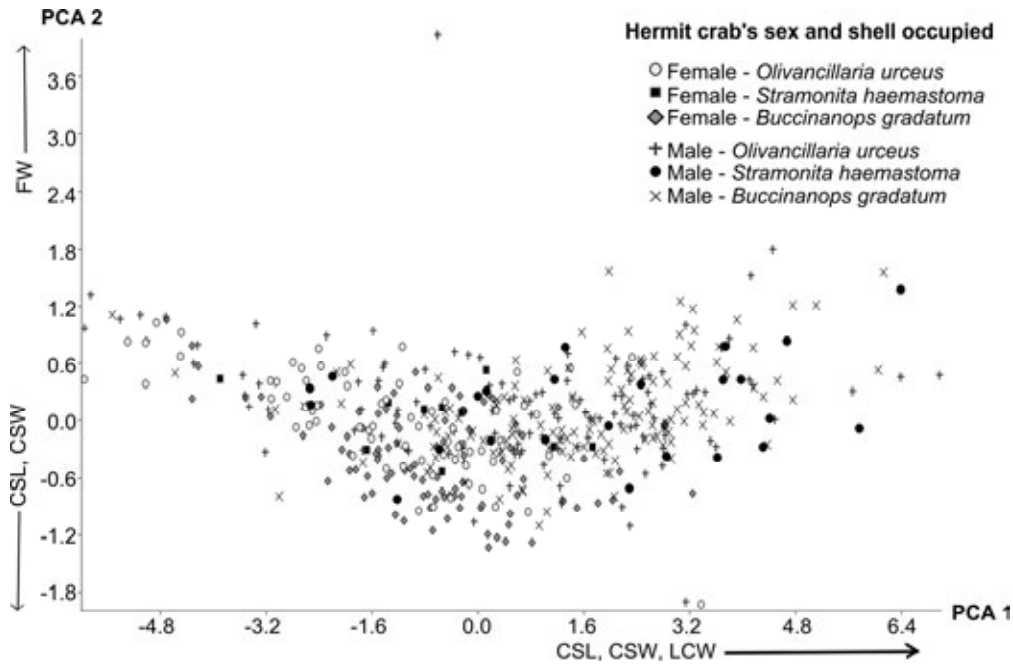


Fig. 4. Principal component analysis (PCA) of the hermit crab *Loxopagurus loxochelis*'s (Diogenidae) attributes in two sampling areas in São Paulo, Brazil. The three attributes with larger scores of each PCA axis are shown next to the axes, and the setae indicate the direction of the increase. LCL = left chela length; LCW = left chela width; CSL = cephalothoracic shield length; CSW = cephalothoracic shield width. These two axes explained 95% of the total variance.

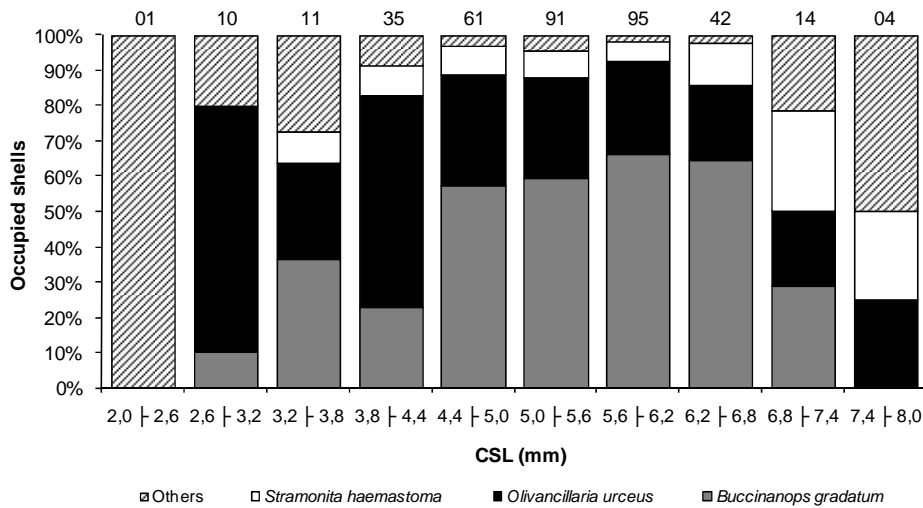


Fig. 5. Pattern of the gastropods' shells' occupation by *Loxopagurus loxochelis* in relation to the size class of the hermit crabs (CSL = cephalothoracic shield length); the number on the bars indicates the amount of individuals in each class. Animals sampled in Caraguatatuba, São Paulo, during July 2002 to June 2003.

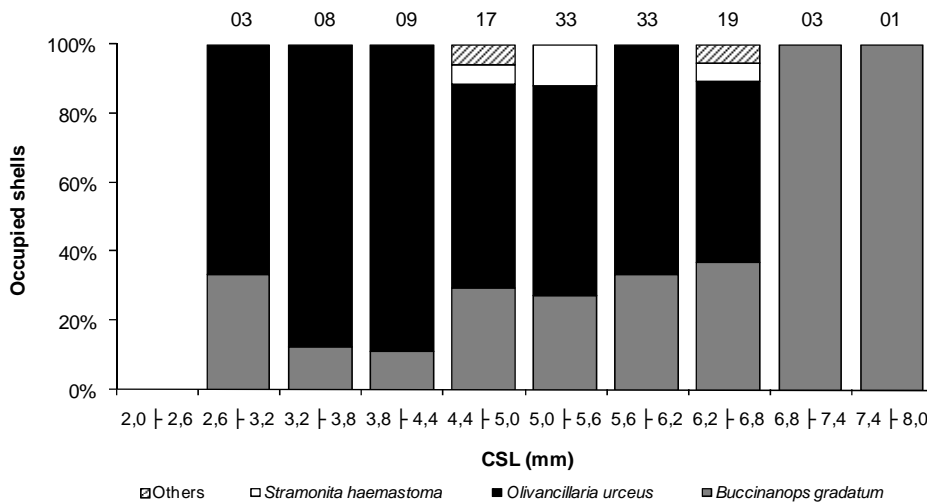


Fig. 6. Pattern of the gastropods' shells' occupation by *Loxopagurus loxochelis* in relation to the class of size of the hermit crabs (CSL = cephalothoracic shield length); the number on the bars indicates the amount of individuals in each class. Animals sampled in Ubatuba, São Paulo, during July 2002 to June 2003.

The regression tree successfully explained the relationship between the hermit crab's characteristics and the internal volume of the inhabited shell, accounting for 77% of the total variance (total of 325 ind.). The first split, separating the juveniles and the small adults - with a shield width smaller than 5.45 mm (193 ind.) - from the larger adults (132 ind.), explained 43% of the variance (Fig. 7). Juveniles and

small adults occupied shells of up to an average 2.3 mm³, depending on their chela length and fresh weight. Large adults with shield length > 7 mm were rare (9 ind.), and represented only 2.7% of the total. These individuals occupied shells of from 6.0 to 8.4 mm³. Those individuals weighing more than 4g inhabited the shells of the largest volume (mean of 8.4 mm³) (Fig. 7).

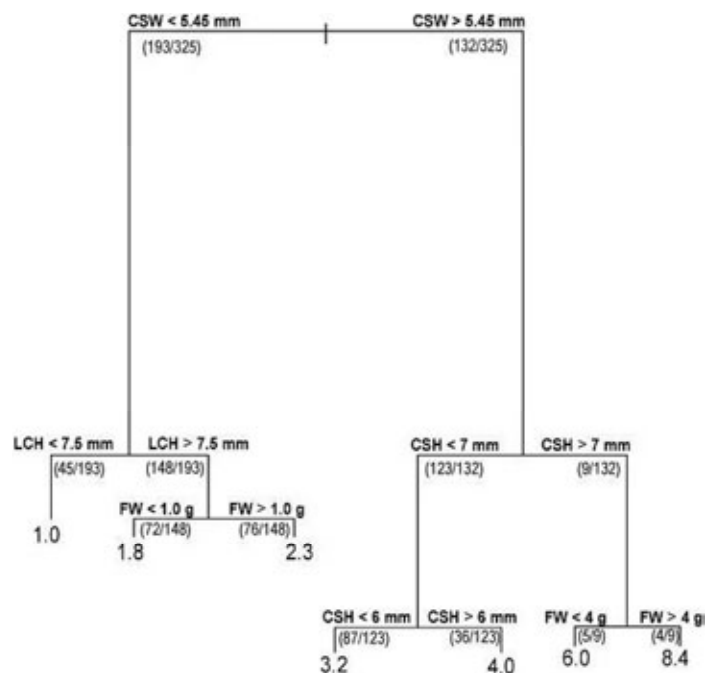


Fig. 7. Relationship between the hermit crab's attributes and the gastropod shell's internal volume (mm^3) accessed through a regression tree model. Numbers in the lowest portions of the tree (leaves) indicate the expected mean internal volume (mm^3) of the shell given the hermit crab attributes indicated in each split, out of the total. The numbers in parenthesis show the number of individuals satisfying the conditions of each split. Vertical lines are proportional to the total amount of the variance explained by each split. CSW = cephalothoracic shield width; CSL = cephalothoracic shield length; LCL = left chela length; FW = fresh weight.

DISCUSSION

The two populations studied here differed with respect to the diversity of the gastropod shells they occupied in two close areas. These population profiles exhibited by *Loxopagurus loxochelis* evidence the importance of the adaptive mechanisms of establishment both in different and in close areas.

The differences in the patterns of shell occupancy between populations of the same species in different areas can be related to the diversity of the gastropod community in each respective area (MANTELATTO et al., 2010). However, it is worth mentioning that an overlap between areas was observed in the present study; Fig. 1 demonstrates that in Caraguatatuba's 15 and 30m depths there was a grouping with transects from Ubatuba, which demonstrates that part of the gastropod diversity overlaps, which would be responsible for some of the similarity in the shell occupation of *L. loxochelis* in the two areas.

Hermit crabs do not necessarily occupy the shells of all existent gastropod species in a given area. Martinelli and Mantelatto (1999), for example,

recorded 16 different shell species in Ubatuba bay, and only six occupied by *L. loxochelis*. *Olivancillaria urceus* and *B. gradatum* are the most abundant gastropods in the Ubatuba and Caraguatatuba regions, respectively. Shells of *O. urceus* are heavier, with a high dry weight, and have a smaller opening width than the *B. gradatum*, as shown in Fig. 2. This characteristic may explain its more intense use in Ubatuba, since this area is more exposed to the ocean than is Caraguatatuba bay, more protected from the forces of the open sea (PIRES-VANIN et al., 1993), due to the presence of São Sebastião Island.

Different populations of the same species may differ greatly in their pattern of shell occupancy as a result of the physical and biological properties of the environment, such as wave strength and habitat heterogeneity (DOMINCIANO et al., 2009) and their indirect effects on shell quality and abundance (SCULLY, 1979). Differences in the shell occupancy patterns between populations of the same species inhabiting environments with different characteristics are very common amongst hermit crabs, and have been widely documented (LEITE et al., 1998; BOTELHO; COSTA, 2000; GARCIA;

MANTELATTO, 2000; MANTELATTO et al., 2007; DOMINCIANO et al., 2009; MANTELATTO et al., 2010). It is important to highlight that both populations have similar physical characteristics, as shown in Fig. 3, which reinforces the idea that other factors, such as environmental pressure or competition with others, play a part in shell selection even though the individuals in the two areas show no differences in their sizes.

The diversity of the hermit species of a given locality is also related to the latitudinal distribution of the gastropod shells, as well as the distribution of other hermit species that may compete for the available shells (MANTELATTO; GARCIA, 2000). Regarding *L. loxochelis*, other hermit crab species occur in the study areas and a sharing of resources with respect to the available shells seems to exist between them. In Ubatuba, there are two other common hermit crab species [*Dardanus insignis* (Saussure, 1858) and *Petrochirus diogenes* (Linnaeus, 1758)] that are similar in size to *L. loxochelis*, but their patterns of shell occupancy are different: *D. insignis* occupies 25% of *B. gradatum* and 28% of *O. urceus*, while *P. diogenes* rarely occupies the shells preferred by *L. loxochelis* (1% in *B. gradatum* and 2% in *O. urceus*) (BERTINI; FRANZOZO, 2000). In Caraguatatuba, *L. loxochelis* coexists with *Isocheles sawayai* (Forest & Saint Laurent, 1968) and *Pagurus exilis* (Benedict, 1892) (FANTUCCI et al., 2008; TEROSSI et al., 2006, respectively). The former uses mainly *S. haemastoma* (*B. gradatum* = 5% and *O. urceus* = 5%) and it is found in shallow waters (5m deep) (FANTUCCI et al., 2008), where *L. loxochelis* occupies the highest diversity of shell types. In relation to *P. exilis*, there is a similarity with *L. loxochelis* in terms of size and distribution (MEIRELES et al., 2006) and, in Caraguatatuba, *P. exilis* uses the shells of 19 gastropod species, 11 of which are also used by *L. loxochelis*, but it shows a marked preference for *B. gradatum* (82%) (TEROSSI et al., 2006).

We cannot, on the basis of these data, dismiss the hypothesis of interspecific competition for the shells, at least at some moment during the life cycle of the coexistent species. This prediction is supported by previous shell availability studies, in which Martinelli and Mantelatto (1999) detected that *O. urceus* is the most available gastropod shell at Ubatuba, and recently, working in different areas of the São Paulo State littoral, confirmed that *O. urceus* and *B. gradatum*, are, respectively, the most available gastropod species in both the regions studied - Caraguatatuba and Ubatuba. The stocks of these resources permit some of the overlapping occupation verified in these species (*L. loxochelis* and *P. exilis*) in the region.

Intraspecific differences in shell selection also take place among hermit crabs, mainly related to reproduction. Light shells with large internal volume are thought to favor ovigerous females, as shell size influences the number of eggs a female can bear. Heavy shells, on the other hand, favor males by offering increased protection from predators during the competition for females (GHERARDI, 1991). Also, when fighting other males for access to a female, males with a larger shell may have an advantage over those in smaller shells (SATO, SENO; 2006). Examples of intraspecific differences have been documented for *Pagurus macclaughlinae* García Gómez, 1982 (TUNBERG et al., 1994); *L. loxochelis* (MARTINELLI; MANTELATTO, 1999; BIAGI et al., 2006); *Pagurus brevidactylus* (Stimpson, 1859) (MANTELATTO; MEIRELES, 2004); *Calcinus tibicen* (Herbst, 1791) (GARCIA; MANTELATTO, 2000), and *Clibanarius vittatus* (Bosc, 1802) (MANTELATTO et al., 2010). In our study, males tended to occupy heavier and larger shells than females (Fig. 4). *Olivancillaria urceus* shells are heavy and present an oval opening, thus being more adequate for males (MARTINELLI; MANTELATTO, 1999). The *Buccinanops gradatum* fusiform shell, the opening of which is wider and consequently has a greater internal volume, is more favorable to females during the egg production period (TORATI; MANTELATTO, 2008). Nonetheless, no intraspecific differences regarding the shell type used were observed in the present study such as those verified for *L. loxochelis* studied in south Brazil (AYRES-PERES et al., 2008). The same trend was observed in *Cestopagurus timidus* (Roux, 1830) by Pessani and Premoli (1993) and in *P. exilis* by Terossi et al. (2006). Interestingly, the differences in shell occupancy between the sexes of *C. tibicen* observed in nature (GARCIA; MANTELATTO, 2000; MANTELATTO; GARCIA, 2000) were not replicated under laboratory conditions (GARCIA; MANTELATTO, 2001), reinforcing the importance of the role of environmental conditions in shaping the hermit crab's shell preference.

According to Garcia and Mantelatto (2000), a sharing of shell resources among individuals probably occurs due to the scarcity of empty shells. The absence of inter sexual variation in the shell occupation pattern in populations of *L. loxochelis* may reflect the abundance and the availability of the most frequently occupied gastropod species' shells in those regions, which thus avoid competition between the sexes, since there are "adequate" shells available for the majority of individuals.

Loxopagurus loxochelis most frequently occupied the shells of *B. gradatum* and *O. urceus*. However, medium-sized individuals were found to occupy a larger diversity of shells than the smaller

ones. Usually, the opposite occurs: the smaller individuals occupying the largest diversity of shells (REESE, 1969; MARTINELLI; MANTELATTO, 1999; GARCIA; MANTELATTO, 2000; MANTELATTO; GARCIA, 2000; MEIRELES; MANTELATTO, 2005), probably because it is easier for them to fit into a variety of shell shapes and sizes (VANCE, 1972a). Terossi et al. (2006) and Fantucci et al. (2008) also reported a higher diversity among medium-sized individuals. Our results reflect the availability of the most frequently occupied shells in all the hermit crabs' size classes.

The regression tree (Fig. 7) - a method that allows the utilization of various quantitative variables at the same time - revealed a close association between the hermit crab's variables and the internal volume of shells, which seems to be the most important determining factor in their occupation by *L. Loxochelis* both in Caraguatatuba and Ubatuba. Different studies identify different characteristics as, for example, the shell opening. In *C. tibicen* and *C. vittatus*, there was a positive relationship between shell weight and the hermit's weight (GARCIA; MANTELATTO, 2000; MANTELATTO et al., 2010). It has been demonstrated that the shell's internal volume is also another important attribute: in *Pagurus pollicaris* Say 1817, the shell preference is determined by the shell's weight and volume and, in the laboratory, the latter attribute was identified as the most important (CONOVER, 1978); more recently, the importance of the shell's volume in *P. exilis* and *I. sawayai* has also been highlighted (TEROSSI et al., 2006; FANTUCCI et al., 2008, respectively); Biagi et al. (2006) observed that the relationship between the shell's aperture and its weight was the one that best reflected the shell's association with *L. loxochelis* in two separated regions in Argentina and Brazil; the same was observed by Ayres-Peres et al. (2008) when evaluating a population of the same species from south Brazil and Carranza et al. (2008) in a study with a population of *L. loxochelis* in Uruguay discovered that the closest relationship was between shell weight and left propodus length.

In the present study it was observed that *L. loxochelis* occupied preferably shells of *B. gradatum* and *O. urceus* in both the study areas, although in Caraguatatuba the hermit crabs used mainly *B. gradatum* and then *O. urceus*, in Ubatuba the pattern was the other way round (*O. urceus* was the most frequently used, followed by *B. gradatum*). The differences between the regions are probably related to the characteristics of each area, as well as to the availability of local shells, reflecting an adjustment of *L. loxochelis* to the resources of the environment. We conclude that the relationship between the morphometry of an individual hermit crab and its shell is not straightforward and cannot be explained just on the basis of direct correlations between the body's and

the shell's characteristics. Actually, shell morphometry and availability are important determinants, as well as the environmental conditions and inter and intraspecific competition. All these factors interact and seem to be taken into consideration by the hermit crabs when choosing a shell, resulting in the diversified pattern of shell occupancy shown here and elsewhere. The outcome of the present study should be to encourage future comparative analysis of the aspects that guide the hermit crabs' use of shells in different areas.

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