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ORIGINAL ARTICLE

Habitat heterogeneity in the assemblages and shell use by the most abundant hermit crabs (Anomura: Diogenidae and Paguridae): does the occupied shell species differ according to gender and species?

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Abstract

The goal of this study was to identify patterns of shell occupation by different species of hermit crabs from the southern Brazilian coast. In total, 644 individuals were collected, represented by six hermit species. *Isocheles sawayai* Forest & Saint Laurent, 1968 showed the highest abundance, with 575 individuals, followed by *Loxopagurus loxochelis* (Moreira, 1901) (n = 56). The other species were *Petrochirus diogenes* (Linnaeus, 1758), *Dardanus insignis* (Saussure, 1858), *Pagurus exilis* (Benedict, 1892) and *Pagurus leptonyx* Forest & Saint Laurent, 1968. *Loxopagurus loxochelis* was found associated with shells of 12 gastropod species, with 75% of males occupying shells of *Olivancilaria urceus* (Roding, 1798) and 78% of females inhabiting shells of *Semicassis granulata* (Born, 1778). Shells of *Semicassis granulata* were the lightest of all gastropod shells, demonstrating differential resource utilization. Additionally, *I. sawayai* occupied shells of 10 species, highlighting *Stramonita haemastoma* (Linnaeus, 1767) with the highest occupation percentage in all demographic classes, confirming a pattern of occupation with a strong relationship to the availability of the resource. The comparison of our results with those of other studies corroborated the influence of region and gastropod diversity on gastropod shell occupation.

Key words

Environmental resource, fitness, sexual selection.

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Introduction

The habitual use of shells by hermit crabs has led this group of crustaceans to develop remarkable behavior in the biological environment and has also contributed to their evolutionary success (Mantelatto and Sousa, 2000).

The diversity of hermit crabs and their abundance in a particular locality is strongly related to the geographic distribution, availability and suitability of gastropod shells (Reese, 1962; Pereira *et al.*, 2009). Thus, the availability of shells constitutes an essential and limiting factor in the population structure of hermit crabs (Meireles *et al.*, 2003). Agonistic conflicts between individuals of the same species or different species over resources (shells) are common in this group (Mantelatto and Garcia, 2000), but the selection and shell occupation do not occur randomly and follow some precepts, such as competition, because the availability of shells is generally low in environment (Bertness, 1980), shell size (Vance, 1972; Bertness, 1981a), internal volume (Conover, 1978), shell weight (Mantelatto and Dominciano, 2002), external architecture and adornments, which increase protection against predation and minimize energy costs transport to the hermit crabs (Vance, 1972; Rotjan *et al.*, 2004).

Therefore, knowledge concerning the availability and variety of shells in the environment provides important information about communities of hermit crabs, because in addition to providing protection, they are closely related to the somatic growth rate, gonadal development and longevity of hermit crabs (Lancaster, 1988).

Thus, the objective of the study was to characterize the patterns of use of gastropod shells by the more abundant hermit crab species in a coastal region of the southern coast of Brazil. For this, we analyzed the percentage of shells of gastropod species that are most commonly used. To detect biometric parameters that provide indications about the occupation of such shells we established a correlation between the shell dimensions (weight and aperture width) and the weight and size of the respective occupants.

Material and Methods

Hermit crabs were collected monthly from July 2010 to June 2011 at five sampling sites parallel to the shoreline and at distinct depths (5, 8, 11, 14 and 17 m). The trawls were conducted during 30-min, in each sampling site, using a shrimp boat outfitted with double-rig nets, in adjacent areas in Babitonga Bay (Fig. 1) (northern coast of the state of Santa Catarina).

Laboratory procedures

After collection, all the specimens were sorted, frozen and transported to the laboratory, where they were removed from their shells, counted, and identified according to Melo (1999). The sexes were recognized by verifying the position of the gonopores (female and male gonopores on the coxae of the third and fifth pairs of pereopods, respectively) and the reproductive condition was observed by the presence of ovigerous females (fertilized eggs attached to pleopodal setae) (Mantelatto and Garcia, 1999). These analyses were performed using a stereomicroscope.

The Cephalothoracic Shield Length (CSL) of the animals was measured with a caliper (0.01 mm), and the Hermit Wet Weight (HWW) was obtained using precision scales (0.01 g). The shells were identified (Rios, 1994; Gofas, 2014), and the largest Shell Aperture Width (SAW) (between inner lip and outer lip) (0.01 mm) and Shell Wet Weight (SWW) were measured with precision scales (0.01 g).

Data analyses

Statistical analyses were performed using the species that were found in more than 10% of samples, i.e., only *Isocheles sawayai* Forest & Saint Laurent, 1968 and *Loxopagurus loxochelis* (Moreira, 1901) that were the most abundant species, mainly in depths of 5 m. The Kruskal-Wallis and Dunn *a posteriori* tests were applied to compare the dimensions of Shell Aperture Width (SAW) and Shell Weight (SW), and to compare the dimensions in the occupied shells by hermit crabs of different sexes. Linear Regressions were performed to evaluate the relationships between parameters of the occupied shells relative to the size of the hermit crabs (Zar, 1999). The values of the variables were log (1+x)-transformed to satisfy the assumptions of the statistical tests (Castilho *et al.*, 2008), which were evaluated at the 5% level of significance.

Results

A total of 644 individuals of six hermit crab species was collected, with four belonging to Diogenidae

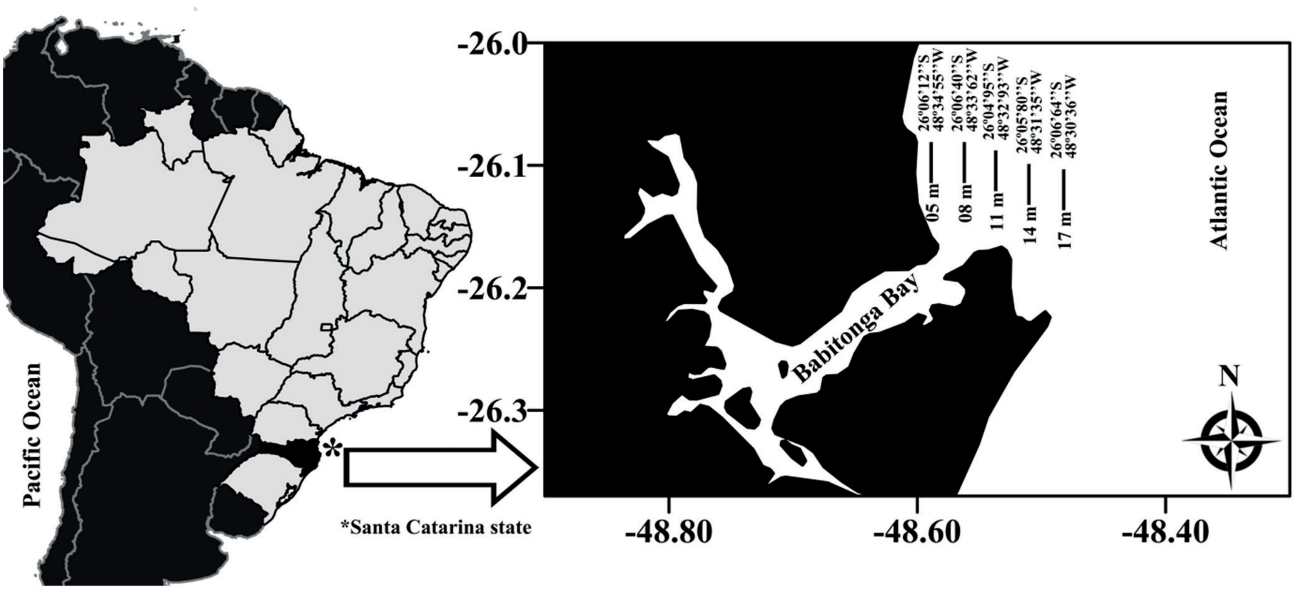

Figure 1. Location of the study area, highlighting the sampled stations in an area adjacent to Babitonga Bay, Santa Catarina, Brazil (source: Grabowski et al., 2014).

and two to Paguridae. Analyses of shell occupation were performed only with the *Isocheles sawayai* and *Loxopagurus loxochelis*, because these species represented 98% of all sampled material, with 575 and 56 individuals, respectively. The other species together totaled 13 individuals (2%) and included *Petrochirus diogenes* (Linnaeus, 1758), *Dardanus insignis* (Saussure, 1858), *Pagurus exilis* (Benedict, 1892) and *Pagurus leptonyx* Forest & Saint Laurent, 1968.

Shell preference

The six hermit crab species occupied shells of 15 gastropod species: *Buccinanops cochlidium* (Dillwyn, 1817), *Monoplex parthenopeus* (Salis Marschlins, 1793), *Buccinanops monilifer* (Kiener, 1834), *Leucozonia nassa* (Gmelin, 1791), *Olivancillaria urceus* (Roding, 1798), *Olivancillaria vesica* (Gmelin, 1791), *Semicassis granulata* (Born, 1778), *Gemophos auritulus* (Link, 1807), *Pisania pusio* (Linnaeus, 1758), *Polinices hepaticus* (Roding, 1798), *Polinices lacteus* (Guilding, 1834), *Siratus tenuivaricosus* (Dautzenberg, 1927), *Stramonita haemastoma* (Linnaeus, 1767), *Strombus pugilis* (Linnaeus, 1758), and *Zidona dufresnei* (Donovan, 1823).

Shells of *Stramonita haemastoma* (38%), *O. urceus* (33%), *S. granulata* (15%), and *P. hepaticus* (10%) were used most often, and *O. urceus* statistically showed the highest SWW and smallest SAW (Kruskal-Wallis, $p < 0.05$, Dunn *a posteriori* test) (Fig. 2). Ovigerous females and males occupied shells with different dimensions (SAW and SWW) (Kruskal-Wallis, $p < 0.05$, Dunn *a posteriori* test).

Isocheles sawayai was represented by 156 females (27%), 103 ovigerous females (18%) and 316 males (55%), which occupied the shells of 10 gastropod species, without differences in occupation between sexes (Kruskal-Wallis, $p > 0.05$). Shells of four gastropod species were utilized by 95% of the individuals collected in the following proportions: *S. haemastoma* (43%), *O. urceus* (31%), *S. granulata* (12%), and *P. hepaticus* (9%) (Tab. 1).

Linear regression: Isocheles sawayai

Linear regressions with animal variables (CSL, HWW) and shell variables (SAW, SWW) were performed with shells of the four most abundant gastropod species, which all resulted in significant relationships ($p < 0.05$). The higher coefficients of determination (*R2*) between CSL vs. SWW and HWW vs. SAW were obtained for shells of *S. haemastoma* (Fig. 3). The regressions performed between HWW vs. SWW showed high coefficients of determination (Fig. 4).

Loxopagurus loxochelis was represented by 24 (43%) females, 31 males (55%) and one ovigerous female (2%). These animals occupied shells of 12 gastropod species. Segregation in the pattern of shell occupation according to the sex was observed; *O. urceus* was occupied by 75% of males, whereas *S. granulata* was

Table 1. Overview in the shell occupation by interest group: females (F), ovigerous females (OF) and males (M) of the hermit crab *Isocheles sawayai* in an area adjacent to Babitonga Bay, Santa Catarina, Brazil.

Shell species	N	% F	% OF	% M	% Species
Stramonita haemastoma	245	10.6	11.3	20.7	42.6
Olivancillaria urceus	180	9.7	3.3	18.3	31.3
Semicassis granulata	67	2.6	1.0	8.0	11.6
Polinices hepaticus	54	3.0	0.9	5.6	9.5
Siratus tenuivaricosus	13	0.5	0.7	1.0	2.2
Buccinanops monilifer	7	0.3	0.2	0.7	1.2
Buccinanops cochlidium	3	0.0	0.2	0.3	0.5
Pisania pusio	3	0.0	0.2	0.3	0.5
Olivancillaria vesica	2	0.2	0.2	0.0	0.4
Leucozonia nassa	1	0.2	0.0	0.0	0.2
Overall total	575	27.1	17.9	55.0	100.0

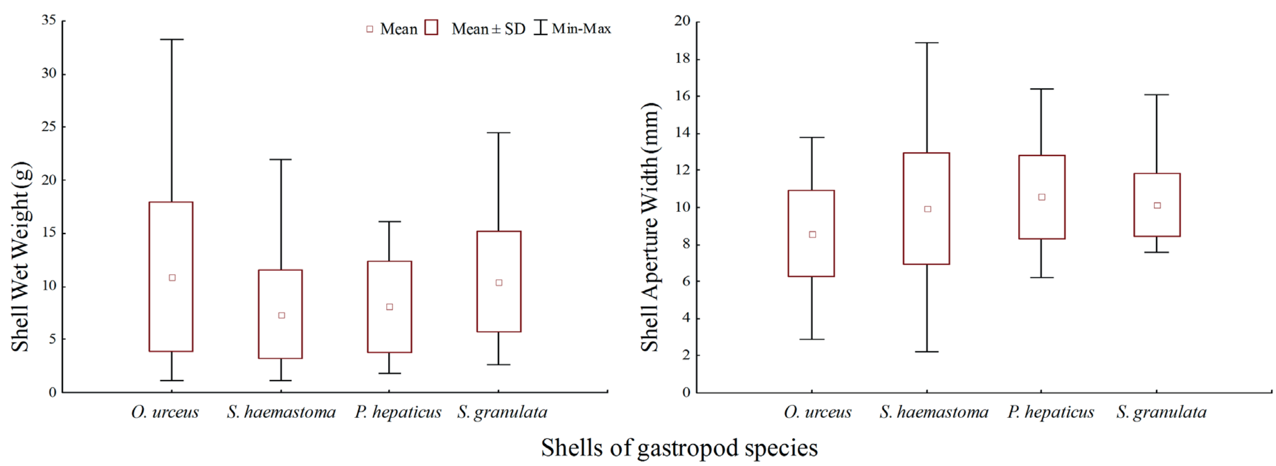

Figure 2. Mean values and standard deviation of Shell Wet Weight and Shell Aperture Width of the four most abundant gastropod species (*Olivancillaria urceus*, *Stramonita haemastoma*, *Polinices hepaticus* and *Semicassis granulata*) during the study period in an area adjacent to Babitonga Bay, Santa Catarina, Brazil.

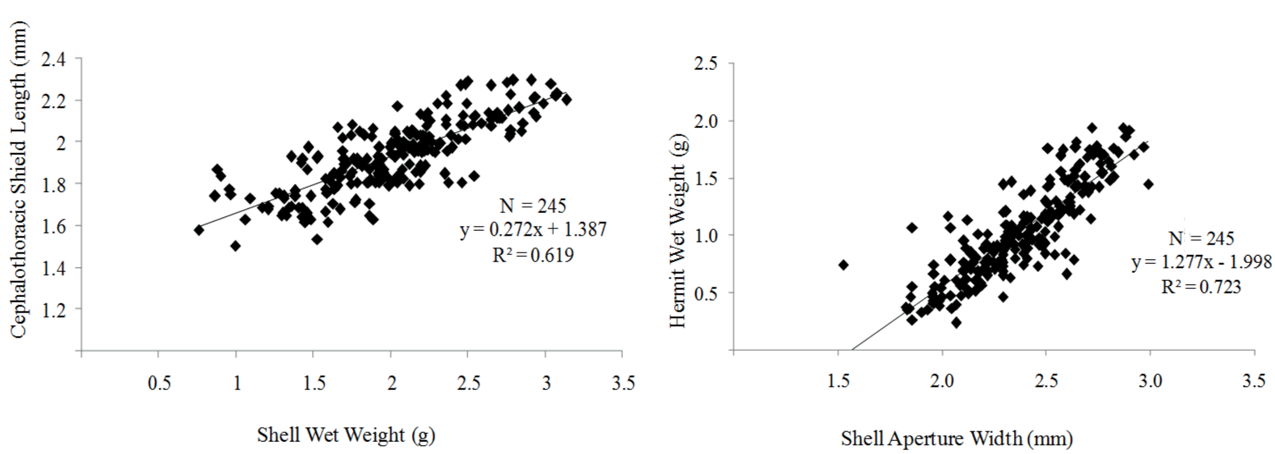

Figure 3. Linear Regression, Cephalothoracic Shield Length (CSL) vs. Shell Wet Weight (SWW) and Hermit Wet Weight (HWW) vs. Shell Aperture Width (SAW) of *Isocheles sawayai* and the gastropod species *Stramonita haemastoma* in an area adjacent to Babitonga Bay, Santa Catarina, Brazil.

used by 78% of females, including ovigerous females (Tab. 2).

Linear regression: Loxopagurus loxochelis

Linear regressions were performed between animal and shell variables for the two most-used shell species. All relationships were significant ($p < 0.05$), especially the HWW vs. SWW of *O. urceus* ($R2 = 0.85$). However, in addition to the HWW vs. SWW correlation ($R2 = 0.84$), the HWW vs. SAW correlation for *S. granulata* was very high ($R2 = 0.78$) (Fig. 5).

Discussion

Interspecific competition should be a non-significant factor in the pattern of shell occupation for the two most abundant and coexistent species of hermit crabs in

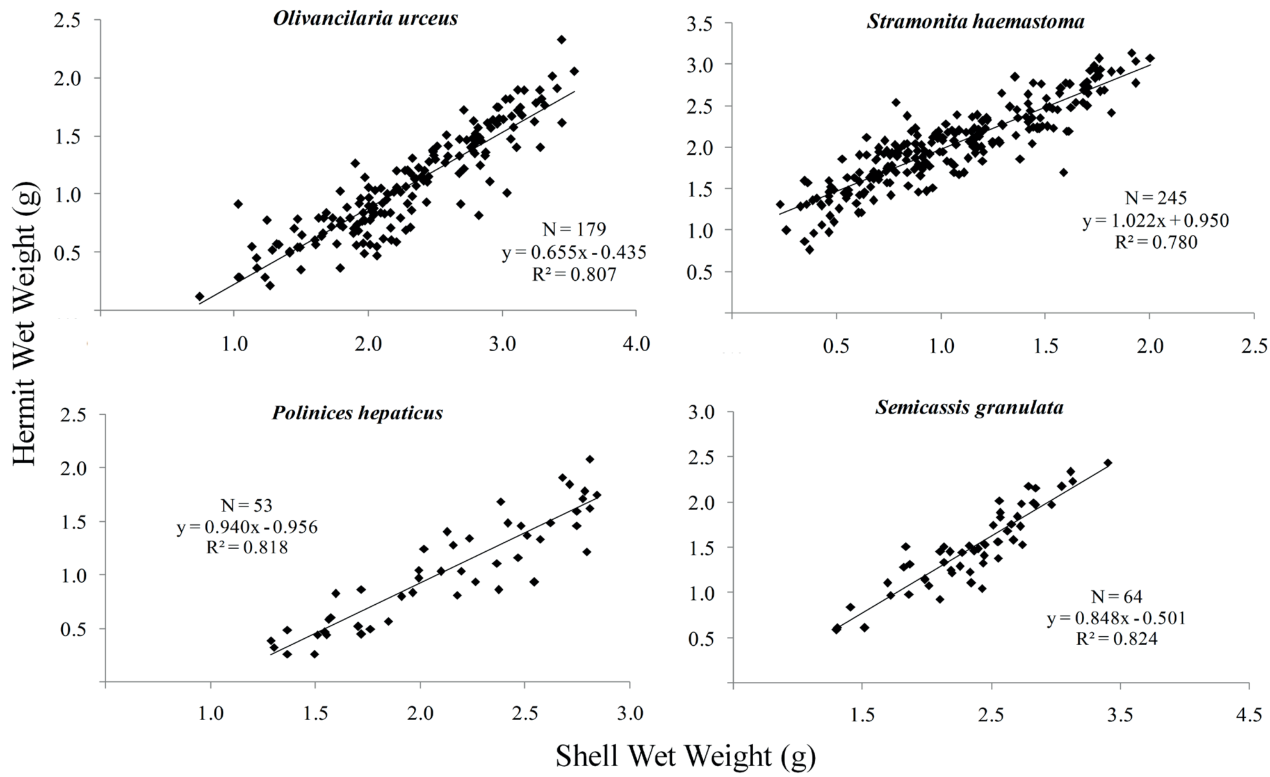

Figure 4. Linear Regression, between Hermit Wet Weight (HWW) vs. Shell Wet Weight (SWW) of gastropod species more occupied by *Isocheles sawayai* during the study in an area adjacent to Babitonga Bay, Santa Catarina, Brazil.

Table 2. Overview in the shell occupation by interest group: females (F), ovigerous females (OF) and males (M) of the hermit crab *Loxopagurus loxochelis* in an area adjacent to Babitonga Bay, Santa Catarina, Brazil.

Shell species	N	% F	% OF	% M	% Species
Olivancillaria urceus	21	8.9	0.0	28.6	37.5
Semicassis granulata	14	17.8	1.8	5.4	25
Buccinanops monilifer	5	5.4	0.0	3.6	8.9
Polinices hepaticus	5	5.4	0.0	3.6	8.9
Stramonita haemastoma	4	3.6	0.0	3.6	7.1
Buccinanops cochlidium	1	0.0	0.0	1.8	1.8
Monoplex parthenopeus	1	0.0	0.0	1.8	1.8
Olivancillaria vesica	1	0.0	0.0	1.8	1.8
Gemophos auritulus	1	0.0	0.0	1.8	1.8
Polinices lacteus	1	0.0	0.0	1.8	1.8
Strombus pugilis	1	1.8	0.0	0.0	1.8
Zidona dufresnei	1	0.0	0.0	1.8	1.8
Overall total	56	42.9	1.8	55.4	100

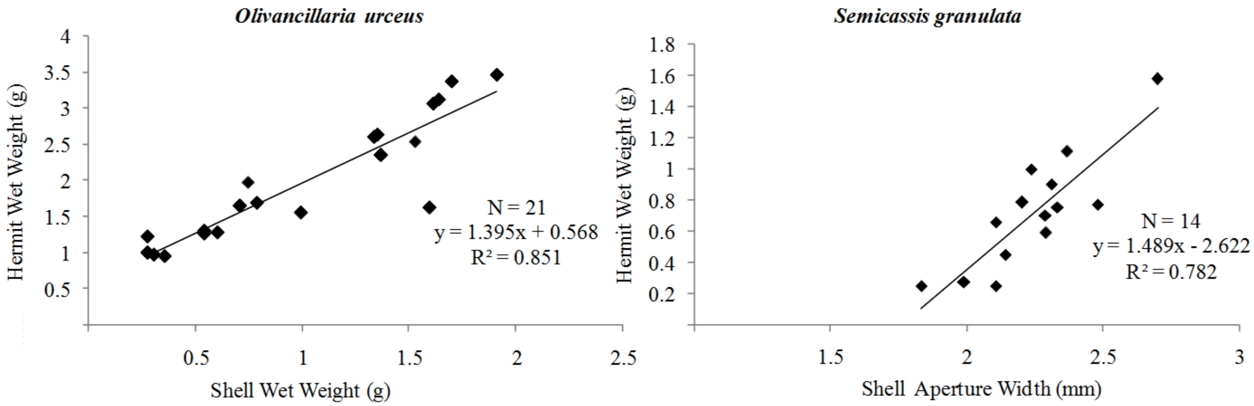

Figure 5. Loxopagurus loxochelis: Linear Regressions between Hermit Wet Weight (HWW) vs. Shell Wet Weight (SWW) of *Olivancillaria urceus*, and HWW vs. Shell Aperture Width (SAW) of *Semicassis granulata* during the study period in the area adjacent to Babitonga Bay, Santa Catarina, Brazil.

the study area. The apparent absence of competition for resources between both species might be a consequence of a difference in their spatial distribution: *Isocheles sawayai* occurs in coastal regions, preferably at sites with depth of 5 m or less (Fantucci *et al.*, 2009), whereas *Loxopagurus loxochelis* is found between 12 and 30 m of depth (Ayres-Peres and Mantelatto, 2008; Fransozo *et al.*, 2008). This spatial occupation difference facilitates coexistence and minimizes niche overlap (Fransozo *et al.*, 1998) in relation to the occupation of resources.

Although the four other species of hermit crabs were represented by few individuals, they demonstrated a spatial overlap with *L. loxochelis*: *Pagurus exilis* inhabits depths from 15 to 35 m (Meireles *et al.*, 2006), *Pagurus leptonyx* from 10 to 20 m (Lemaitre *et al.*, 1982), and *Dardanus insignis* and *Petrochirus diogenes* are found in areas deeper than 20 m (Fransozo *et al.*, 2008). Despite some overlap in certain deep areas, Meireles *et al.* (2012) proposed that the competition for resources among species is more pronounced in the juvenile stage when individuals have similar body sizes, and thus, compete for empty shells with the same dimensions. According to these authors, competition for resources tends to decrease in the adult phase, because *L. loxochelis*, *D. insignis* and *P. diogenes* reach larger sizes than *P. exilis* and *P. leptonyx*.

Males and females of all species occupied shells of different dimensions (weight and aperture width). This is because the sexes have different sizes, with males being larger than females, which has already been described in several studies on hermit crabs (Branco *et al.*, 2002). In general, two hypotheses have been proposed for the size difference (see references below): males invest more energy in growth to reach larger sizes than females, allowing them to use larger and heavier shells, whereas females direct energy into the production of eggs and incubation, resulting in less somatic growth and therefore, they occupy lighter shells that require less energy to carry (Bertness, 1981a). Alternatively, the difference in body size might be the result of an evolutionary selection of reproduction prowess, where hermit crabs compete for reproductive partners and the largest individuals tend to win intraspecific combats, which might represent a selective factor over generations (Bertness, 1981a; Abrams, 1988, Mantelatto and Sousa, 2000; Garcia and Mantelatto, 2001; Branco *et al.*, 2002; Martinelli *et al.*, 2002; Mantelatto *et al.*, 2005; Biagi *et al.*, 2006; Ayres-Peres *et al.*, 2008).

Another factor that benefits the population is differential growth. Manjón-Cabeza and García-Raso (1998) confirmed that the growth period of males of *Dardanus pugilator* (Roux, 1829) begins about five months before that of females, which privileges their development and avoids competition for shells between the sexes at the juvenile stage.

Therefore, the difference in body size according to sex reduces the intraspecific competition for shelter among demographic groups and other resources possibly become beneficial and decisive factors for the establishment, growth and maintenance of the population in the environment (Yoshino *et al.*, 2001).

This appears to be the case for the species studied here.

Isocheles sawayai

The richness of empty shells (10 species of gastropods) occupied by *I. sawayai* in the study area (26ºS) was greater than that described by Pinheiro *et al.* (1993), in Ubatuba, São Paulo (23ºS) (six species), but was lower than that identified at the same latitude by Fantucci *et al.* (2008) (17 species) in a neighboring area (Caraguatatuba), and was similar to that found by Masunari *et al.* (2008) (eight species) on the Paraná coast (25ºS), thereby demonstrating the absence of a latitudinal pattern in determining shell occupation. The competence in using resources is probably directly linked to the regional abiotic and biotic conditions and the plasticity of species of hermit crab to occupy gastropod shells of different species (Galindo *et al.*, 2008). This plasticity might be related to the body size of the hermit crab, with small animals such as *I. sawayai* having an enormous variety of species of gastropod shells available, because smaller shells are commonly found for many species in the natural environment (Bertini and Fransozo, 2000) and are rarely damaged, enabling their widespread use (FLM, pers. obs.).

The shells of *Stramonita haemastoma* were occupied at a high percentage by all demographic groups (males, females and ovigerous females), similar to the pattern found by Masunari *et al.* (2008) (males 57.14% and females 62.33%) and suggesting that no competition between the sexes exists for the higher availability of this resource in the environment (Abrams, 1988). In contrast, Mantelatto and Dominciano (2002) described a different shell occupation pattern by *Paguristes tortugae* Schmitt, 1933, with low coefficient of determination: *Pisania auritula* (Link, 1807) ($R2$ = 0.46), *Cerithium atratum* (Born, 1778) ($R2$ = 0.51), and *Morula nodulosa* (Adams, 1845) ($R2$ = 0.45). This is due to the lack of adequate shells available in the environment, which generates intense intraspecific competition in species that occupy rocky shore areas.

The shell of *S. haemastoma* provided the best fit for *I. sawayai*, as shown by the higher coefficients of determination for the animal variables CSL and HWW with the shell variables (CSL vs. SWW; HWW vs. SAW) and the excellent association between the variables HWW vs. SWW. High biometric coefficients were also identified by other authors for *I. sawayai* and *S. haemastoma*, for example, Pinheiro *et al.* (1993) (CSL vs. SAW, $R2$ = 0.72), and Fantucci *et al.* (2008) (CSL vs. SWW, $R2$ = 0.76).

An appropriate balance between the dimensions of the animal and the shell is extremely important for the occupation choice. However, the shell dimension might be of secondary importance after the availability of this resource in the environment (Mantelatto and Meireles, 2004). This explains the high occupation of *S. haemastoma* recorded in this study, because it combines a high availability in the environment and provides the most suitable dimensions for occupation by hermit crabs.

Olivancillaria urceus was the second most abundant shell used (31.3%), and was the most available species on the coast of São Paulo state, especially in the Ubatuba region (Ayres-Peres *et al.*, 2012). The availability of this gastropod in the study area is probably similarly high, as also observed on the coast of Paraná (southern Brazil) (Masunari *et al.*, 2008). Shells of *O. urceus* possessed a smaller aperture than the other gastropod shells. During intra or inter-specific fighting for the shell or predator attack, hermit crabs are removed from their shells through the aperture (Turra *et al.*, 2005). Therefore, a smaller aperture hinders their removal and provides greater protection (Bertini and Fransozo, 2000). Another feature of this shell is its statistically higher weight and thicker wall than similar-sized shells of other species (Ayres-Peres *et al.*, 2012), which might provide better protection against predators that break shells, and be more robust against adverse environmental conditions, such as wave action (Reese, 1962; Bertness, 1981b). The weight of this shell might also contribute to the improved stability of hermit crabs on an unconsolidated substrate, thus preventing the animal being dragged along by the tide or water current (Masunari *et al.*, 2008).

The disadvantage of the use of a heavy shell by the hermit crab is that it requires higher energy expenditure in movement (Siu and Lee, 1992); however, *I. sawayai* remains half-buried, with only its antennae protruding from the substrate to obtain food particles in suspension (Melo, 1999), which potentially requires a low energy expenditure. Babitonga Bay forms the largest estuarine complex on the Santa Catarina coast, that provides a widespread and constant circulation of materials in suspension for the coastal region and abundant food for benthic suspension feeder species (D'Aquino *et al.*, 2011), conditions that are favorable for the establishment of *I. sawayai* in the region.

Loxopagurus loxochelis

Loxopagurus loxochelis occupied a considerable number of shells of gastropod species (12), similar to the numbers registered by Ayres-Peres *et al.* (2012) (14 species) and Frameschi *et al.* (2013) (10 species), also on the North coast of São Paulo state. *Olivancillaria urceus* was one of main resources used by this species in this study (37.5%), compared with a frequency in previous studies of 77.7% (Ayres-Peres *et al.*, 2012) and 31.3% (Frameschi *et al.*, 2013). According to Wait and Schoeman (2012), shell selection is a process that involves individual and sexual preferences in different dimensions, with the aim of providing the best protection for the hermit crab and sufficient space for the development of embryos and their oxygenation, because females that inhabit very small shells show difficulties in reproducing or reduced rates of reproduction (Fantucci *et al.*, 2008). Thus, the observed highlighted differential shell occupation by *L. loxochelis* is potentially explained by the physiological demands of each sex during the life cycle, i.e., most males occupied *O. urceus* that were heavy, with thick walls, to obtain protection against mechanical abrasion (Reese, 1969). On the other hand, the higher occupancy of *Semicassis granulata* shells by females suggests an intimate relationship with the weight of the shell (which are on average lighter than those of *O. urceus*), which facilitates transport, especially during the breeding season when the females carry embryos in the abdomen (Elwood *et al.*, 1995).

Shells of the other species used by *L. loxochelis* are probably occupied sporadically, due to the immediate need of the animal to find a shelter when other more appropriate resources are not available for occupation.

It has been demonstrated here that specific preferences exist in the species of shell occupied; some shells are selected according to type, shape or weight, emphasizing that success in selecting this feature is related not only to the availability of the resource in the environment, but also to variation in shape and size. In many cases, the relationship between the morphology of the animal and the shell dimensions is not sufficient alone to explain the choice of a particular shell by the hermit crab species in the natural environment, but it is necessary to take into account potential ecological interactions, such as inter and intra-specific competition that might occur (Biagi *et al.*, 2006). Thus, the study of the gastropod community and hermit crabs becomes essential to draw more accurate conclusions concerning the fascinating mechanisms of availability and shell occupation, as well as the inter or intra-specific ecological processes that determine shell occupation patterns in nature.

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References

Abrams, P.A. 1988. Sexual difference in resource use in hermit crabs: consequences and causes, p.283–296. In: G. Chelazzi and M. Vannini (eds), *Behavioural adaptations to the intertidal life*. New York, Plenum Press.

Ayres-Peres, L. and Mantelatto, F.L. 2008. Patterns of distribution of the hermit crab *Loxopagurus loxochelis* (Moreira, 1901) (Decapoda, Diogenidae) in two coastal areas of southern Brazil. *Revista de Biología Marina y Oceanografía*, 43(2): 399–411.

Ayres-Peres, L.; Quadros, L.F. and Mantelatto, F.L. 2012. Comparative analysis of shell occupation by two southern populations of the hermit crab *Loxopagurus loxochelis* (Decapoda, Diogenidae). *Brazilian Journal of Oceanography*, 60(3): 299–310.

Ayres-Peres, L.; Sokolowicz, C.C.; Kotzian, C.B.; Rieger, P.J and Santos, S. 2008. Ocupação de conchas de gastrópodes por ermitões (Decapoda, Anomura) no litoral de Rio Grande, Rio Grande do Sul, Brasil. *Iheringia, Série Zoologia*, 98(2): 218–24.

Bertini, G. and Fransozo, A. 2000. Patterns of shell utilization in *Petrochirus diogenes* (Decapoda, Anomura, Diogenidae) in the Ubatuba Region, São Paulo, Brazil. *Journal of Crustacean Biology*, 20(3): 468–473.

Bertness, M.D. 1980. Shell preference and utilization patterns in littoral hermit crabs of the Bay of Panama. *Journal of Experimental Marine Biology and Ecology*, 48(1): 1–16.

Bertness, M.D. 1981a. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). *Crustaceana*, 40(2): 197–205.

Bertness, M.D. 1981b. Crab shell-crushing predation and gastropod architectural defense. *Journal of Experimental Marine Biology and Ecology*, 50(2–3): 213–230.

Biagi, R.; Meireles, A.L and Mantelatto, F.L. 2006. Bio-ecological aspects of the hermit crab *Paguristes calliopsis* (Crustacea, Diogenidae) from Anchieta Island, Brazil. *Anais da Academia Brasileira de Ciências*, 78(3): 451–462.

Branco, J.O.; Turra, A. and Souto, F.X. 2002. Population biology and growth of the hermit crab *Dardanus insignis* at Armação do Itapocoroy, Southern Brazil. *Journal of Marine Biology*, 82(4): 597–603.

Castilho, A.L.; Furlan, M.; Costa, R.C. and Fransozo, A. 2008. Abundance and temporal-spatial distribution of the rock shrimp *Sicyonia dorsalis* Kingsley, 1878 (Decapoda, Penaeoidea) from the northern coast of São Paulo State, Brazil. *Senckenbergiana Maritima*, 38(1):75–83.

Conover, M.R. 1978. The importance of various shell characteristics to the shell-selection behavior of hermit crabs. *Journal of Experimental Marine Biology and Ecology*, 32(2): 131–142.

D'Aquino, C.A.; Neto, J.S.A.; Barreto, G.A.M. and Schettini, C.A.F. 2011. Caracterização Oceanográfica e do transporte de sedimentos em suspensão no estuário do rio Mampituba, SC. *Revista Brasileira de Geofísica*, 29(2): 217–230.

Elwood, R.W.; Marks, N. and Dick, J.T.A. 1995. Consequences of shell-species preferences for female reproductive success in the hermit crab *Pagurus bernhardus*. *Marine Biology*, 123(3): 431–434.

Fantucci, M.Z.; Biagi, R. and Mantelatto, F.L. 2008. Shell occupation by the endemic Western Atlantic hermit crab *Isocheles sawayai* (Diogenidae) from Caraguatatuba, Brazil. *Brazilian Journal of Biology*, 68(4): 859–867.

Fantucci, M.Z.; Biagi, R.; Meireles, A.L. and Mantelatto, F.L. 2009. Influence of biological and environmental factors on the spatial and temporal distribution of the hermit crab *Isocheles sawayai* Forest & Saint-Laurent, 1968 (Anomura, Diogenidae). *Nauplius*, 17(1): 37–47.

Frameschi, I.F.; Andrade, L.S.; Alencar, C.E.R.D.; Fransozo, V.; Teixeira, G.M. and Fernandes-Góes, L.C. 2013. Shell occupation by the South Atlantic endemic hermit crab *Loxopagurus loxochelis* (Moreira, 1901) (Anomura: Diogenidae). *Nauplius*, 21(2): 137–149.

Fransozo, A.; Bertini, G.; Braga, A.C.A. and Negreiros-Fransozo, M.L. 2008. Ecological aspects of hermit crabs (Crustacea, Anomura, Paguroidea) off the northern coast of São Paulo state Brazil. *Aquatic Ecology*, 42(3): 437–448.

Fransozo, A.; Mantelatto, F.L.; Bertini, G.; Fernandez-Góes, L.C. and Martinelli, J.M. 1998. Distribution and assemblages of anomuran crustaceans in Ubatuba Bay, north coast of São Paulo State, Brazil. *Acta Biologica Venezuelica*, 18(4): 17–25.

Galindo, L.A.; Bolaños, J.A. and Mantelatto, F.L. 2008. Shell utilization pattern by the hermit crab *Isocheles sawayai* (Anomura, Diogenidae) from Margarita Island, Caribbean Sea, Venezuela. *Gulf and Caribbean Research*, 20(1): 49–57.

Garcia, R.B. and Mantelatto, F.L. 2001. Shell selection by the tropical hermit crab *Calcinus tibicen* (Herbst, 1791) (Anomura, Diogenidae) from Southern Brazil. *Journal of Experimental Marine Biology and Ecology*, 265(1): 1–14.

Gofas, S. 2014. Gastropoda. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=101 on 2015-03-02.

Grabowski, R.C.; Simões, S.M. and Castilho, A.L. 2014. Population structure, sex ratio and growth of the seabob shrimp *Xiphopenaeus kroyeri* (Decapoda, Penaeidae) from coastal waters of southern Brazil. *ZooKeys*, 457: 253–269.

Lancaster, I. 1988. *Pagurus bernhardus* (L.). An introduction to the natural history of hermit crabs. *Field Studies*, 7: 189–238.

Lemaitre, R.; McLaughlin, P.A. and García-Gomez, J. 1982. The provenzanoi group of hermit crabs (Crustacea, Decapoda, Paguridae) in the Western Atlantic. Part IV. A review of the group, with notes on variations and abnormalities. *Bulletin of Marine Science*, 32(3): 670–701.

Manjón-Cabeza, M.E. and García-Raso, J.E. 1998. Population structure and growth of the hermit crab *Diogenes pugilator* (Decapoda: Anomura: Diogenidae) from the Northeastern Atlantic. *Journal of Crustacean Biology*, 18(4): 753–762.

Mantelatto, F.L.; Christofoletti, R.A. and Valenti, W.C. 2005. Population structure and growth of the hermit crab *Pagurus brevidactylus* (Anomura: Paguridae) from the northern coast of São Paulo, Brazil. *Journal of the Marine Biology Association of United Kingdom*, 85(1): 127–128.

Mantelatto, F.L. and Dominciano, L.C.C. 2002. Pattern of shell utilization by the hermit crab *Paguristes tortugae* (Diogenidae) from Anchieta Island, southern Brazil. *Scientia Marina*, 66(3): 265–272.

Mantelatto, F.L. and Garcia, R.B. 1999. Reproductive potential of the hermit crab *Calcinus tibicen* (Anomura) from Ubatuba, São Paulo, Brazil. *Journal of Crustacean Biology*, 19(2): 268–275.

Mantelatto, F.L. and Garcia, R.B. 2000. Shell utilization pattern of the hermit crab *Calcinus tibicen* (Diogenidae) from southern Brazil. *Journal of Crustacean Biology*, 20(3): 460–467.

Mantelatto, F.L. and Meireles, A.L. 2004. The importance of shell occupation and shell availability in the hermit crab *Pagurus brevidactylus* (Stimpson, 1859) (Paguridae) population from the southern Atlantic. *Bulletin of Marine Science*, 75(1): 27–35.

Mantelatto, F.L. and Sousa, L.M. 2000. Population biology of the hermit crab *Paguristes tortugae* Schmitt, 1933 (Anomura, Diogenidae) from Anchieta Island, Ubatuba, Brazil. *Nauplius*, 8(2): 185–193.

Martinelli, J.M.; Mantelatto, F.L. and Fransozo, A. 2002. Population structure and breeding season of the South Atlantic hermit crab, *Loxopagurus loxochelis* (Anomura, Diogenidae) from the Ubatuba region, Brazil. *Crustaceana*, 75(6): 791–802.

Masunari, S.; Fontanelli, A.M. and Sampaio, S.R. 2008. Morphometric relationships between the hermit crab *Isocheles sawayai* (Forest & Saint Laurent) (Crustacea Anomura Diogenidae) and its shell from Southern Brazil. *The Open Marine Biology Journal*, 2: 13–20.

Meireles, A.L.; Biagi R.; Fransozo, A. and Mantelatto, F.L. 2012. Os Ermitões (Crustacea, Anomura). p. 479–488. In: A.C.Z. Amaral and S.A.H. Nallin (orgs), Biodiversidade e ecossistemas bentônicos marinhos do Litoral Norte de São Paulo - Sudeste do Brasil. Campinas, IB/UNICAMP, E-book - ISBN:978-85-85783-24-2 http://www.bibliotecadigital.unicamp.br/document/?code=000812694&opt=1

Meireles, A.L.; Biagi, R. and Mantelatto, F.L. 2003. Gastropod shell availability as a potential resource for the hermit crab infralittoral fauna of Anchieta Island (SP), Brazil. *Nauplius,* 11(2): 99–105.

Meireles, A.L.; Terossi, M.; Biagi, R. and Mantelatto, F.L. 2006. Spatial and seasonal distribution of the hermit crab *Pagurus exilis* (Benedict, 1892) (Decapoda: Paguridae) in the southwestern coast of Brazil. *Revista de Biología Marina y Oceanografía*, 41(1): 87–95.

Melo, G.A.S. 1999. Manual de identificação dos Crustacea Decapoda do litoral brasileiro: Anomura, Thalassinidea, Palinuridea e Astacidea. São Paulo, Editora Plêiade, 551p.

Pereira, P.H.C.; Junior, J.Z.O. and Jacobucci, G.B. 2009. Ocupação de conchas e utilização de microambientes por caranguejos ermitões (Decapoda, Anomura) na Praia da Fortaleza, Ubatuba, São Paulo. *Biotemas*, 22(2): 65–75.

Pinheiro, M.A.A.; Fransozo, A. and Negreiros-Fransozo, M.L. 1993. Seleção e relação com a concha em *Isocheles sawayai* Forest e Saint-Laurent, 1967 (Crustacea, Anomura, Diogenidae). *Arquivos de Biologia e Tecnologia*, 36(4): 745–752.

Reese, E. 1962. Shell selection behaviour of hermit crabs. *Animal Behaviour*, 10: 347–360.

Rios, E.C. 1994. Sea shells of Brazil. Rio Grande do Sul. Fundação Cidade do Rio Grande, Instituto Acqua, Museu Oceanográfico de Rio Grande, Universidade de Rio Grande, 2nd Ed., 368p.

Rotjan, R.D.; Blum, J. and Lewis, S.M. 2004. Shell choice in *Pagurus longicarpus* hermit crabs: does predation threat influence shell selection behavior? *Behavioral Ecology and Sociobiology*, 56(2): 171–176.

Siu, B.F.C. and Lee, S.Y. 1992. Shell preference and utilization pattern in two hermit crabs, *Pagurus trigonocheirus* (Stimpson) and *Clibanarius bimaculatus* (de Haan), on a sheltered rocky shore in Hong Kong. *Asian Marine Biology*, 9: 205–216.

Turra, A.; Denadai, M.R. and Leite, F.P.P. 2005. Predation on gastropods by shell-breaking crabs: effects on shell availability to hermit crabs. *Marine Ecology Progress Series*, 286(1): 279–291.

Vance, R.R. 1972. The role of shell adequacy in behavioral interactions involving hermit crabs. *Ecology*, 53(6): 1075–1083.

Wait, M. and Schoeman, D.S. 2012. Shell use, population structure, and reproduction of the hermit crab, *Clibanarius virescens* (Kraus, 1843) at Cape Recife, South Africa. *Journal of Crustacean Biology*, 32(2): 203–214.

Yoshino, K.; Goshima, S. and Nakao, S. 2001. Sexual difference in shell use in the hermit crab *Pagurus filholi* from northern Japan. *Crustacean Research*, 30: 55–64.

Zar, J.H. 1999. Biostatistical analysis. 4th Ed. New Jersey, Prentice-Hall, 663 p.