Gastropod shell utilisation pattern by the hermit crab *Clibanarius symmetricus* (Anomura: Diogenidae) in an Equatorial Amazon estuary

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**ABSTRACT**

*Clibanarius symmetricus* is a diogenid hermit crab that is highly abundant in rocky intertidal environments, including the rock outcrops of Amazon estuaries. This study characterises the *C. symmetricus* shell utilisation pattern in the Marapanim River estuary, Pará, Equatorial Amazon, based on the hypothesis that occupancy patterns would differ, in relation to biometry and diversity of occupied shells, from those of other regions in the range of this species due to the distinct and unique environmental characteristics of equatorial estuaries. Monthly samplings were carried out from August 2006 to July 2007, in the upper and lower areas of the mid-littoral during low tides. A total of seven gastropod species were found as shells occupied by hermit crabs: 93.33% were *Thaissella trinitatensis* shells, 2.00% *Nassarius vibex*, 2.00% *Neritina virginea*, 1.33% *Natica marochiensis*, 0.67% *Parvanachis obesa*, and, occasionally, *Littorina flava* and *Phalium granulatum* shells, each with only one occurrence (0.33%). Juveniles (cephalothoracic shield length (CL) of less than 3.6 mm) occupied a higher variety of shells, while adults occupied shells with larger meristic variation. Males occupied larger shells. The length of the animal was influenced by shell measurements (total width, aperture width and weight). *Clibanarius symmetricus* showed occupancy patterns generally similar to those of specimens of the same species previously studied in the Brazilian subtropical region, and this occupancy is explained by shell availability, shell size and weight, and hermit size. However, this study showed lower occupied shell species diversity, and the species with highest occupancy frequency (*T. trinitatensis*) was not reported in any previous studies on this hermit crab. In addition, the studied population differed in occupancy patterns, with differences between males and females, and between juveniles and adults.

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**Introduction**

Hermit crabs are anomuran decapod crustaceans that use empty gastropod shells as shelter and as protection for their fragile non-calciﬁed, soft abdomen. This occupancy mechanism is a way of protecting against predators, physical stress, osmotic stress and
wave action (Biagi et al. 2006a). Gastropod shells constitute a vital resource for hermit crabs (Conover 1978; Garcia and Mantelatto 2000), allowing crustaceans to adapt to diverse types of marine environments, and are also one of the main reasons for the evolutionary success of these organisms (Conover 1978; Hazlett 1981; Garcia and Mantelatto 2001). However, despite the importance of shell utilisation by the hermit crab, experiments have proven that they only occupy empty shells that are available in the environment, since they are incapable of removing live gastropods from their shells, as this activity would demand a strength beyond that of a hermit crab (Laidre 2011).

Gastropod shell utilisation strongly influences all aspects of hermit crab biology (Hazlett 1981), such as body morphology (Turra and Leite 2002), population dynamics, and population maintenance in a particular environment (Biagi et al. 2006b). Moreover, shell utilisation influences fecundity, reproduction and population growth patterns (Fotheringham 1976; Bertness 1981; Mantelatto et al. 2002; lossi et al. 2005; Sant’Anna et al. 2008).

Shell occupancy does not occur randomly, but is rather influenced by several factors, such as shell availability in nature, weight, size, shape and/or internal shell volume, suitability of shell size and shape, or even intra- and interspecific competition among hermit crabs (Martinelli and Mantelatto 1999; Mantelatto and Garcia 2000; Garcia and Mantelatto 2001; Meireles et al. 2003; Dominiciano and Mantelatto 2004; Mantelatto and Meireles 2004; Meireles and Mantelatto 2005; Biagi et al. 2006b; Sant’Anna et al. 2006a; Fransozo et al. 2008). The presence of epibionts on shells is also a factor that may provide camouflage in combination with the substrate and influence the shell selection by hermit crabs (Martinelli and Mantelatto 1998; Ayres-Peres and Mantelatto 2010; Ribeiro et al. 2015). Shell occupancy might also vary between sexes due to differential energy investment or differential growth, or even competition between sexes (Mantelatto and Martinelli 2001; Fantucci et al. 2008). Shell utilisation, in turn, might differ among environments occupied by hermit crabs, due to abiotic fluctuations, for example the water dynamics (Garcia and Mantelatto 2000), and to differences in shell availability (Terossi et al. 2006).

In Amazon estuaries, the most frequent hermit crab species found in intertidal environments was Clibanarius symmetricus (Randall, 1840) (Morais and Lee 2014). Considering how extensive the Brazilian coastal area is, studies developed with the purpose of defining gastropod shell utilisation patterns by hermit crab C. symmetricus are still scarce. Studies on this topic observed that shell availability was a determining factor in occupancy (Negreiros-Fransozo et al. 1991); determined that occupancy will depend mainly on hermit size and shell architecture (Turra and Leite 2002, 2004); and showed that occupancy varies with occurrence site, shell availability, and shell features, such as length and weight (Sant’Anna et al. 2006a, 2006b); with occupancy patterns varying between sex groups and occurrence areas (Mantelatto et al. 2010); and with occupancy patterns mainly influenced by shell architecture (Sampaio and Masunari 2010). On the other hand, these studies were restricted to subtropical areas of the Brazilian coast, and nothing has been reported about the shell occupancy pattern of this species on the equatorial Amazon coast.

Thus, our study aimed to describe gastropod shell occupancy patterns in relation to the biometry and diversity of shells occupied by a population of C. symmetricus in an equatorial estuary, with emphasis on relationships between the size (length) and weight of hermit crabs and the shell morphometrics and occupied gastropod shell species. Our
hypothesis was that occupancy patterns differed between development stages (juveniles and adults), between sexes and between different regions in Brazil. We expected to find a lower diversity of occupied shells in the Amazon estuary than in estuaries of tropical and subtropical regions, since there is lower population evenness as an overall ecological pattern in the equatorial region, despite the high amount of biomass, and some species have a higher degree of dominance compared to the rest of the assemblage (Boltovsksy et al. 1999).

**Material and methods**

**Study area**

The Marapanim River estuary is located in the Amazon coastal zone, northern Brazil, between Extractive Reserves ‘Mãe Grande de Curuçá’ and ‘Maracanã’ and near Environmental Protection Area Algodoal/Maiandeua (east of the Marapanim estuary). This region acts as an important nursery area for many fish and crustacean species, and is classified as an extremely high-priority area for the conservation and partitioning of Brazilian biodiversity benefits (MMA 2007).

This region is situated east of the Amazon River mouth; it has a free connection with the Atlantic Ocean and is dominated by a semi-diurnal macro-tidal regime, with amplitudes ranging from 3.5 to 6 m. Combined with water and sedimentary discharges from the Amazon River, it promotes an environment with mixing of waters that influences coastal dynamics and estuarine channel morphology (Berrêdo et al. 2008).

The climate in this region is tropical wet, with mean annual temperature of around 27°C with no large variations throughout the year, and total annual rainfall between 2400 and 3300 mm (Moraes et al. 2005). Climatic seasons are defined according to rainfall; there are generally two distinct seasonal periods: a dry season from July to December, and a wet season from January to June (Moraes et al. 2005).

**Sampling and analysis of biological material**

Sampling was conducted at daytime during low neap tide at four locations of the rock outcrops in the intertidal zone of the estuary, limited by coordinates A1 (0°38’S, 47°38’W), A2 (0°42’S, 47°41’W), B1 (0°38’S, 47°34’W) and B2 (0°43’S, 47°38’W). Localities were determined by the combination of stretch (downstream: low estuary, and upstream: upper medium estuary), and estuary margin (western margin and eastern margin), with monthly periodicity from August 2006 to July 2007. At each location, three random samplings using a 0.5 × 0.5 m quadrat were performed in the upper and lower intertidal zones of the mid littoral.

Individuals of *C. symmetricus* including burrowing individuals (approx. 5 cm in depth) were collected. In the same quadrat where hermit crabs were sampled, empty gastropod shells were also collected so as to check shell availability in the environment. In the laboratory, hermit crabs were carefully removed from their shells or, alternatively, their shells were gently cracked open with a bench vise. The species identification was based on Negri et al. (2014).
Sex of *C. symmetricus* specimens was identified based on the position of gonopores; males have gonopores on the coxae of the fifth pereiopods whereas females have gonopores on the coxae of the third pair. Intersex individuals have gonopores on the coxae of both third and fifth pereiopods. Individuals with unidentifiable sex were categorised as undetermined sex. The cephalothoracic shield length (CL) was measured using a pair of digital calipers, accuracy to 0.01 mm (DIGIMESS, model 200 mm).

The gastropod shells (voucher numbers 120849–120854, Museum of Zoology of the University of São Paulo) were identified to the species level with the help of specific literature (Rios 1994, 2009; Simone 1998, 2011). Shell aperture length (SAL), shell aperture width (SAW), total shell length (TSL) and total shell width (SW) were then measured using the same pair of digital calipers. The shell dry weight (DW) was determined using a digital scale with accuracy to 0.01 g (MARTE, model AS1000c) after the shells were dried in an oven for 24 hours at 60°C.

**Data analysis**

A total of 300 hermit crabs and their respective shells were used for the analyses, since only intact shells with no damage to their surface were selected. Shell species utilisation pattern by *C. symmetricus* was assessed with relative frequency in 1 mm size classes. To separate juveniles from adults, a 3.6 mm CL value was used as the size of sexual maturity for this population, found by a regression analysis between cephalothoracic shield width and length, based on the breakpoint in the regression line (unpub. data).

In order to determine which shell measurements were more representative of the occupancy pattern by hermit crabs, a principal component analysis (PCA) was performed according to Borcard et al. (2011) and Legendre and Legendre (2012). Data were standardised for this analysis since they were at different scales, and a correlation matrix was calculated based on 9999 randomisations, where a correlation coefficient was generated indicating which variables were explained by the principal component axes. Scores generated for sampling units and loadings generated for variables were extracted from the results obtained. In addition, self-values, the explanation percentage of each axis, and values from the broken-stick model were obtained. Axes with self-values higher than predicted by broken-stick were considered the ones that best explained data variations. To generate a graph with spatial distribution of the data, scores generated for sampling units were plotted on axes 1 and 2, as well as categorical variables (occupied gastropod species and development stage – juveniles and adults).

To assess whether hermit crab size varied significantly in relation to shell size or weight, a multiple regression was performed, with CL as the dependent variable, and biometric variables of shells as independent variables. For that purpose, data were log-transformed (x + 1), since they did not show a normal distribution. This analysis yielded a global correlation coefficient and a correlation for each variable, which indicates the degree of association between the variables analysed, ranging from −1 (highly negative correlation) through 0 (absence of correlation) to 1 (highly positive correlation).
Results

A total of 1040 available empty gastropod shells were collected, belonging to six species. Of those, 74.43% were *Thaisella trinitatensis* (Guppy, 1869), 11.54% *Neritina virginea* (Linnaeus, 1758), 5.38% *Parvanachis obesa* (Adams, 1845), 4.62% *Nassarius vibex* (Say 1822), 2.4% *Natica marochiensis* (Gmelin, 1791) and 1.63% *Littorina flavia* (King & Broderip, 1832).

The hermit crabs *C. symmetricus* occupied seven gastropod species (Table 1), of which *T. trinitatensis* shells had the highest occupancy rate, with 93.33% of the total, and were occupied by hermit crabs in all size classes, except for the smallest individuals (0.1–1 mm) (Figure 1).

Shells occupied by adult hermit crabs had a broader range of biometric variables. For TSL, SW and SAL, hermit crab size is directly proportional to shell size. However, for SAW and DW, there is no significant difference in shell occupancy between juveniles and adults (Figure 2).

Of the total hermit crabs, 145 were males, 97 were females, 14 were intersex individuals and 44 were of undetermined sex. The highest occupancy percentage was

| Table 1. Descriptive statistics of morphometric data of gastropod shells occupied by *Clibanarius symmetricus* in the Marapanim River estuary (Brazil-Pará) from August 2006 to July 2007. |
|-----------------------------------------------|
| Species                       | N | TSL   | SW   | SAL   | SAW  | DW  |
| Littorina flavia             | 1 | 7.91  | 7.11 | 5.52  | 3.84 | 0.09|
| TSL  | SW   | SAL   | SAW  | DW  |
| 10.87 | 10.87 | 10.87 | 10.87 | 10.87 |
| Nassarius vibex             | 6 | 11.8  | 7.93 | 7.24  | 3.59 | 0.21|
| TSL  | SW   | SAL   | SAW  | DW  |
| 16.23 | 16.23 | 16.23 | 16.23 | 16.23 |
| 12.49 | 12.49 | 12.49 | 12.49 | 12.49 |
| Parvanachis obesa            | 2 | 5.24  | 2.62 | 2.82  | 1.34 | 0.01|
| TSL  | SW   | SAL   | SAW  | DW  |
| 5.55 | 5.55 | 5.55 | 5.55 | 5.55 |
| 2.63 | 2.63 | 2.63 | 2.63 | 2.63 |
| 2.89 | 2.89 | 2.89 | 2.89 | 2.89 |
| Thaisella trinitatensis       | 280 | 4.71  | 3.1  | 3.17  | 1.47 | 0.01|
| TSL  | SW   | SAL   | SAW  | DW  |
| 42.22 | 42.22 | 42.22 | 42.22 | 42.22 |
| 14.67 | 14.67 | 14.67 | 14.67 | 14.67 |
| 6.94 | 6.94 | 6.94 | 6.94 | 6.94 |

N = number of individuals; SD = standard deviation; TSL = total length; SW = total width; SAL = aperture length; SAW = aperture width; DW = dry weight; Min = minimum; Max = maximum.
Figure 1. Shell utilization frequency of different gastropod species relative to CL size (Cephalothoracic shield length, in mm) of *Clibanarius symmetricus* in Marapanim River estuary (Brazil-Pará).

Figure 2. Biometric variables of gastropod shells occupied by *Clibanarius symmetricus* in the Marapanim River estuary (Brazil-Pará). (TSL= total shell length; SW= total shell width; SAL= shell aperture length; SAW= shell aperture width; and DW= dry weight).
in *T. trinitatensis*; however, hermit crabs of undetermined sex occupied the smallest shells. Two gastropod species were occupied exclusively by males: *N. marochiensis* and *Phalium granulatum* (Born, 1778) (Table 2).

In the PCA, all biometric analyses had R values higher than 0.9, indicating that they were significantly contributing to the shell occupancy patterns by the hermit crabs. In addition, only axis 1 explained the variation in the data, with 94.43% of variation accommodated by the axis. Data were plotted on a graph with gastropod species as a categorical variable, and the juvenile bar indicating the part of the data where 100% of the hermit crabs were smaller than 3.6 mm CL (unpub. data) (Figure 3). Therefore, the juveniles used a broader variety of shell species (five species) compared to adults (three

**Table 2.** Gastropod species occupied by *Clibanarius symmetricus* in the Marapanim river estuary (Brazil-Pará) from August 2006 to July 2007.

| Species             | Total | Male | Female | Intersex | Undetermined |
|---------------------|-------|------|--------|----------|--------------|
|                     | N %   | N %  | N %    | N %      | N %          |
| *Littorina flavia*  | 1 0.33| 0 0  | 0 0    | 0 0      | 1 0.33       |
| *Nassarius vibex*   | 6 2.00| 3 1  | 1 0.33 | 0 0      | 2 0.67       |
| *Natica marochiensis* | 4 1.33| 4 1.33| 0 0    | 0 0      | 0 0          |
| *Neritina virginea* | 6 2.00| 1 0.33| 3 1    | 1 0.33   | 1 0.33       |
| *Parvanachis obesa* | 2 0.67| 0 0  | 0 0    | 0 0      | 2 0.67       |
| *Phalium granulatum*| 1 0.33| 1 0.33| 0 0    | 0 0      | 0 0          |
| *Thaisella trinitatensis* | 280 93.33| 136 45.33| 93 31  | 13 4.33  | 38 12.67     |
| Total               | 300 100| 145 48.33| 97 32.33| 14 4.66  | 44 14.67     |

*N* = number of individuals.

**Figure 3.** Principal component analysis of morphometric data of gastropod shells occupied by *Clibanarius symmetricus* in the Marapanim River estuary (Brazil-Pará). TSL = total shell length; SW = total shell width; SAL = shell aperture length; SAW = shell aperture width; DW = dry weight.
species); some shell species were occupied exclusively by juveniles (P. obesa, L. flava, N. virginea and N. vibex), and two other species were exclusively occupied by adult individuals (N. marochiensis and P. granulatum).

Multiple regression analysis between shell biometric variables and size measurements of hermit crabs (CL) of the entire population explained 95% of the data (R = 0.95); they were significant for SW, SAW and DW (p < 0.001; p = 0.03; p < 0.001, respectively; and r² = 0.9), indicating that these were the variables that best explained shell occupancy by the hermit crab. When males and females were compared separately, the significant variables for females were SAL (b = 0.44; p = 0.01; r² = 0.90) and DW (b = 0.12; p = 0.04; r² = 0.90); for males the significant variable was SW (b = 0.85; p < 0.001; r² = 0.94). The multiple regression analysis was also performed between development stages (juveniles and adults), and the CL of hermit crabs showed a dependence relationship with total shell width (SW) for both development stages (p < 0.001 e r² = 0.86 in juveniles; p < 0.001 and r² = 0.88 for adults; Table 3).

Discussion

Hermit crabs occupied seven species of gastropod shell in the Marapanim equatorial Amazon estuary. Thaisella trinitatensis shell was the most frequently used, and this species had the highest frequency among the empty shells present at the sampling sites. Of the studies previously carried out in the Brazilian subtropical region, Negreiros-Fransozo et al. (1991) found that 100% of the hermit crabs C. symmetricus (vittatus) occupied shells of the genus Thaisella (Thais). In other studies, the gastropod shell species most frequently used by C. symmetricus in a natural environment was Stramonita haemastoma (Linnaeus, 1767) (Reigada and Santos 1997; Sant’Anna et al. 2006a, 2006b; Mantelatto et al. 2010; Sampaio and Masunari 2010). The preference for S. haemastoma was reported in laboratory experiments by Turra and Leite (2002). In studies on other hermit crab species in natural environments, S. haemastoma was also the most frequently used species, as well as Calcinus tibicen (Herbst, 1791) (Mantelatto and Garcia 2000), Isocheles sawayai (Forest & Saint Laurent 1968) (Sant’Anna et al. 2006a; Fantucci et al. 2008) and Loxopagurus loxochelis (Moreira 1901) (Sant’Anna et al. 2006a). However, S. haemastoma not was found in this study; this suggests that occupancy is intimately linked to shell availability in the environment.

The diversity of occupied shells and the number of shells available for occupancy by hermit crabs might work as a potential biodiversity index for the ecosystem inhabited by the hermit crab and also for neighbouring ecosystems (Legendre and Legendre 2012).

Table 3. Regression summary for dependent variables and cephalothoracic shield length (CL) for different groups. Significant values in bold script.

| Variables | Groups | Beta | SE of Beta | B  | SE of B | t(294) | p level |
|-----------|--------|------|------------|----|---------|--------|---------|
| SW        | Male   | 1.04 | 0.23       | 0.86| 0.19    | 4.60   | 0.00    |
| SAL       | Male   | −0.07| 0.17       | −0.07| 0.16    | −0.44  | 0.66    |
| DW        | Male   | −0.05| 0.09       | −0.03| 0.05    | −0.51  | 0.61    |
| SW        | Juvenile | 0.66 | 0.19       | 0.43| 0.13    | 3.38   | 0.00    |
| SW        | Adult  | 0.92 | 0.20       | 0.75| 0.16    | 4.65   | 0.00    |

SAL = aperture length; SE = standard error; SW = total width; DW = dry weight.
The seven gastropod shell species occupied by *C. symmetricus* in the present study represent a lower species diversity than found in other studies in Brazilian subtropical regions: from nine to 13 species in the coastal zone of São Paulo (Mantelatto et al. 2010; Sant’Anna et al. 2006b; respectively), and 12 species on the coast of Paraná (Sampaio and Masunari 2010). However, it was generally similar to the amount of occupied species in Piauí, north-eastern Brazil, with a total of six occupied species (Mantelatto et al. 2010) (Table 4). The high frequency of *T. trinitatensis* shell occupancy, which was not found in previous studies, indicates a different occupancy pattern for this region, clearly affected by the local diversity of empty gastropod shells in the environment, since *T. trinitatensis* is the most abundant shell species in Marapanim estuary.

Hermit crabs frequently choose shells that best suit their body size and/or due to suitable shell weight (Martinelli and Mantelatto 1999; Dominciano and Mantelatto 2004). It is likely that hermit crabs from the studied estuary are occupying species that are available and not only the most suitable ones, and shell availability in the environment is an important factor for occupancy by hermit crabs (Mantelatto and Meireles 2004; Biagi et al. 2006a; Fantucci et al. 2008; Sampaio and Masunari 2010).

Table 4. Gastropod shell occupancy by *Clibanarius symmetricus* (*vittatus*) at different latitudes (%). Significant values in bold script (high frequency of shell occupancy).

| Species                     | Sant’Anna et al. (2006b) | Mantelatto et al. (2010) | Sampaio and Masunari (2010) | Present study          |
|-----------------------------|--------------------------|--------------------------|-----------------------------|------------------------|
|                            | São Paulo 23°58’S         | Piauí 02°05’S            | São Paulo 23°48’S           | Paraná 25°52’S         |
| Achatina fulica             | 0.89                     | –                        | 0.34                        | 0.08                   |
| Astrea olfersii             | –                        | –                        | 1.35                        | –                      |
| Buccinanops gradatatum      | 0.17                     | –                        | –                           | –                      |
| Buccinanops lamarckii       | –                        | –                        | –                           | –                      |
| Cerithium atratum           | 0.05                     | 0.43                     | –                           | 0.76                   |
| Chicoereus brevifrons       | –                        | 0.43                     | –                           | –                      |
| Chicoereus senegalensis     | –                        | –                        | 0.42                        | –                      |
| Chicoereus tenuivariicosus  | –                        | –                        | 29.05                       | –                      |
| Cymatium parthenopeum       | 2.13                     | –                        | 4.39                        | 0.42                   |
| Dorsanum moniliferum        | 0.43                     | –                        | –                           | 5.48                   |
| Fusinus brasiliensis        | –                        | –                        | 1.35                        | –                      |
| Leucozonia nassa            | 0.08                     | 0.85                     | 3.04                        | –                      |
| Littorina flava             | –                        | –                        | –                           | 0.33                   |
| Nassarius vibex             | 0.13                     | –                        | –                           | 2.00                   |
| Natica marochiensis         | –                        | –                        | –                           | 1.33                   |
| Neritina virginia           | –                        | –                        | –                           | 2.00                   |
| Olivancillaria steeria      | –                        | –                        | –                           | 0.08                   |
| Olivancillaria urceus       | 0.30                     | –                        | –                           | 26.47                  |
| Olivancillaria uretai       | –                        | –                        | –                           | 0.08                   |
| Parvanachis obesa           | –                        | –                        | –                           | 0.67                   |
| Phalium granulatum          | 0.05                     | –                        | –                           | 0.33                   |
| Pisania pusio               | 0.05                     | –                        | –                           | –                      |
| Polinices hepaticus         | 0.38                     | –                        | 1.01                        | 0.59                   |
| Pugilina morio              | –                        | 57.45                    | –                           | –                      |
| Semicassis granulatum       | –                        | –                        | –                           | 0.84                   |
| Stramonita haemastoma       | 95.26                    | 40.43                    | 48.31                       | 64.61                  |
| Strombus pugilis            | –                        | –                        | 11.15                       | –                      |
| Thaisella trinitatensis     | –                        | –                        | –                           | 93.33                  |
| Tegula viridula             | 0.08                     | –                        | –                           | –                      |
| Turbinella laevigata        | –                        | 0.43                     | –                           | –                      |
| Zidona dufresnei            | –                        | –                        | 0.17                        | –                      |
Shell utilisation pattern is related to habitat, resulting from different availability of shells in the field (Terossi et al. 2006). Thus, the occupancy for one species or another might vary according to the occurrence site and to their geographical distribution, since it depends on shell availability (Negreiros-Fransozo et al. 1991; Garcia and Mantelatto 2000). Moreover, occupancy pattern might also vary according to environmental variations, as shells provide protection against predation, osmotic stress and wave action (Biagi et al. 2006a).

Unfortunately, there are no studies listing gastropod biodiversity in the Marapanim estuary. Empty gastropod shells found in this estuary belonged mostly (75%) to *T. trinitatensis*. However, Morais and Lee (2014) listed the benthonic fauna in an adjacent estuary (Ilha de Areuá, Pará), including gastropods; *T. trinitatensis* was also one of the species with the highest occurrence frequency (> 40%) in the region. Although a high number of *S. haemastoma* were collected in a nearby estuary (Morais and Lee 2014), this species was not occupied by *C. symmetricus* here and was not found among the shell species available in the Marapanim estuary.

Even if our study has identified a different shell species from the ones usually used by *C. symmetricus* at other sites, it is likely that the choice for *T. trinitatensis* wasn’t random; this species has architecture similar to *S. haemastoma* (shell shape and spiralisation more elongated). Occupancy of shells with similar morphology to *S. haemastoma* was also reported by Sampaio and Masunari (2010) for *C. symmetricus* (*vittatus*), indicating that shell attributes are the most important factor in shell occupancy by these hermit crabs. This agrees with Turra and Leite (2004), who proposed that shell occupancy by the hermit crab *C. symmetricus* (*vittatus*) is more related to shell architecture than to shell length or weight. Moreover, the degree of shell elongation or spiralisation can be an important factor in shell use by hermit crabs (Teoh and Chong 2014).

Adult hermit crabs occupied shells with measurements corresponding to the shells occupied by juveniles, indicating that young hermit crabs might be occupying shells that are larger than the suitable size, and this might be considered a strategy to allow for their future growth, as observed by Dominiano and Mantelatto (2004) for other hermit crab species, such as *Paguristes tortugae* Schmitt, 1933. Although the shell is a factor that affects the fecundity, reproduction and population growth patterns of hermit crabs (Fotheringham 1976; Bertness 1981; Mantelatto et al. 2002; Iossi et al. 2005; Sant’Anna et al. 2008), in certain situations it does not seem to determine the size of the hermit crab inside; large individuals might occupy small/light shells, and small individuals might occupy large/heavy shells (Turra 2003). However, when hermit crabs are confined to shells that are too small for them, their growth rate can decrease significantly, and can increase the risk of predation, and consequently of mortality (Fotheringham 1976; Angel 2000).

The difference in variety of gastropod shell species occupied by juvenile individuals (five species) compared to adult individuals (three species) and the exclusive occupancy of certain species by both groups might be determined by their likely preference for certain shell types throughout their development. This result corroborates shell preference experiments conducted with hermit crabs *Pagurus hirsutiusculus* (Dana, 1851) and *P. granosimanus* (Stimpson, 1859) by Straughan and Gosselin (2014); they observed that the diversity of occupied shells decreased as the size of these hermit crabs increased. Therefore, the preference for shell type is an important determining factor in shell
occupancy by hermit crabs, and it changes throughout the ontogeny of the hermit crab (Straughan and Gosselin 2014).

Among the shell parameters assessed, shell weight was an important factor for shell occupancy by *C. symmetricus*. In general, heavier shells ensure greater stability to the animal against currents, and protection against predators (Mantelatto and Dominiano 2002).

Males and females occupied the same gastropod shell species; however, males occupied the two species with larger sizes, *N. marochiensis* and *P. granulatum*. This might be explained by the sexual dimorphism present in *C. symmetricus*; males reach larger sizes than females (Turra and Leite 2000; Sampaio et al. 2009; Sant’Anna et al. 2009; Mantelatto et al. 2010).

Males and females had different shell occupancy patterns, which have already been reported in other studies (Sant’Anna et al. 2006b; Fantucci et al. 2008; Mantelatto et al. 2010; Teoh and Chong 2014). This might be explained by the difference in energy expenditure, that males possibly have a higher growth rate than females, since females would be investing more energy in reproduction; and this reduces competition for shell occupancy (Mantelatto et al. 2010). Furthermore, different growth patterns might influence the probable difference in occupancy (Fantucci et al. 2008), associated with the possible competitive dominance of males over females in the fight for shells due to the difference in sizes among them (Yoshino and Goshima 2002).

Hence, the gastropod shell utilisation pattern by *C. symmetricus* in the Marapanim River estuary did not differ from the pattern observed in subtropical regions, which relates occupancy variation to shell availability in the environment. However, hermit crabs occupied *T. trinitatensis* more frequently in the estuary studied, where there was a high availability of these empty shells. This shell was not reported in other studies on the same hermit crab species, confirming that occupancy pattern might vary according to geographical distribution. In addition, our study also observed differences in occupancy according to development stage; this is the first time this information was reported for this species.

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No potential conflict of interest was reported by the authors.

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