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Population ecology of the hermit crab *Clibanarius symmetricus* (Anomura: Diogenidae) on an exposed beach of the Brazilian Amazon coast

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ABSTRACT

The hermit crab *Clibanarius symmetricus* is a conspicuous species in the intertidal zone of several environments along the Western Atlantic. Low salinity has been suggested as a major factor that affects the population structure of *C. symmetricus*, causing absence/scarcity of ovigerous females and juveniles. The marked seasonal variation in rainfall provides the opportunity to assess salinity-related patterns of temporal density, and population dynamics (growth, mortality, and secondary production) of *C. symmetricus* in a low rocky outcrop of an equatorial exposed dissipative sandy beach. The results showed that *C. symmetricus* density reached high values ($\sim$25 ind. m^{-2}) and increased with increasing salinity. As opposed to previous studies, our data indicate that salinity did not inhibit the simultaneous presence of age and sex categories. The constant presence of ovigerous females and juveniles indicated continuous reproduction. The larger size of males compared to females was due to their lower mortality and longer life span. The high production-to-biomass ratio (P/B = 2.44 $year^{-1}$) indicates a rapid biomass replacement for this equatorial population. Shelter provided by the rocky outcrop on this exposed dissipative beach is a key factor in the success of this population. These data are relevant to build a general overview of *C. symmetricus* life history traits, since knowledge of this species is generally limited to subtropical populations.

1. Introduction

Hermit crabs are conspicuous macrofauna components in an array of environments ranging from polar to tropical seas, inhabiting primarily intertidal environments. They have become a successful group in these environments as gastropod shell occupation allows for an effective response to desiccation, temperature variation, and predation (Reese, 1969; Hazlett, 1981; Pretterebner et al., 2012). From an ecological perspective, these organisms play an important role in marine trophic webs and nutrient cycling, acting as prominent scavengers and deposit feeders (Negreiros-Fransozo et al., 1997; Fransozo and Mantelatto, 1998). Additionally, the hard and motile substratum provided by hermit crab-occupied shells are important islands for the attachment of epifauna, increasing its biodiversity, especially in soft bottom environments (Brooks and Mariscal, 1986; Balazy and Kuklinski, 2013).

The diogenid hermit crab *Clibanarius symmetricus* (Randall, 1840), a species previously misidentified as *Clibanarius vittatus* (Bosc, 1802), has a wide geographical distribution along the Western Atlantic, ranging from the Caribbean Sea to southern Brazil (Negri et al., 2014). Most ecological studies on *C. symmetricus* populations have been conducted in subtropical and low hydrodynamic environments such as sheltered sandy beaches and tidal flats (Turra and Leite, 2000; Sant'Anna et al., 2009) and only recently has this species been studied in a tropical region (Mantelatto et al., 2010; Rodrigues and Martinelli-Lemos, 2016, 2019).

Clibanarius symmetricus is often reported as an abundant species in different intertidal environments, yet the main factors that regulate density variation are still poorly known (but see Rodrigues and Martinelli-Lemos, 2019). For instance, the absence of population categories such as ovigerous females and juveniles

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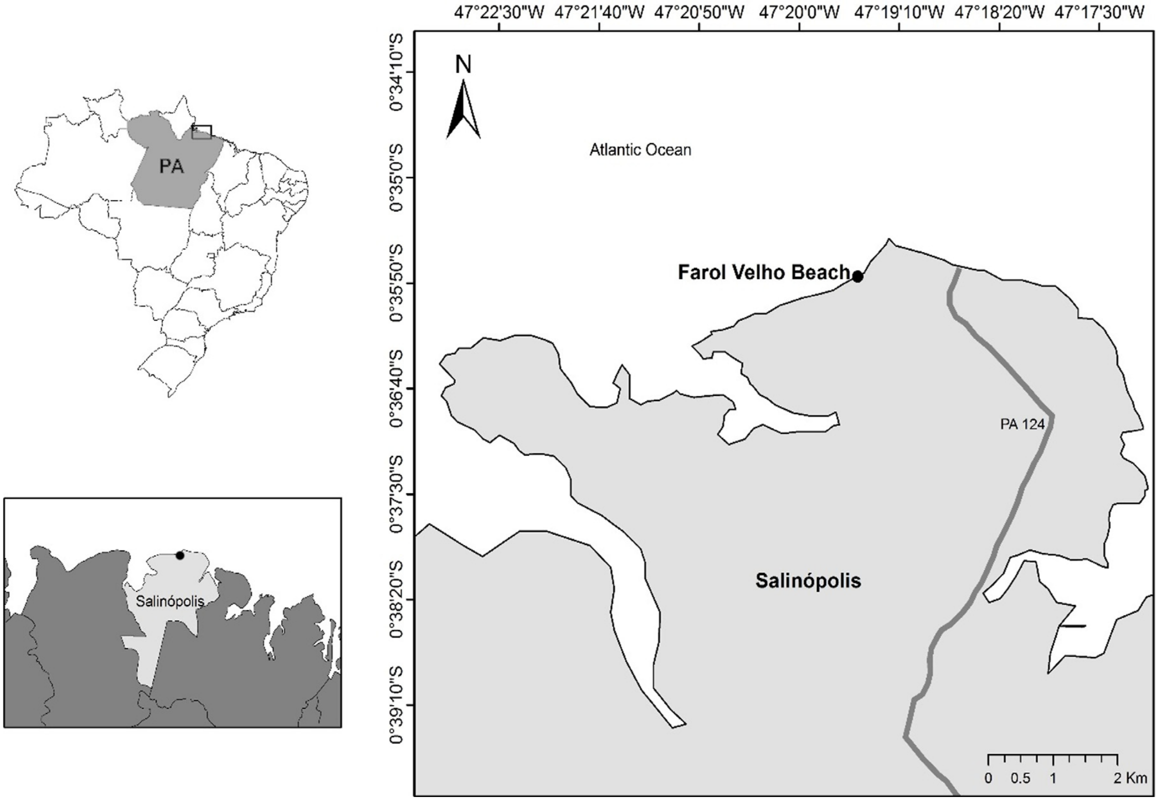

Fig. 1. Location of Farol Velho Beach, on the Brazilian Amazon coast. Top-left corner: Brazil — Pará state (gray) and Salinópolis city region (rectangular selection); bottom left corner: Salinópolis city (dot); right: Farol Velho Beach at Salinópolis city.

is frequently reported, explained by several assumptions, among which is low salinity (Sant'Anna et al., 2009; Mantelatto et al., 2010; Rodrigues and Martinelli-Lemos, 2019). Although it is quite reasonable to assume salinity is an important control factor, it has only been shown (Young and Hazlett, 1978) to influence the larval development of the congeneric *C. vittatus*.

The frequently reported absence/scarcity of females, both ovigerous and non-ovigerous, and juveniles (Turra and Leite, 2000; Sant'Anna et al., 2009; Sampaio et al., 2009; Rodrigues and Martinelli-Lemos, 2019) leads to contrasting population parameter estimates (e.g., sex ratio and size structure) for this hermit crab, hampering the development of solid population ecological parameters at local and larger scales. In addition, there is an important knowledge gap of other life history traits of *C. symmetricus*, e.g., mortality and secondary production estimates, which are important functional measurements for population, community, and environmental approaches (Brey, 1999; Dolbeth et al., 2012).

It is therefore striking that there is no information on this population ecology on equatorial exposed sandy beaches. This is also true for most species of the Amazon coast; even the most simple density data are restricted to a single study (Rodrigues and Martinelli-Lemos, 2019). Low latitudes represent a climatic limit for distribution, with stable temperature year-round resulting in environmental features that enable an analysis of the influence of basic environmental factors on population dynamics. The Amazon coast has peculiar environmental characteristics such as high river discharge, macrotidal regime, and rainfall regime, the latter characterized by two contrasting periods (Moraes et al., 2005), which lead to marked salinity variation in coastal environments. This study area, therefore, provides an opportunity to assess the potential effect of salinity on the density of this hermit crab. In addition, the presence of a large *C. symmetricus* population in a rocky outcrop of an exposed macrotidal sandy beach located in the Brazilian Amazon coast enabled a comprehensive study on population structure and dynamic in this unique equatorial environment.

2. Material and methods

2.1. Study area

This study was conducted on Farol Velho Beach (0°35′30.4″S and 47°19′20.9″W), located in Salinópolis, Pará State, in the Brazilian Amazon coast (Fig. 1). Climate in this region is tropical wet with total annual rainfall ranging from 2400 to 3330 mm and mean annual temperature of 27 °C. There are generally two different seasons based on the rainfall measures of the last few decades: rainy season (from December to May) and a drier season (from June to November) (Moraes et al., 2005).

The study place is a dissipative, exposed, macrotidal (4 to 5.3 m) sandy beach, with gentle slope (1–1.40°), sediment predominantly comprised of fine sands (2.6 to 2.8 phi) and wave heights below 0.90 m (Ranieri and El-Robrini, 2016). Low rocky outcrops are exposed on the lower beach face during low tides, creating tidal pools inhabited by the hermit crab *C. symmetricus*. In spring low tides, the lower limit of the outcrop is situated, approximately, ten meters from the waterline.

2.2. Sampling and laboratory procedures

Monthly samplings were carried out from October 2015 to September 2016, during spring low tide periods. A 30 m-long and 36 m-wide sampling station (parallel to the waterline) was fixed with its beginning in the lower limit of the rocky outcrop. The lower intertidal zone of the outcrop was included, as this zone is predominantly occupied by *C. symmetricus*, which was observed

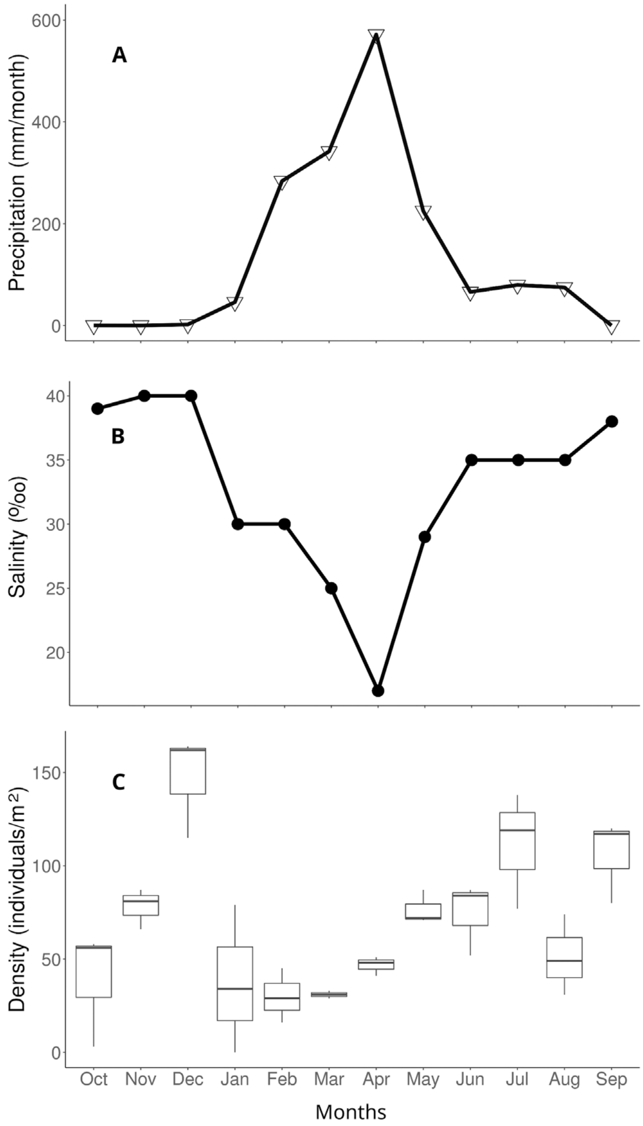

Fig. 2. Monthly variation of (A) rainfall (mm/month), (B) salinity (‰) and (C) density (ind. m^{-2}) of *Clibanarius symmetricus* (Randall, 1840).

before and during the samplings. The fact that the sampling station corresponded to a homogeneous flat area allowed the sampling of hermit crabs, which can hide in inaccessible, sharp crevices between high rocks, and sometimes, even below them. Three transects perpendicular to the waterline were randomly defined within this sampling station. Along each transect, five equidistant levels were established 6 m apart from each other. Five contiguous quadrats (0.25 m^2) were sampled at each level in each transect (totaling 1.25 m^2 of area per level/transect). The hermit crabs sampled were frozen and stored. Water temperature and salinity were measured in the beginning of each sampling using a thermometer and an optical refractometer, respectively. Monthly rainfall was collected online at the INMET portal (Instituto Nacional de Meteorologia — http://www.inmet.gov.br).

In the laboratory, the hermit crabs were defrosted at environmental temperature, and manually removed from shells with a bench vice. Their cephalothoracic shield length (CLS) was measured from the tip of the rostrum to the midpoint of the cervical groove, using a vernier caliper. Individuals were categorized in juveniles (sexually immature individuals), males and females (sexually immature individuals), and intersex. Juveniles were categorized as individuals smaller than the smallest ovigerous female (2.6 mm of CSL), following the criteria frequently used to distinguish juveniles from adults of hermit crab species (e.g., Patton and Robertson, 1980; Garcia and Mantelatto, 2001; Teoh and Chong, 2014). Adult individuals (≥2.6 mm CSL) were sexed based on the presence of gonopores on the coxae of the third (females) and fifth pairs (males) of pereiopods. Individuals with gonopores on the coxae of both third and fifth pereiopods were categorized as intersex individuals. Intersex individuals smaller than 2.6 mm were not categorized as juveniles in order not to underestimate their frequency in the population, which was compared to other *C. symmetricus* populations.

To obtain ash-free dry mass, used to estimate mass–length relationship, individuals were dried at 70 °C for 48 h (dry mass, DM). The dried mass was burnt in a muffle furnace for 4 h at 500 °C (ash mass, AM). Ash-free dry mass (AFDM) was calculated by subtracting ash mass from dry mass.

2.3. Data analysis

The relationship between rainfall and salinity was estimated using a linear model. Due to the close relationship between these variables, and assuming that salinity would be a more limiting factor than rainfall from a biological perspective, salinity was used in further ecological analyses. *Clibanarius symmetricus* density was modeled according to salinity and sexual characterization (juvenile — J; female — F; male — M). The initial full, ordinary linear model was submitted to a backwards, stepwise selection using a hypothesis test, where possible, or Akaike Information Criteria (AIC) values. The models considered and compared were: Full Model (i.e., with Interaction; Density ∼ Salinity*Sex), Without Interaction (i.e., Density ∼ Salinity+Sex), Salinity only (Density ∼ Salinity), and Sexual characterization only (Density ∼ Sex). Assumption violations, identified using residual distribution patterns, were corrected with a proper generalized model (hereby the Generalized Least Square — GLS). For this analysis, ovigerous females were pooled with females, and intersex individuals were not included due to their low frequencies.

Differences in mean size (CSL) between sexes was assessed using a *t*-test for unequal variances. This approach aimed to confirm the sexual dimorphism of this species, with males relatively larger than females. Density and mean size of transects were used as replicates in these population structure analyses.

Due to this kind of dimorphism, size–frequency trend analyses were performed to estimate body growth parameters separately for males and females. Therefore, length–frequency distribution of females and males were grouped into 0.5 mm size classes; juveniles were divided equally between sexes and months. Age–length keys were not sound enough to allow for precise estimates of body growth parameters. Thus, the ELEFAN I (Electronic Length–Frequency Analysis) routine of the FISAT II package was used (FAO-ICLARM Stock Assessment Tools) (Gayanilo et al., 2005). ELEFAN assumes that growth is described by the Von Bertalanffy growth function (VBGF) (Somers, 1988; García-Berthou et al., 2012), accounting for seasonal oscillation (Pauly and Gaschutz, 1979). The growth index phi prime (Φ'), calculated as $\Phi' = 2\log_{10}(L_\infty) + \log_{10}K$ (Pauly and Munro, 1984), was used to compare growth performance between males and females, and between the *C. symmetricus* population on Farol Velho beach and other populations of this species. Instantaneous mortality rate (Z) was also calculated for each sex using the length-converted catch curve method (Pauly et al., 1995), also from the FISAT package. To compare Z between sexes, a *t-test* was performed *for slope difference* (Zar, 2005). Life span ($t_{\max}$) was estimated using

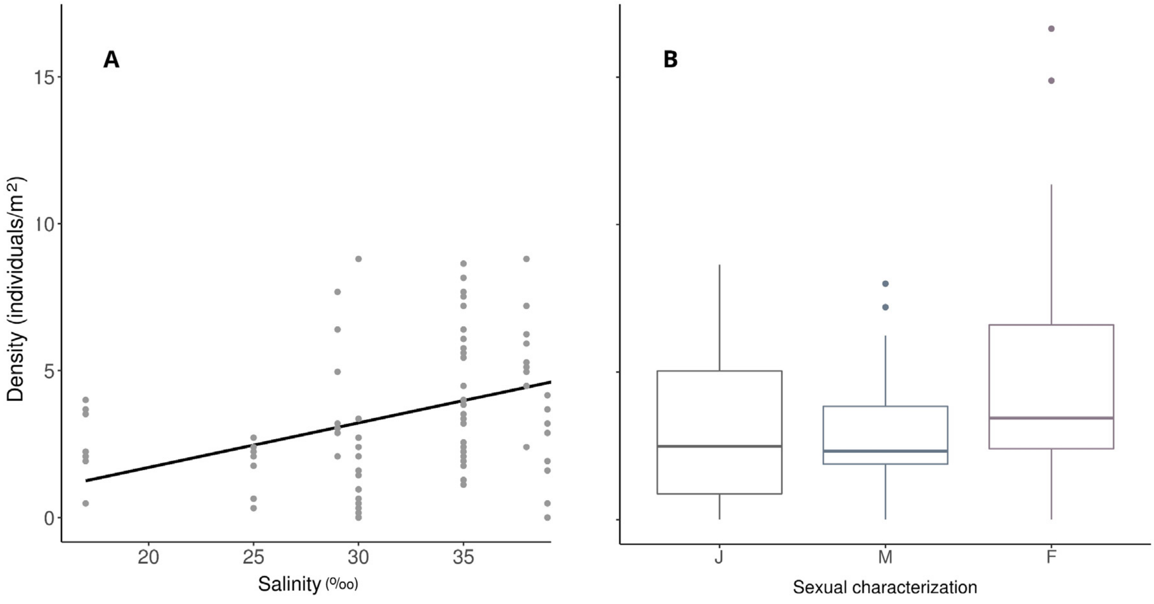

Fig. 3. Significant factors of density as a function of salinity and sex characterization of *Clibanarius symmetricus* (Randall, 1840) (juveniles — J, males — M and females — F) according to the GLS model: (A) density of individuals according to salinity (‰) and (B) median, quartiles/deciles of juvenile, male, and female densities.

the 99th percentile length of the population ($L_{99\%}$) (Sparre et al., 1989).

Biomass and secondary production were estimated using the power function $M = aL^b$, where M is AFDM per individual (g), L is the CLS (mm), and *a* and *b* are constants. An analysis of covariance (ANCOVA) was used to compare length–mass relationship between sexes. Data were log-transformed to fulfill ANCOVA assumptions. The annual somatic production (P) of population (males and females separately) was estimated using the mass-specific growth rate method. In this method, production is calculated based on length–frequency distribution (obtained from all pooled samples), length–mass relationship, and the von Bertalanffy growth function parameters (Crisp, 1984; Brey, 2001). P/B ratio was calculated by the ratio between somatic production (P) and mean biomass (B). All analyses considered a 0.05 significance level.

3. Results

3.1. Physical factors and population structure

Monthly rainfall varied from 0 (November) to 571.8 mm (April). Typically marked seasons were observed from January to June (rainy) and from July to December (dry), with salinity ranging from 17 (April) to 40‰(November and December) (Fig. 2). Seawater temperature was almost constant throughout the study period (29 °C–31 °C), which is also typical of this region. The relationship between rainfall and salinity was significant, negative, and high ($F = 83.6$; d.f. = 1,10; $p < 0.01$; $r^2 = 0.89$).

The overall annual mean density of *C. symmetricus* was estimated as 11.05 ind. m^{-2} ± 6.47 SD. The relationship of density with salinity and sexual characterization resulted in a GLS model because data were heteroscedastic density variance increased according to salinity values. Both salinity and sex significantly influenced mean hermit crab density, with no interaction between these factors ($t = 3.93$, d.f. = 1, $p < 0.01$; Fig. 3A). Females were generally more abundant than males ($t = 2.54$, d.f. = 1, $p = 0.01$), with an overall mean density 1.6 times as high. Juveniles were marginally less abundant than females ($t = 1.96$, d.f = 1, $p = 0.05$) and as abundant as males ($t = 0.59$, d.f. = 1, $p = 0.56$; Fig. 3B) (see Table 1).

Table 1
Stepwise model selection results of the relationship of density with salinity and sexual characterization (juveniles — J, males — M, and females — F). *Full — with interaction between factors; LM — Ordinary linear model; GLS — General least squares; AIC — Akaike information criteria.

Models compared	Model selection result
Full LM × Full GLS	**AIC** 535 × 527
GLS	Likelihood Ratio (LR) test
Full GLS × Without interaction	LR = 5.23; d.f. = 2; p = 0.07
Without interaction × Salinity only	LR = 7.12; d.f. = 2; p = 0.02
Without interaction × Sexual characterization only	LR = 14.99; d.f. = 1; $p < 0.01$
Summary: *Selected model: density ~ salinity + sexual characterization* Variance structure: fixed weights ~ salinity	

Among females, 8.73% were ovigerous, and intersex characteristics were observed in only 1.20% of the 2,486 individuals sampled. Regarding monthly occurrences, high ovigerous female frequencies were observed at the end of the drier season and beginning of rainy season (December 2015–March 2016). Ovigerous females were absent only in October 2015 (Fig. 4). Juvenile frequency increased during the drier period, mostly from April to June. Intersex individuals were also sampled throughout the sampling period, except for August. The lowest relative juvenile frequency occurred in February, and one ovigerous intersex individual was also found in this month.

The cephalothoracic shield lengths (CSL) of the smallest and the largest individuals were 0.6 (juvenile) and 12.0 mm (male), respectively (Table 2). Sexual dimorphism was identified, i.e. males were significantly larger than females ($t = 7.01$, d.f. = 50, $p < 0.001$).

3.2. Population dynamics

The asymptotic length (L_∞) of the von Bertalanffy growth function (VBGF) of males was higher (12.6 mm) than that of females (9.3 mm) and they had similar curvature parameters (K) (0.48 and 0.47 yr^{-1}, respectively) (Fig. 5). No seasonal oscillation

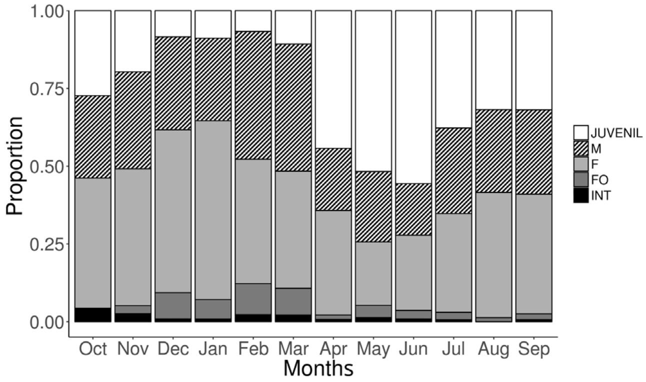

Fig. 4. *Clibanarius symmetricus* (Randall, 1840). Monthly proportion of occurrence of juveniles, males, non-ovigerous females, ovigerous females, intersexes and ovigerous intersex.

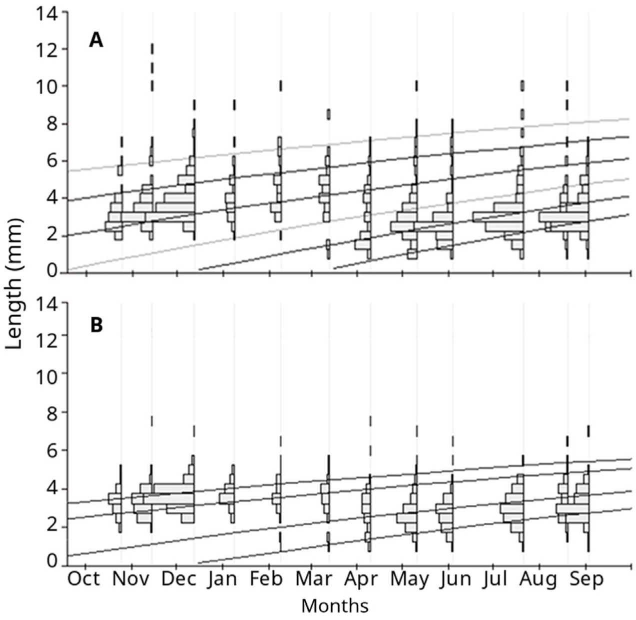

Fig. 5. *Clibanarius symmetricus* (Randall, 1840). Frequency distribution of cephalothoracic shield length and growth curves of von Bertalanffy for males (A) and females (B).

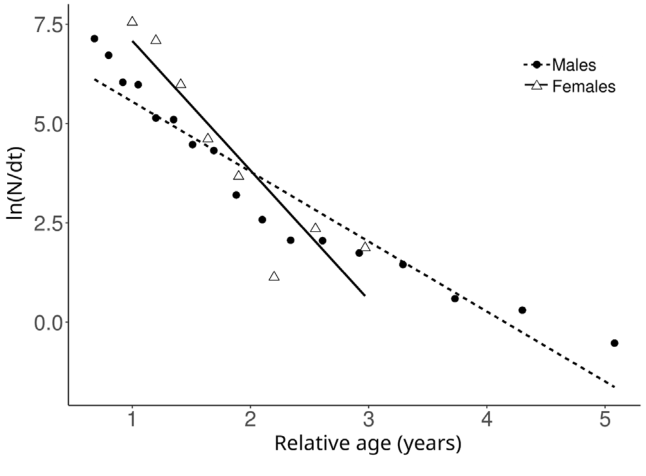

Fig. 6. *Clibanarius symmetricus* (Randall, 1840). Results of length-converted catch curve (Total mortality –Z) of males and females.

Table 2
Clibanarius symmetricus (Randal, 1840). Number, size range, and mean size of cephalothoracic shield length (mm) in population categories.

Categories	N	Min	Max	Mean ± SD
Juveniles	722	0.6	2.5	2.04 ± 0.30
Males	677	2.6	12.0	3.96 ± 0.40
Non-ovigerous females	957	2.6	7.2	3.40 ± 0.20
Ovigerous females	100	2.6	6.5	3.69 ± 0.49
Intersex	30	1.9	4.0	2.93 ± 0.45
Total	2486	0.6	12	3.20 ± 0.80

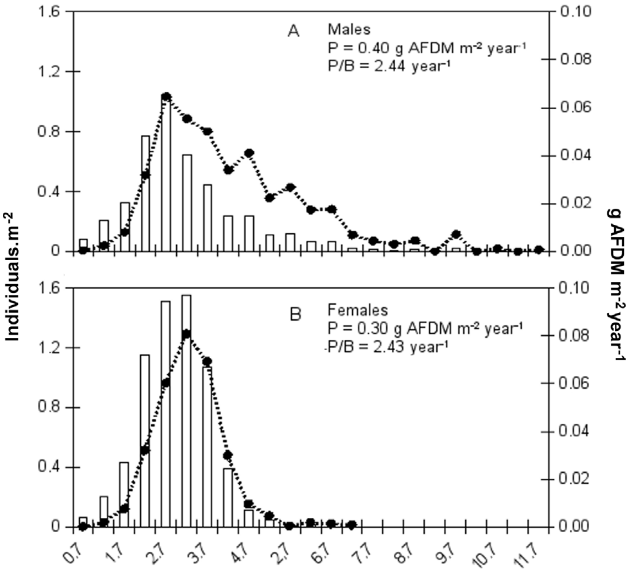

Fig. 7. *Clibanarius symmetricus* (Randall, 1840). Annual distribution of density and production of males and females across length classes.

in growth was observed in this population, i.e. C = 0. The growth index, phi prime (Φ'), of males (1.88) was higher than that of females (1.61). The instantaneous mortality, Z, of males (1.76 yr^{-1}) was significantly lower than that of females (3.26 yr^{-1}) ($t = -3.93$, d.f. = 21, $p < 0.05$) (Fig. 6), and conversely, the life span of males (2.51 yr) was longer than that of females (1.61 yr).

3.3. Mass–length relationship and secondary production

The relationship between cephalothoracic shield length (CSL) and ash-free dry mass (g AFDM) of males ($y = 0.0004\times^{3.275}$; $n = 46$, $r^2 = 0.95$) and females ($y = 0.0005\times^{3.097}$; $n = 37$, $r^2 = 0.95$) did not differ (ANCOVA, F = 1.84, d.f. = 1, 84, p = 0.18).

The mean annual biomass population was 0.29 g AFDM m^{-2}, with a slightly higher estimate for males (0.16 g AFDM m^{-2}) than for females (0.12 g AFDM m^{-2}). Annual population production was estimated as 0.70 g AFDM m^{-2} yr^{-1}(males: 0.40; females: 0.30 g AFDM m^{-2} yr^{-1}). Males and females had similar P/B ratio (~2.44 yr^{-1}). The highest production peak occurred around the 2| −3 (females) and 3| −4 mm (males) size classes. Since only males were observed within size classes from 8| −9 onwards, all the secondary production estimated based on larger-sized individuals is attributed to males. Individuals between 0.7 and 3.7 mm contributed with more than 50 and 80% of male production and female production, respectively. Higher production values followed density peaks (Fig. 7).

4. Discussion

Most ecological studies available on the hermit crab *C. symmetricus* (hereafter considered as synonymous of *C. vitattus* in studies in South America before 2014 (Negri et al., 2014) encompassed opportunistic sampling approaches. Therefore, the scope of comparison among density data is limited. According to the information available, it is possible to determine that the density of this hermit crab in this rocky outcrop was considerably high compared to other data in South America (5 ind. m^{-2}: Swennen et al., 1982; 0.02 ind. m^{-2} Nucci et al., 2001; 5 ind. m^{-2}: Rodrigues and Martinelli-Lemos, 2019). In North America, higher density of *C. vittatus* was found, although this is currently assumed to be a different species (22.46 ± 49.52 ind. m^{-2}: Lowery and Nelson, 1988). Along with the constant presence of juveniles and ovigerous females, our results indicate that the outcrop environment within a dissipative exposed beach, i.e. moderate swash climate, is suitable for the presence of *C. symmetricus.* Its occurrence is related to less harsh hydrodynamic conditions, such as sheltered sandy beaches and tidal flats. Despite the lack of systematic studies on the density of this hermit crab, *Clibanarius* species have been recognized as conspicuous and abundant members of the macrofauna in very gently sloping, dissipative beaches (McLachlan and Defeo, 2018), such as Farol Velho. Our data indicate the relevant role played by the rocky outcrop, as it offers microhabitats that provide shelter, food, and protection to hermit crabs against desiccation and wave action (*sensu* Kostylev et al., 2005). In addition, this environment also provides a high source of gastropods shells, an essential resource for hermit crabs such as *C. symmetricus*.

Low salinity has been frequently suggested as a trigger for the migration of ovigerous females of *C. symmetricus* toward high salinity sites, resulting in absence/low abundance of ovigerous females (Sant'Anna et al., 2006, 2009). This assumption is largely based on the larval development of the congeneric *Clibanarius vittatus*, which was shown to reach optimal conditions with higher salinities, ranging from 25 to 35 (Young and Hazlett, 1978). Another factor attributed to the absence/scarcity of juveniles is habitat partitioning according to size (Turra and Leite, 2000). The population of the present study generally showed a positive trend with increased salinity, meaning they benefit from drier periods in this Amazon coastal region. This trend was observed regardless of maturity stage or sex. Adult abundance peak in December (dry) and the recruitment of juveniles mostly in April (rainy) indicated a trend toward interaction, as assumed by the marginal rejection of the full model (i.e., $p = 0.07$). This scenario may confirm the habitat-partitioning hypothesis, yet it may stem only from reproduction peaks. The latter perspective seems more plausible for Farol Velho due to the co-occurrence of juveniles and adults, both males and females.

The nearly year-round presence of ovigerous females and juveniles also indicates a continuous reproductive pattern, as observed for other tropical hermit crab populations, including two tropical populations of *C. symmetricus* (e.g., Reese, 1968; Turra and Leite, 2000; Litulo, 2005; Mantelatto et al., 2010; Teoh and Chong, 2014; Rodrigues and Martinelli-Lemos, 2019). On the other hand, subtropical *C. symmetricus* populations have discontinuous reproduction (Mantelatto et al., 2010), reinforcing the effect of latitude (temperature) on the reproductive period of crustaceans, which is well documented for sandy beach crustaceans (Abele, 1982; Defeo and McLachlan, 2005; Petracco et al., 2010). The smallest ovigerous female of *C. symmetricus* (2.6 mm CSL) was recorded on Farol Velho, which indicates an earlier sexual maturity reached by tropical populations, since high temperatures allow for premature maturity. This latitudinal trend of the smallest ovigerous female of *C. symmetricus* has been previously suggested by Rodrigues and Martinelli-Lemos (2019) based on the difference in the smallest ovigerous females between an Amazon estuary (3.6 mm: obtained from relative growth analysis) and subtropical populations (3.9–5.0 mm). This assumption is supported by the fact that the smallest ovigerous females of *C. symmetricus* have been collected here so far.

Overall sex ratio skewed toward females has been found in other hermit crab species (Lowery and Nelson, 1988; Manjón-Cabeza and García-Raso, 1998; Mantelatto et al., 2007) including *Clibanarius* as *C. symmetricus* (Turra and Leite, 2000; Sant'Anna et al., 2009). Sex ratio skewed toward females has been assumed to result from higher mortality of males or habitat partitioning (Turra and Leite, 2000). Our results do not support the first hypothesis since females showed higher mortality than males, as well as shorter life span. Therefore, higher proportion of females than males seems to be the general pattern in *C. symmetricus*, either due to habitat partitioning, even if partial, or because it is genetically determined (Turra and Leite, 2000). Additionally, environmental factors, especially the complex interaction between shells and *C. symmetricus*, can influence sex ratio (Mantelatto et al., 2010). There are a few reports of sex ratio skewed toward males in some *C. symmetricus* populations (Sampaio et al., 2009; Mantelatto et al., 2010). Some studies use opportunistic sampling methods, and sex ratio should thus be considered with caution. Males are larger on average (Turra and Leite, 2000; Sant'Anna et al., 2009), and thus easier to be found. Ovigerous females, on the other hand, probably remain more sheltered due to their higher vulnerability.

Intersexuality has been recorded in 17 hermit crab species around the world (Sant'Anna et al., 2010). The presence of intersex, as the present study reports, is common in *C. symmetricus*, although it occurs in low percentage (0.5 to 7%) (Mantelatto et al., 2010; Sant'Anna et al., 2009; Rodrigues and Martinelli-Lemos, 2019). Intersex *C. symmetricus* individuals were initially considered as functional males due to their ability to copulate with females (Turra, 2004). However, the occurrence of ovigerous intersex indicates that these organisms can also act as functional females (Turra, 2007), which is also observed in the present study. Based on a reproductive system analysis of *C. symmetricus*, Sant'Anna et al. (2010) suggested that this species can show a true sequential hermaphroditic process, although what triggers this phenomenon has not been fully understood so far.

A systematic approach and the presence of all sexual categories in this study allowed for estimating growth curves of individual sexes. The larger size of males on Farol beach is supported by their lower mortality, higher growth index (phi prime: Φ'), and longer life span, which enable them to reach larger sizes than females, resulting in the well-known sexual size dimorphism. Higher L_∞ and Φ' of males agree with a subtropical population (Sant'Anna et al., 2008), although these authors did not estimate mortality rate and observed a slightly longer life span in females, as opposed to the population on Farol beach (Sant'Anna et al., 2008).

Growth parameters, $L\infty$ and K (curvature parameter), are expected to be inversely correlated, insofar as any strict interpretation of each parameter alone between populations tends to be problematic (Pauly, 1981; Cardoso and Defeo, 2004). Hence, the use of phi prime, Φ', a measure of the intensity of growth, is a more suitable parameter to compare growth among populations. A lower phi prime of the equatorial *C. symmetricus* population than those on subtropical beaches (Turra and Leite, 2000) suggests that milder subtropical temperatures allow this hermit crab to reach higher growth than in the equatorial region.

The shorter life span observed in the tropical population of Farol beach compared to a subtropical region is supported by the latitudinal paradigm of species population dynamics, according to which the life cycle of tropical crustacean populations is shorter at higher latitudes (Defeo and McLachlan, 2005). Although there are no mortality estimates for subtropical *C. symmetricus* populations, this shorter life span suggests a higher mortality of tropical populations of this hermit crab. However, this same latitudinal paradigm implies larger maximum sizes at higher latitudes, and higher length compared to other subtropical populations was unexpectedly observed here (Turra and Leite, 2000). Unexpected and marked variations in the largest *C. symmetricus* individuals is probably due to differences in availability of larger shells for hermit crab populations as hypothesized by Mantelatto (2010). Lower availability or suitability of shells for equatorial populations can also lead to differences in body growth (Bertness, 1981; Alcaraz et al., 2015). Therefore, local-scale factors such as shell availability for *C. symmetricus* can mask or overcome macroscale trends of this hermit crab.

Regarding the secondary production of *C. symmetricus*, higher values of males mirrors their larger mean size and higher biomass, despite the higher density of females. The high contribution of juveniles, smaller females and males indicates that these organisms are very important in *C. symmetricus* somatic production. Smaller individuals grow faster than larger individuals, reaching higher mass-specific growth rates (Brey, 2001). Therefore, despite their lower biomass, smaller individuals can contribute more to population production than larger individuals. *Clibanarius symmetricus* production (0.70 g AFDM m^{-2} yr^{-1}) is very similar to the global median estimated for sandy beach macrofauna (0.74 g AFDM m^{-2} yr^{-1}), and higher than the estimated for sandy beach crustaceans (0.45 g AFDM m^{-2} yr^{-1}).

The similar P/B values estimated for males and females ($\sim$2.44 yr^{-1}) reflect their similar growth constant (K). These values are also similar to the median values of sandy beach crustaceans (2.33 yr^{-1}) estimated by Petracco et al. (2013). This P/B value indicates that this *C. symmetricus* population incorporates more than twice its mean annual biomass over a year or, in other words, that it incorporates a biomass that is equal to its mean biomass over approximately six months. This population turnover rate can be considered high as it shows some features related to low P/B, e.g., low motility (*sensu* Cusson and Bourget, 2005) and a considerable life span for an equatorial crustacean population (Petracco et al., 2012, 2013). The use of an empirical relationship between P/B and life span in a large dataset of sandy beach crustaceans ($P/B = 3.94$ life span $^{-1.09}$: Petracco et al., 2013) resulted in a P/B ratio of 1.85 yr^{-1} for a population with life span of 2 yr, i.e. lower than that estimated for *C. symmetricus*. The high proportion of juveniles with low biomass yet with higher turnover rate than adults contributes with this considerable P/B value. Both *C. symmetricus* production and P/B ratio show that this hermit crab plays an important role in the energy flux of Farol Velho Beach.

The marked difference in rainfall between seasons in the Amazon coast helps to identify an evident, positive trend between hermit crab density and salinity in all maturity stages and sexes. The constant presence of juveniles and ovigerous females indicates that salinity did not inhibit the simultaneous presence of age and sex categories. This study confirms the continuous reproductive pattern and shorter life span of tropical macrofauna populations. It provides the first secondary production estimate for this species, and the high P/B indicates a rapid biomass replacement in this population. Studies conducted on the Amazon Coast are essential to define global population distribution patterns and/or paradigms due to their latitudinal position and climate peculiarities, as highlighted by the clean-cut trends identified here.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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