Spatiotemporal distribution and population structure of *Clibanarius symmetricus* (Randall, 1840) (Crustacea, Diogenidae) in an Amazon estuary

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**Abstract:** Rocky outcrops in the intertidal zones of estuaries often contain a highly diverse microbenthic community which includes the hermit crab, *Clibanarius symmetricus*, an abundant species on the equatorial Amazon coast. However, the ecology of this anomuran is poorly understood. Given this, the present study investigated the spatiotemporal distribution and structure of the *C. symmetricus* populations that inhabit the rocky outcrops of the Marapanim estuary in northern Brazil. Samples were collected monthly over a yearly cycle covering both the dry and rainy seasons in the upper and lower midlittoral zones during low tide. The distribution and abundance of *C. symmetricus* were affected directly by environmental factors such as temperature, seasonality, the intertidal zone, and salinity. The population presented sexual dimorphism, with males being larger than females, a male-biased sex ratio (1.5:1), a nonnormal and unimodal distribution, continuous reproduction, and sexual maturation at a cephalothoracic shield length of 3.6 mm. Despite the unique characteristics of the Amazon coast and the study estuary, the spatiotemporal distribution and structure of the *C. symmetricus* population were similar to those recorded at higher latitudes.

**Key words:** Abundance, Anomura, macrobenthos, sex ratio, size classes

1. Introduction

The hermit crabs of the genus *Clibanarius* Dana, 1852 are common benthic anomurans that inhabit the intertidal zone in tropical and subtropical regions (Melo, 1999; Mantelatto et al., 2010), where they play an important role in the marine food chain and nutrient cycling (Negreiros-Fransozo et al., 1997; Fransozo and Mantelatto, 1998). These crabs are also important indicators of environmental change in the intertidal zone (Dunbar et al., 2003). A total of 60 valid *Clibanarius* species have been described from around the world (McLaughlin et al., 2010; Negri et al., 2014). One species, *Clibanarius symmetricus* (Randall, 1840), is distributed along the Caribbean coast of Central America, and ranges over the northern and eastern coasts of South America, as far south as Santa Catarina, Brazil (Negri et al., 2014).

Populations studies provide important insights into the distribution of a species and the adaptive mechanisms that determine this distribution, as well as the abundance of the organism (Mantelatto et al., 2010). However, in the specific case of *C. symmetricus*, population studies have been restricted mainly to the subtropical coast of southern Brazil (e.g., Sampaio et al., 2009; Sant'Anna et al., 2009; Mantelatto et al., 2010), and no ecological data are available from the equatorial region.

Reproductive patterns, sex ratios, and density may vary considerably among the different populations of *C. symmetricus*. Seasonal breeding has been recorded in subtropical populations, for example (Turra and Leite, 2000; Sant'Anna et al., 2009; Mantelatto et al., 2010), whereas continuous reproduction has been reported from tropical South America (Mantelatto et al., 2010), with more intense reproductive activity being recorded in warmer months (Sant'Anna et al., 2009). The species is sexually dimorphic, with males being larger than females (Turra and Leite, 2000; Sampaio et al., 2009; Sant'Anna et al., 2009; Mantelatto et al., 2010), and while most populations have a biased sex ratio, there is no systematic pattern with the bias favoring either the males or the females in different populations (Negreiros-Fransozo et al., 1991; Turra and Leite, 2000; Sant'Anna et al., 2009; Mantelatto et al., 2010).

Temperature is considered the principal abiotic factor determining reproductive patterns in this species; it also acts as a regulator of metabolic, biochemical, and hormonal activity (Sant'Anna et al., 2009). Salinity is also a factor determining the abundance and distribution of *C. symmetricus*.
symmetricus (Sant’Anna et al., 2006a), given that ovigerous females tend to migrate to more saline waters (Sant’Anna et al., 2008). Other factors may also affect the distribution of these organisms in the environment, e.g., type of substrate (Franoso et al., 1998; Meireles et al., 2006) and the availability of gastropod shells in the environment (Meireles et al., 2003; Biagi et al., 2006a).

The lack of data on the C. symmetricus populations of the equatorial Amazon coast limits the understanding of the functional variation in the ecology of the species across different latitudes. As the equatorial coast of Brazil has a distinct configuration of climate and sedimentation patterns, as well as the influence of macrotides (=4–6 m), it presents unique conditions in comparison with other latitudes. Given this, the present study investigated the spatiotemporal variation in the density and population structure of the hermit crab C. symmetricus in the rocky outcrops found in an estuary of the equatorial Amazon coast. The data were used to test the hypothesis that the species presents distinct distribution patterns and population structure in this region, in comparison with other latitudes in which it has been studied.

2. Materials and methods

2.1. Study area

The estuary of the Marapanim River discharges directly into the Atlantic Ocean to the east of the mouth of the Amazon River and covers an area of 2500 km². This estuary is strongly influenced by the local semidiurnal macrotidal regime, with a tidal amplitude of between 3.5 and 6 m (Silva et al., 2009). Saline marine waters encroach 60 km into the estuary during the period of reduced rainfall (Berrêdo et al., 2008) between July and December.

The region is located within the Intertropical Convergence Zone (ITCZ), where the local climate is regulated by low atmospheric pressure and high humidity (annual rainfall of 2400–3300 mm) and mean temperatures of approximately 27 °C (Moraes et al., 2005; Berrêdo et al., 2008). There are two seasons associated with distinct rainfall levels, with a dry season from July to December and a rainy season from January to June (Moraes et al., 2005). Based on the data from the National Water Agency (ANA 2007, http://www.ana.gov.br), however, the period of the present study was atypical, with a lack of rain in January. For the purposes of the present study, then, the dry season was defined as the period between August and January, and the rainy season as that between February and July.

The estuary is a mixed-water environment, determined by the influence of tidal activity and sedimentary discharge, which combine to determine the physical dynamics of the coastal environment, such as sedimentation patterns (Berrêdo et al., 2008; Silva et al., 2009). The morphology and hydrodynamics of this estuary, and its sedimentation patterns, reflect the unique features of the equatorial Amazon region.

Four sites were selected for the present study to represent the salinity gradient found within the estuary and the variation in substrates and anthropogenic impacts (Figure 1). The most anthropogenic sites were located on the left (western) margin of the estuary, near the village of Marudá (site A1) and the town of Marapanim (site A2). The sites with the least human impact are located on the eastern margin of the estuary, adjacent to the well-preserved Algodoal Island (site B1) and the village of Cazéal (site B2).

The northernmost sites (A1 and B1), located in the lower estuary (sector 1), are the most saline due to the influence of marine waters, whereas those further south (A2 and B2) are located within the intermediate (middle) estuarine zone (sector 2), where salinity is invariably lower due to the input of freshwater from the Marapanim River. The characteristics of the substrate also vary between sectors, with the lower estuary (sector 1) being characterized by a higher density of larger rock fragments. Rocks of similar size are found at site B2, but they are more ferruginous and crumble easily, while at site A2, the rocks are relatively small and covered partially by mud (Silva and Martinelli-Lemos, 2012).

2.2. Sampling and analysis of hermit crabs

Hermit crabs were sampled each month from August 2006 to July 2007, which included both the dry (August to January) and rainy (February to July) seasons. The specimens were collected from the consolidated substrate of the upper and lower midlittoral zone at each site (Figure 1).

Three random samples were collected at each site in the daytime 1 h after the lowest spring tide. For this, 3 quadrats (0.5 m × 0.5 m) were established haphazardly at each site, and all hermit crabs found within each quadrat were collected manually. As no other hermit crab species is sympatric with C. symmetricus in the study area, the identification of the specimens was unequivocal. During specimen collection, the salinity of the water in the pool water was determined using an optical refractometer, while its temperature was measured using a mercury thermometer.

In the laboratory, the crabs were removed carefully from their shells or, when this was impossible, the shell was cracked open gently in a bench vise. The species was identified based on Melo (1999), and subsequently corrected according to Negri et al. (2014). The sex of the specimens was determined based on the position of the gonopores: in the male, the gonopores are located on the coxae of the fifth pleopods, whereas in the female, they are found on the coxae of the third pair. Intersex individuals had gonopores on the coxae of both the third
and the fifth pereiopods. Specimens whose sex could not be confirmed were assigned to the “undetermined” category. The cephalothoracic shield length (CSL) and width (CSW) were measured using a pair of digital calipers accurate to 0.01 mm, and total wet weight (TW) was determined using a digital scale (precision of 0.01 g). Only intact specimens were measured and weighed.

2.3. Data analysis
The density of *C. symmetricus* was calculated by dividing the number of individuals recorded (ind.) by the size of the quadrat area sampled (0.25 m²). Mean salinity and water temperature were compared among sites (A1, A2, B1, and B2), and between intertidal zones (upper and lower zone of the midlittoral) using an analysis of variance (one-way ANOVA). The correlation between hermit crab density and environmental variables (temperature and water salinity) was investigated using a multiple regression analysis.

As the data did not satisfy the assumptions of normality or homoscedasticity, even after transformation, differences in *C. symmetricus* density among treatments (season, sector, margin, and zone) were analyzed using a permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations (Anderson, 2005). These analyses were based on matrices of Bray–Curtis similarity scores, using log (x + 1) transformed density values.

For the analysis of the body size–frequency distribution of the hermit crabs, the specimens were grouped into 2-mm CSL interval classes. The normality of the distribution (total and grouped by sex) was verified using the Kolmogorov–Smirnov test. The difference in body size between the sexes was tested using Student’s t-test. The sex ratio was analyzed among size classes and months using chi-square $\chi^2$ (specimens with undetermined sex were excluded from this analysis).

The cephalothoracic shield length size that corresponds to the onset of morphological sexual maturity was estimated according to the regression breakpoints, i.e. the point at which the slope either becomes discontinuous or changes direction, marking the transition from the juvenile to the adult phase (Mantelatto and Martinelli, 2001). The CSW (dependent variable) vs. CSL (independent variable) ratio was determined using a linear regression analysis adjusted to the formula $Y = a + b.X$. The analyses were run in Statistica* 12.7 (STATSOFT, 2015) and Primer* 6.0

Figure 1. Geographical location of the study area, showing the 4 sampling sites in the Marapanim estuary: A1 and A2 (western margin), B1 and B2 (eastern margin).
(Clarke and Warwick, 1994), and an α = 0.05 significance level was adopted for all procedures.

3. Results

3.1. Abiotic factors

Water temperature varied little during the sampling period, ranging between 27.6 °C and 29.7 °C. The temperature of the water was significantly higher in the inner estuary (sector 2) in comparison with the outer estuary, i.e. sites A1 and B1 (ANOVA, F = 101.29; P < 0.0001). However, temperature did not vary significantly between margins or midlittoral zones (P > 0.05).

The lowest salinity (0) was recorded in March 2007, while the highest value (44) was registered in October 2006 (Table 1). Mean salinity was also significantly higher in the lower estuary (21.53) in comparison with the middle estuary, where it was 13.21 (ANOVA, F = 77.33; P < 0.0001). Mean salinity was also significantly lower on the western margin (15.27), i.e. sites A1 and A2, in comparison with the eastern margin (sites B1 and B2), where it was 19.45 (ANOVA, F = 10.4; P = 0.001). No significant variation was found, however, between the lower (mean salinity = 17.21) and upper (17.87) zones of the midlittoral.

3.2. Spatiotemporal distribution of *C. symmetricus*

A total of 380 *C. symmetricus* specimens were collected during the study period. Hermit crab density varied significantly between seasons (dry and rainy; P < 0.01), sector (lower and middle; P < 0.01), and zone (upper and lower midlittoral; P < 0.01). However, no significant variation was found between the estuary margins (A and B; P = 0.46) or in the interaction between the abiotic factors analyzed (Table 1).

The mean total density recorded during the study period was 5.28 ± 11.69 ind./m². Factors associated with different densities were plotted to verify how they influenced the distribution of the species in the environment. This showed that the density of *C. symmetricus* was higher during the rainy season (Figure 2a) and in the lower estuary (sector 1), and highest on the eastern margin (B1) and lowest on the western margin at site A2 (Figure 2b), and highest in the lower midlittoral zone (Figure 2c).

The mean density of hermit crabs, as well as the temperature and salinity of the water, varied considerably during the study period (Figure 3). The multiple regression analysis showed a significant negative correlation between hermit crab density and temperature (β = –0.37; P =

### Table 1. Results of the PERMANOVA comparing *Clibanarius symmetricus* densities among sampling points in the equatorial Marapanim estuary, Pará, Brazil.

| Factor     | DF | SS    | MS    | pseudo-F | P (perm) |
|------------|----|-------|-------|----------|----------|
| Seasons    | 1  | 5837.70 | 5837.70 | 10.430   | 0.001    |
| Sectors    | 1  | 23877  | 23877  | 42.661   | <0.001   |
| Margins    | 1  | 312.79  | 312.79  | 0.559    | 0.460    |
| Zones      | 1  | 5915.80 | 5915.80 | 10.570   | 0.001    |
| Se × Sc    | 1  | 1695.90 | 1695.90 | 3.030    | 0.076    |
| Se × Ma    | 1  | 189.15  | 189.15  | 0.337    | 0.576    |
| Se × Zo    | 1  | 646.98  | 646.98  | 1.156    | 0.272    |
| Sc × Ma    | 1  | 72.79   | 72.79   | 0.054    | 0.758    |
| Sc × Zo    | 1  | 1282.10 | 1282.10 | 2.291    | 0.127    |
| Ma × Zo    | 1  | 61.65   | 61.65   | 0.110    | 0.790    |
| Se × Sc × Ma | 1 | 1901   | 1901   | 3.396    | 0.064    |
| Se × Sc × Zo | 1 | 1384.40 | 1384.40 | 2.473    | 0.115    |
| Se × Ma × Zo | 1 | 1182.90 | 1182.90 | 2.095    | 0.151    |
| Sc × Ma × Zo | 1 | 626.21  | 626.21  | 1.188    | 0.285    |
| Se × Sc × Ma × Zo | 1 | 998.21 | 998.21 | 1.783    | 0.186    |
| Residues   | 272 | 152,240 | 559.70 |          |          |
| Total      | 287 | 198,210 |        |          |          |

(Se) seasons (dry and rainy), (Sc) sectors (lower [1] and middle [2]), (Ma) margins (A and B), and (Zo) zones (lower [L] and upper [U]). DF = degrees of freedom, SS = sum of squares, MS = mean squares. P = probability (α = 0.05). Significant values are highlighted in bold.
0.009), but little relationship with salinity ($\beta = 0.18; P = 0.18$). This analysis explained 39% of the variation in the data ($R = 0.39$).

3.3. Population structure of C. symmetricus in the study area

It was possible to examine 336 C. symmetricus specimens for sex determination, and the sex was identified in 287 cases, including 163 males (56.80%), 103 nonovigerous females (35.89%), 5 ovigerous females (1.74%), and 16 intersex individuals (5.57%). The sex of a further 49 individuals could not be identified; these specimens were designated as undetermined sex. Ovigerous females were present in September, November, July, and March, i.e. during both the dry and the rainy seasons (Figure 4). Two ovigerous intersex specimens were collected in August.

The CSL ranged from 0.99 mm (in a specimen of undetermined sex) to 8.91 mm (male), while the smallest ovigerous females had a CSL of 4.51 mm (Table 2). Size did not vary significantly between males and females overall ($t = 1.86; P = 0.06$), although the mean CSL of the males was significantly longer than that of nonovigerous females ($t = 2.47; P = 0.01$), but significantly shorter than that of ovigerous females ($t = -2.08; P = 0.03$). Nonovigerous females were also significantly smaller than ovigerous females ($t = -3.48; P < 0.001$). Intersex hermit crabs were significantly larger, on average, than both males ($t = -2.28; P = 0.02$) and females ($t = -3.75; P < 0.001$).

The smallest size (CSL) class contained only individuals of undetermined sex (Figure 5). Both males and females were present in almost all CSL classes except for the largest one (8–9 mm), which was comprised exclusively of males. All the females in the largest classes (4–5 mm and above) were ovigerous. A unimodal size distribution was recorded in most months (Figure 6), with continuous...
juvenile recruitment throughout the year, which was more intense from April through September. The sex ratio was significantly male biased (1.5:1; χ² = 11.53; P < 0.01) in all rainy season months except March (Table 3).

The CSW vs. CSL ratio presented the breakpoint in 3.6 mm (CSW: –0.24 + 0.89*CSL, R² = 0.98), indicating a shift in the growth pattern that shows that this is the size at which *C. symmetricus* reaches morphological sexual maturity.

4. Discussion
4.1. Spatiotemporal distribution of *C. symmetricus*

The distribution of *C. symmetricus* in the Marapanim estuary is influenced directly by environmental factors such as temperature, which may influence a number of aspects of the biology of the species, such as reproduction and growth patterns, and sexual maturation. The variation in crab density found between seasons and in the different sectors and zones of the Marapanim estuary during different periods reflects the spatiotemporal variation in environmental factors.

While no significant correlation was found between the density of crabs and salinity in the present study, the abundance of *C. symmetricus* was greatest where the water was most saline. Sant'Anna et al. (2009) found evidence that salinity may have an important influence on the reproductive patterns of this species. Although no data are available on the influence of salinity on the development of *C. symmetricus* larvae, high salinity is known to be a requirement for the adequate development of the eggs and larvae of *Clibanarius vittatus* (Fotheringham and Bagnall, 1976; Lowery and Nelson, 1988; Kelly and Turner, 2011).

Given the observations in the present study, it would be reasonable to assume that *C. symmetricus* may also require more saline environments, which would restrict its presence in the inner sectors of the estuary. In a study of anomuran larvae in the Marapanim estuary, Oliveira and Martinelli-Lemos (unpub. data) found a positive correlation between the density of these organisms and salinity, with higher densities being recorded in the lower estuary, adjacent to the open sea. While all the evidence points to a preference for more saline conditions, the lack of a significant correlation in the present study may be related to the small numbers of larvae collected.
One other factor that may limit the presence of these organisms to the lower estuary is the sediment. As the lower estuary has rock fragments of larger size (Silva and Martinelli-Lemos, 2012), this may favor the occurrence of the organisms by providing refuge from high temperatures and the physical stress of breaking waves. This may also account for the higher density of *C. symmetricus* recorded in the lower midlittoral zone, which is less exposed to the sun during the tidal cycle than the upper zone, where relatively high temperatures may cause heat stress and increase the risk of desiccation.

In addition to providing protection, rocky substrates provide a wider variety of microhabitats, in which many organisms that provide nutritional resources can be found (Franzozo et al., 2008). The rocky outcrops of the estuaries of the Amazon coast harbor a wealth of decapod crustaceans (Oliveira et al., 2012; Silva and Martinelli-Lemos, 2012; Oliveira et al., 2013; Morais and Lee, 2014; Sampaio and Martinelli-Lemos, 2014; Rodrigues and Martinelli-Lemos, 2016; Nóbrega and Martinelli-Lemos, 2016), which may create an environment favorable for the development of hermit crabs.

The variation in temperature in the study region is small; however, the density of *C. symmetricus* was correlated negatively with water temperature. Hermit crabs may suffer considerably from heat stress in this environment, and during hotter periods, they may actively seek out a cooler environment. Sant'Anna et al. (2009) considered temperature to be an important factor in determining the reproductive patterns in this species, as well as acting as a regulator of metabolic and biochemical activity, and a hormonal cue.

The hermit crab *C. symmetricus* was least abundant at site A2 (western margin, middle estuary). In addition to the site having less-saline waters, the substrate at this site—small rocks partially covered by mud—appears to be less favorable to the species. The site is also influenced by the presence of urban development, i.e. the town of Marapanim and the village of Marudá, which are not only residential areas but also function as centers of tourism, especially during vacation periods, further intensifying the potential impact on the structure of the *C. symmetricus* populations found in this area.

Overall, then, the evidence implies that *C. symmetricus* tends to occur in areas with more saline water, substrates with larger rocks, and less anthropogenic impact. Migration patterns may be related to the need to find optimal locations for development. Fotheringham (1975) first highlighted the influence of seasonal and reproductive factors on migratory behavior; hermit crabs may also migrate in search of important resources such as appropriate empty shells (see Gherardi et al., 1990).

The availability of gastropod shells and competition for this resource are also important factors influencing the distribution of hermit crab populations (Hazlett, 1981; Martinelli and Mantelatto, 1999; Bertini and Franzozo, 2000; Franzozo et al., 2008), including *C. symmetricus* (Sant'Anna et al., 2006b; Rodrigues and Martinelli-Lemos, 2016). Variation in the availability of food sources and the feeding behavior of the crabs may also have an important

### Table 2.
Basic parameters of cephalothoracic shield length (CSL) of the *Clibanarius symmetricus* specimens collected in the Marapanim estuary, Pará, Brazil (SD: standard deviation).

| Groups              | N  | Minimum | Maximum | Mean ± SD |
|---------------------|----|---------|---------|-----------|
| Undetermined        | 49 | 0.99    | 2.12    | 1.54 ± 0.28 |
| Males               | 163| 1.72    | 8.91    | 3.82 ± 1.61 |
| Nonovigerous females | 103| 1.86    | 7.14    | 3.39 ± 1.23 |
| Ovigerous females   | 5  | 4.51    | 6.27    | 5.33 ± 0.76  |
| Intersex individuals| 16 | 2.56    | 7.18    | 4.77 ± 1.32 |
| TOTAL               | 336| 0.99    | 8.91    | 3.44 ± 1.60  |

### Figure 5.
Frequency of occurrence of *Clibanarius symmetricus* specimens of nonovigerous females (F), ovigerous females (OF), males (M), and intersex individuals (INT) by size class (cephalothoracic shield length, in mm), collected in the Marapanim estuary, Pará, Brazil.
influence on the large-scale distribution of *C. symmetricus* (Dunbar et al., 2003).

4.2. Population structure of *C. symmetricus*

Ovigerous *C. symmetricus* females were relatively rare overall (1.74% of total abundance); however, as they were not absent altogether, reproduction does appear to be occurring in the population. It seems likely that most ovigerous females may have migrated to locations closer to the mouth of the estuary than the outermost sampling points surveyed in the present study (sites A1 and B1).

![Figure 6](image)

**Figure 6.** Frequency distribution of cephalothoracic shield length (in mm) classes of the *Clibanarius symmetricus* specimens collected in the Marapanim estuary, Pará, Brazil. The vertical line represents the onset of sexual maturity (3.6 mm).
in search of more saline water and more appropriate substrates (larger rocks), as well as optimal salinity for spawning (Sant’Anna et al., 2009).

The relative rarity of intersex individuals (5.57%) appears to be a common feature of C. symmetricus populations throughout its geographic range. Turra and Leite (2000) found that 5%–7% of a population in a subtropical region was intersex, and even lower frequencies have been recorded in other tropical and subtropical areas, with Sant’Anna et al. (2009) recording a frequency of 2.5%, Sampaio et al. (2009) recording one of 1.9%, and Mantelatto et al. (2010) only 0.3%.

Intersex individuals were long considered to be functional males, given that female sexual features are only present in the external morphology (Turra, 2004), until Turra (2007) found an ovigerous intersex individual. Ovigerous intersex individuals were also collected in the present study, indicating that they may also be functional females. Intersexuality may thus represent a form of hermaphroditism involving the simultaneous presence of both female and male gonads in the same individual (Sant’Anna et al., 2010), although this requires further investigation.

The sexual dimorphism recorded in the present study population is consistent with that found in the species at other latitudes (Reigada and Santos, 1997; Turra and Leite, 2000; Sampaio et al., 2009; Sant’Anna et al., 2009; Mantelatto et al., 2010). Sexual dimorphism appears to be a characteristic common to all hermit crabs (e.g., Mantelatto and Martinelli, 2001; Bertini et al., 2004; Biagi et al., 2006a; Ayres-Peres and Mantelatto, 2008; Fantucci et al., 2009). This may be related to the difference in energy available for growth, with males having more energy available for somatic growth in comparison with females, who must dedicate more energy to the production of eggs. Larger males may also be able to outcompete smaller males in mating combats, and thus gain access to more reproductive partners, as described by Abrams (1988).

Morphological sexual maturity estimated from the analysis of relative growth patterns shows smaller size than that recorded in tropical and subtropical regions (Table 4). Relative growth is often used to determine sexual maturity in hermit crabs, and is considered a reliable criterion for this purpose (Biagi et al., 2006b). The earlier sexual maturity recorded in the present study may be related to the higher temperatures found in the equatorial Marapanim estuary, which may favor growth and development. The Bergmann rule, which explains latitudinal body size variation in vertebrates (later adopted to invertebrates), postulates that animals at higher latitudes tend to be larger in size to better tolerate colder temperatures (Bergmann, 1847). As reproductive potential is defined by the body size and rate of growth of an organism, reproductive age will decrease with decreasing growth rates (Giesel, 1976).

A nonnormal, unimodal distribution of body size has also been recorded in C. symmetricus in other regions

Table 3. Sex ratio (SR) of the Clibanarius symmetricus specimens collected in the Marapanim estuary, Pará, Brazil.

| Months    | Males | Females | SR   | $\chi^2$ | P       |
|-----------|-------|---------|------|----------|---------|
| August    | 22    | 19      | 1.15:1 | 0.22     | 0.64    |
| September | 14    | 16      | 0.8:1 | 0.13     | 0.71    |
| October   | 05    | 03      | 1.6:1 | -        | -       |
| November  | 10    | 09      | 1.11:1| 0.05     | 0.82    |
| December  | 04    | 08      | 0.5:1 | 1.33     | 0.25    |
| January*  | -     | -       | -    | -        | -       |
| February  | 12    | 04      | 3:1   | 4.00     | 0.04    |
| March     | 06    | 07      | 0.85:1| 0.07     | 0.78    |
| April     | 18    | 07      | 2.57:1| 4.84     | 0.02    |
| May       | 37    | 21      | 1.76:1| 4.41     | 0.03    |
| June      | 14    | 05      | 2.8:1 | 4.41     | 0.03    |
| July      | 21    | 09      | 2.3:1 | 4.80     | 0.02    |
| Total     | 163   | 108     | 1.5:1 | 11.53    | <0.001  |

$\chi^2$ = chi-square; $P$ = probability ($\alpha = 0.05$). Significant values are highlighted in bold.

* In January, only intersex and undetermined individuals were encountered.

Table 4. Mean CSL (in mm) and the smallest ovigerous female (OF) recorded in studies of Clibanarius symmetricus at different latitudes along the Brazilian coast.

|                | Turra and Leite (2000) | Sampaio et al. (2009) | Sant’Anna et al. (2009) | Mantelatto et al. (2010) | Present study |
|----------------|------------------------|-----------------------|--------------------------|--------------------------|---------------|
| São Paulo      | 23°49’S                | 25°52’S               | 23°58’S                  | 23°48’S                  | 0°28’05’S     |
| Paraná         | 6.98 ± 1.04            | 5.86 ± 1.32           | 7.32 ± 1.74              | 7.60 ± 1.17              | 8.47 ± 2.49   |
| Smallest OF    | 5.07                   | 3.95                  | 4.9                      | 4.0                      | 4.51          |

χ² = chi-square; $P$ = probability ($α = 0.05$). Significant values are highlighted in bold.

* In January, only intersex and undetermined individuals were encountered.
The presence of juvenile individuals throughout the year reflects a continuous reproductive process in the present study population. The high frequency of juveniles recorded in the present study indicates that they inhabit the same areas as the adults, in contrast with the findings of Sant’Anna et al. (2009), who reported that the adults inhabited an area distinct from that of recruitment. This indicates that the Marapanim estuary is suitable for the development of the entire population, making it an important site for the conservation of *C. symmetricus*.

Mantelatto et al. (2010) also recorded continuous reproduction in a population in tropical northeastern Brazil, which indicates that this may be the typical pattern for *C. symmetricus* in tropical and equatorial regions. In subtropical regions, however, seasonal breeding is the norm (Turra and Leite, 2000; Sampaio et al., 2009; Sant’Anna et al., 2009; Mantelatto et al., 2010). This indicates that the breeding pattern of these hermit crabs varies by latitude, as observed by van de Kerk et al. (2016), who concluded that the reproductive strategies of a species, such as its breeding frequency, may vary along a latitudinal gradient.

A male-biased sex ratio has been recorded in *C. symmetricus* populations in southern (Sampaio et al., 2009) and southeastern Brazil (Mantelatto et al., 2010). However, a female-biased sex ratio was recorded in *C. symmetricus* populations in southeastern (Negreiros-Fransozo et al., 1991; Turra and Leite, 2000; Sant’Anna et al., 2009) and northeastern Brazil (Mantelatto et al., 2010). A male-biased sex ratio may be the result of differential survival or life expectancy, but may also represent an adaptive strategy that permits each female to mate with more than one male (Ayres-Peres and Mantelatto, 2008). Other determinants may include differential sexual migration (Wenner, 1972). This may have been a factor in the present study, given the predominance of males during the rainy season, and the scarcity of ovigerous females throughout the year. Differential migration between males and females was also reported by Sampaio et al. (2009), on the subtropical southern coast of Brazil. Differential migration patterns between the sexes have also been observed in *C. vittatus* in Texas, in the United States, where there is a predominance of males during the winter (Fotheringham, 1975).

In conclusion, the distribution of *C. symmetricus* was influenced by temperature, season, the intertidal zone, and salinity. The study population was characterized by male-oriented sexual dimorphism, a nonnormal and unimodal distribution, continuous reproduction, and a male-biased sex ratio. The distribution patterns (according to the variables tested) and population structure of *C. symmetricus* were similar to those recorded in previous studies at higher latitudes, which partially contradicts the hypothesis of a possible latitudinal gradient. However, the specimens collected in the present study were smaller in size on average than those collected in previous studies, and sexual maturation was earlier, reflecting the influence of the higher temperatures of the equatorial study region, which favor early sexual maturity in comparison with populations at higher, cooler latitudes.

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**References**

Abrams PA (1988). Sexual difference in resources use in hermit crabs: consequences and causes. In: Chelazzi, G, Vannini, M, editors. Behavioral Adaptations to Intertidal Life. New York, NY, USA: Plenum Press, pp. 283-296.

Anderson MJ (2005). PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Auckland, New Zealand: Department of Statistics, University of Auckland.

Ayres-Peres L, Mantelatto FL (2008). Análise comparativa da estrutura populacional do ermitão endêmico do Atlântico Ocidental *Loxopagurus loxochelis* (Decapoda, Anomura) em duas regiões do Estado de São Paulo, Brasil. Iheringia, Sér Zool 98: 28-35 (in Portuguese).

Bergmann C (1847). Über die verhältnisse der warmeökonomie der thiere zuhrer grösse. Gottinger Studien I: 595-708 (in German).

Berrêdo JF, Costa ML, Progene MPS (2008). Efeitos das variações sazonais do clima tropical úmido sobre as águas e sedimentos de manguezais do estuário do rio Marapanim, costa nordeste do Estado do Pará. Acta Amaz 38: 473-482 (in Portuguese).

Bertini G, Fransozo A (2000). Patterns of shell utilization in *Petrochirus diogenes* (Decapoda, Anomura, Diogenidae) in the Ubatuba region, São Paulo, Brazil. J Crustacean Biol 20: 468-473.

Bertini G, Fransozo A, Braga A (2004). Ecological distribution and reproductive period of the hermit crab *Loxopagurus loxochelis* (Anomura, Diogenidae) on the northern coast of São Paulo State, Brazil. J Nat Hist 38: 2331-2344.

Biagi R, Meireles AL, Mantelatto FL (2006a). Bio-ecological aspects of the hermit crab *Paguristes calliopsis* (Crustacea, Diogenidae) from Anchieta Island, Brazil. An Acad Bras Ciênc 78: 451-462.
Biagi R, Meireles AL, Mantelatto FL (2006b). Relative growth and sexual maturity of the hermit crab Paguristes erythrops (Anomura, Diogenidae) from South Atlantic. Hydrobiologia 559: 247-254.

Clarke KR, Warwick RM (1994). Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth, UK: Plymouth Marine Laboratory, Natural Environment Research Council.

Dana JD (1852). Crustacea. Part I. United States Exploring Expedition During the Years 1838, 1839, 1840, 1841, 1842 Under the Command of Charles Wilkes, U. S. N. Vol. 13: i-viii, 1-685. Philadelphia: C. Sherman (reprinted Antiquariaat Junk, Lochem, 1972).

Dunbar SG, Coates M, Kay A (2003). Marine hermit crabs as indicators of freshwater inundation on tropical shores. Memoirs of Museum Victoria 60: 27-34.

Fantiuzzi MZ, Biagi R, Mantelatto FL (2009). Use of pleopod morphology to determine sexual dimorphism and maturity in hermit crabs: Isocheles sawayai as a model. Helgol Mar Res 63: 169-175.

Fransozo A, Bertini G, Braga AA, Negreiros-Fransozo ML (2008). Ecological aspects of hermit crabs (Crustacea, Anomura, Paguroidea) off the northern coast of São Paulo State, Brazil. Aquat Ecol 42: 437-448.

Fransozo A, Mantelatto FLM (1998). Population structure and reproductive period of the tropical hermit crab Calcinus tibicen (Decapoda: Diogenidae) in the region of Ubatuba, São Paulo, Brazil. J Crustacean Biol 18: 738-745.

Fotheringham N (1975). Structure of seasonal migrations of the littoral hermit crab Clibanarius vittatus (Bosc). J Exp Mar Biol Ecol 18: 47-53.

Fotheringham N, Bagnal RA (1976). Seasonal variation in the occurrence of planktonic larvae of sympatric hermit crabs. J Exp Mar Biol Ecol 21: 279-287.

Gherardi F, Micheli F, Vannini M (1990). Movement patterns and dispersal of the hermit crab Clibanarius longitarsus in a mangrove swamp. Mar Behav Physiol 16: 209-223.

Giesel JT (1976). Reproductive strategies as adaptations to life in temporally heterogeneous environments. Ann Rev Ecol Syst 7: 57-79.

Hazlett BA (1981). The behavioral ecology of hermit crabs. Annu Rev Ecol Syst 12: 1-22.

Kelly CJ, Turner RL (2011). Distribution of the hermit crabs Clibanarius vittatus and Pagurus maclaughlinae in the northern Indian River Lagoon, Florida: a reassessment after 30 years. J Crustacean Biol 31: 296-303.

Lowery WA, Nelson WG (1988). Population ecology of the hermit crab Clibanarius vittatus (Decapoda: Diogenidae) at Sebastian Inlet, Florida. J Crustacean Biol 8: 548-556.

Mantelatto FL, Fernandes-Góes LC, Fantiuzzi MZ, Biagi R, Pardo LM, Góes JM (2010). A comparative study of population traits between two South American populations of the striped-legged hermit crab Clibanarius vittatus. Acta Oecol 36: 10-15.

Mantelatto FL, Martinelli JM (2001). Relative growth and sexual dimorphism of the South Atlantic hermit crab Loxopagurus loxochelis (Anomura, Diogenidae) from Ubatuba, Brazil. J Nat Hist 35: 429-437.

Martinelli JM, Mantelatto, FLM (1999). Shell utilization by the hermit crab Loxopagurus loxochelis (Diogenidae) in Ubatuba Bay, Brazil. Crustaceans and the Biodiversity Crisis, Crustacea 1: 719-731.

Meireles AL, Biagi R, Mantelatto FL (2003). Gastropod shell availability as a potential resource for the hermit crab infra-litoral fauna of Anchieta Island (SP), Brazil. Nauplius 11(2): 99-105.

Meireles AL, Terossi M, Biagi R, Mantelatto FL (2006). Spatial and seasonal distribution of the hermit crab Pagurus exilis (Benedict, 1892) (Decapoda: Paguridae) in the Southwestern coast of Brazil. Rev Biol Mar Oceanogr 14(1): 87-95.

McLaughlin PA, Boyko CB, Crandall K, Akomai T, Lemaître R, Osawa M, Rahayu DL (2010). Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidea of the Galatheidea) – preamble and scope. Raffles Bull Zool 23: 1-4.

Melo GAS (1999). Manual de Identificação dos Crustáceos Decápodos do Litoral Brasileiro: Anomura, Thalassinidea, Palinuridea e Astacidea. São Paulo: Plêiade/FAPESP (in Portuguese).

Moraes BC, Costa JMN, Costa ACL, Costa MH (2005). Variação espacial e temporal da precipitação no estado do Pará. Acta Amaz 35: 207-214 (in Portuguese).

Negreiros-Fransozo ML, Fransozo A, Hebling NJ (1991). Estrutura populacional e determinação do tamanho da concha em quatro espécies de ermitões (Crustacea, Decapoda, Anomura) do litoral paulista. Biotemas 4: 135-148 (in Portuguese).

Negreiros-Fransozo ML, Fransozo A, Mantelatto FL, Santos S (1997). Anomura species (Crustacea, Decapoda) and their ecological distribution at Fortaleza Bay sublittoral, Ubatuba, São Paulo, Brazil. Iheringia, Sér Zool 83: 187-194.

Negri M, Lemaître R, Mantelatto FL (2014). Molecular and morphological resurrection of Clibanarius symmetricus (Randall, 1840), a cryptic species hiding under the name for the “thinstripe” hermit crab C. vittatus (Bosc, 1802) (Decapoda: Anomura: Diogenidae). J Crustacean Biol 34: 848-861.

Nóbrega PSV, Martinelli-Lemos JM (2016). Composition and spatio-temporal variation in the density of the Brachyura (Decapoda, Pleocyemata) in the rocky substrates of an Amazonian estuary. Crustacea 89: 1447-1466.

Oliveira DB, Silva DC, Martinelli JM (2012). Density of larval and adult forms of the burrowing crustaceans Lepidophthalmus siriboia (Callianassidae) and Upogebia vasquezi (Upogebiidae) in an Amazon estuary, northern Brazil. J Mar Biol Assoc U K 92: 295-303.

Reigada ALD, Santos S (1997). Biologia e relação com a concha em Clibanarius vittatus (Bosc, 1802) (Crustacea, Diogenidae) em São Vicente, SP, Brasil. Braz Arch Biol Technol 40: 941-952 (in Portuguese).
Rodrigues ACM, Martinelli-Lemos JM (2016). Gastropod shell utilisation pattern by the hermit crab *Clibanarius symmetricus* (Anomura: Diogenidae) in an equatorial Amazon estuary. J Nat Hist 50: 2657-2671.

Sampaio SR, Masunari S, Haseyama KLF (2009). Distribuição temporal do ermitão *Clibanarius vittatus* (Anomura, Diogenidae) no litoral do Paraná. Iheringia, Sér Zool 99: 276-280 (in Portuguese).

Sant'Anna BS, Zangrande CM, Reigada ALD, Severino-Rodrigues E (2006a). Spatial distribution and shell utilization in three sympatric hermit crabs at non-consolidated sublittoral of estuarine-bay complex in São Vicente, São Paulo, Brazil. Rev Biol Mar Oceanogr 41: 141-146.

Sant'Anna BS, Zangrande CM, Reigada ALD, Pinheiro MAA (2006b). Shell utilization pattern of the hermit crab *Clibanarius vittatus* (Crustacea, Anomura) in an estuary at São Vicente, State of São Paulo, Brazil. Iheringia, Sér Zool 96: 261-266.

Sant'Anna BS, Christofoletti RA, Zangrande CM, Reigada ALD (2008). Growth of the hermit crab *Clibanarius vittatus* (Bosc, 1802) (Crustacea, Anomura, Diogenidae) at São Vicente, São Paulo, Brazil. Braz Arch Biol Technol 51: 547-550.

Sant'Anna BS, Reigada ALD, Pinheiro MAA (2009). Population biology and reproduction of the hermit crab *Clibanarius vittatus* (Decapoda: Anomura) in an estuarine region of southern Brazil. J Mar Biol Assoc UK 89: 761-767.

Sant'Anna BS, Turra A, Zara FJ (2010). Simultaneous activity of male and female gonads in intersex hermit crabs. Aquat Biol 10: 201-209.

Silva AC, Souza Filho PWM, Rodrigues SWP (2009). Morphology and modern sedimentary deposits of the macrotidal Marapanim Estuary (Amazon, Brazil). Cont Shelf Res 29: 619-623.

Silva DC, Martinelli-Lemos JM (2012). Species composition and abundance of the benthic community of Axiidea and Gebiidea (Crustacea: Decapoda) in the Marapanim Bay, Amazon estuary, northern Brazil. Zoologia (Curitiba) 29: 144-158.

Turra A (2004). Intersexuality in hermit crabs: reproductive role and fate of gonopores in intersex individuals. J Mar Biol Assoc UK 84: 757-759.

Turra A (2007). Reproductive role of intersex hermit crabs. Crustaceana 80(4): 491-494.

Turra A, Leite FPP (2000). Population biology and growth of three sympatric species of intertidal hermit crabs in southeastern Brazil. J Mar Biol Assoc UK 80: 1061-1069.

van de Kerk M, Jones Littles C, Saucedo O, Lorenzen K (2016). The effect of latitudinal variation on shrimp reproductive strategies. PLoS ONE 11(5): e0155266. doi: 10.1371/journal.pone.0155266.

Wenner AM (1972). Sex ratio as a function of size in marine Crustacea. Am Nat 106: 321-350.