UNIVERSIDADE FEDERAL DO PARÁ
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
EMBRAPA AMAZÔNIA ORIENTAL
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

ANA PAULA FERREIRA DANIN

Ecologia populacional de *Clibanarius symmetricus* (Anomura: Diogenidae) em uma praia exposta da Costa Amazônica Brasileira

Belém
2017

ANA PAULA FERREIRA DANIN

Ecologia populacional de *Clibanarius symmetricus* (Anomura: Diogenidae) em uma praia exposta da Costa Amazônica Brasileira

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia do convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para obtenção do título de Mestre em Ecologia.
Área de concentração: Ecologia.
Linha de Pesquisa: Ecologia de Organismos e Populações.

Orientador: Prof. Dr. Marcelo Petracco
Coorientador: Dr. Cléverson Ranieri dos Santos

Belém
2017

Dados Internacionais de Catalogação na Publicação (CIP) de acordo com ISBD
Sistema de Bibliotecas da Universidade Federal do Pará
Gerada automaticamente pelo módulo Ficat, mediante os dados fornecidos pelo(a) autor(a)

D183e Danin, Ana Paula Ferreira
Ecologia populacional de Clibanarius symmetricus (Anomura: Diogenidae) em uma praia exposta da Costa Amazônica Brasileira / Ana Paula Ferreira Danin. — 2017.
40 f. : il.

Orientador(a): Prof. Dr. Marcelo Petracco
Coorientador(a): Prof. Dr. Cléverson Rannieri Meira dos Santos
Dissertação (Mestrado) - Programa de Pós-Graduação em Ecologia, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, 2017.

1. Ecologia costeira. 2. Caranguejo Ermitão. 3. Costa Amazônica. I. Título.

CDD 574.5248

ANA PAULA FERREIRA DANIN

Ecologia populacional de *Clibanarius symmetricus* (Anomura: Diogenidae) em uma praia exposta da Costa Amazônica Brasileira

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia do convênio da Universidade Federal do Pará e Embrapa Amazônia Oriental, como requisito parcial para obtenção do título de Mestre em Ecologia pela Comissão Julgadora composta pelos membros:

COMISSÃO JULGADORA

Prof. Dr. Fernando Luis Medina Mantelatto
Universidade de São Paulo

Prof. Dra. Maíra Pombo
Universidade Federal do Amapá

Prof. Dr. Bruno Sampaio Sant'Anna
Universidade Federal do Amazonas

Prof. Dr. Leandro Juen
Universidade Federal do Pará

Prof. Dr. Raphael Ligeiro Barroso Santos
Universidade Federal do Pará

Aprovada em: 06 de junho de 2017.
Local da defesa: SAT-2 do Instituto de Ciências Biológicas da Universidade Federal do Pará.

À minha mãe, Adélia, meu amor
maior.

AGRADECIMENTOS

Ao meu orientador Prof. Dr. Marcelo Petracco pela confiança, paciência, dedicação e incentivo, obrigada ainda pelos valorosos conhecimentos transmitidos ao longo desta orientação os quais me tornaram uma pessoa e cientista melhor. Ao coorientador Dr. Cleverson Ranieri pela contribuição no desenvolvimento deste estudo. À Prof. Dra. Jussara Martinelli Lemos pelos comentários e sugestões ao longo do desenvolvimento deste estudo. À Prof. Dra. Maíra Pombo pela boa vontade e atenção sempre que requisitada. Ao Prof. Dr. José Eduardo Martinelli pelo apoio laboratorial e apoio na realização das saídas de campo. À Dra. Daiane Aviz pelo auxílio estatístico e as ótimas ideias que levaram ao aprimoramento deste trabalho. Ao Dr. Luiz Simone pelo auxílio na identificação das conchas de gastrópodes.

À CAPES, pela concessão da bolsa de estudos.

À Universidade Federal do Pará, ao Programa de Pós-graduação em Ecologia e seu corpo docente, pela oportunidade e aprendizado.

A todos os amigos do Laboratório de Oceanografia Biológica, sem os quais esses dois anos teriam sido muito menos divertidos, obrigada pelos bons momentos no laboratório: Alysson, Arnaldo, Felipe, Leo, Mayk, Rose, Vanessa e Mayara. E em especial à equipe oficial de campo e “aventuras”: Denys pela boa vontade e responsabilidade em nos levar para Salinas, Stéfany por todo o trabalho atencioso e pelas boas músicas, Diego por ser uma “enciclopédia ambulante” pronta para tirar qualquer dúvida, Santino pelas valorosas horas (e playlists) passadas no laboratório e Gabriel pela dedicação no trabalho. Agradeço também a todos que participaram dos trabalhos em campo nem que apenas uma vez: Abdul, John, Lidi, Dani, Alexandre, Felipe, Priscila e Rosângela.

Às amigas: Karina, pelas melhores conversas, caronas e abraços; Kelly, pelas risadas compartilhadas mesmo em períodos difíceis; Marina, pelo apoio e melhores piadas e Raque, pelo incentivo e por sempre acreditar em mim. Obrigada por terem aparecido na minha vida e serem as melhores amigas que alguém pode ter.

À minha família, em especial meus pais, irmãos e avós. Em particular, à minha mãe Adélia, por ser a maior fonte de amor e apoio incondicional; minha vó Tetê, por toda a ajuda ao longo destes anos; minha tia Anete, pelas palavras de incentivo e à minha irmã Amanda, por ser meu maior exemplo e inspiração. Obrigada por tudo o que fizeram por mim, espero sempre poder retribuí-las.

“I can still feel that leap of enthusiasm, and real joy, at the prospect of finally getting out to the beach, and running around. But probably the most important thing, to me, aside from just the freedom of it and the power of it, was the kind of creatures that you could see along the beach, that you can't find anywhere else."

Dra. Sylvia Earle

Ecologia populacional de *Clibanarius symmetricus* (Anomura: Diogenidae) em uma praia exposta da Costa Amazônica Brasileira.

RESUMO

O caranguejo ermitão *Clibanarius symmetricus* possui ampla distribuição geográfica ao longo do Atlântico Ocidental, sendo uma espécie conspícua em águas rasas e intertidais de diversos ecossistemas como praias arenosas, planícies de maré, manguezais e costões rochosos. No entanto, informações acerca da história de vida desta espécie são em geral limitadas as regiões subtropicais. Neste estudo, é acessado a estrutura e dinâmica populacional, e o padrão de ocupação de conchas de uma população de *C. symmetricus* habitando um afloramento rochoso de uma praia arenosa exposta na Costa Amazônica. Para isso, amostragens mensais foram realizadas de Outubro de 2015 a Setembro de 2016. Maior densidade de *C. symmetricus* foi registrada na estação seca e a constante presença de fêmeas ovígeras sugere reprodução contínua. A proporção sexual total foi favorável as fêmeas (0.6:1, M:F) e dimorfismo sexual de tamanho foi observado. Machos e fêmeas obtiveram curvaturas similares, mas o índice de performance de crescimento foi menor que de populações subtropicais. A taxa de renovação (P/B) também foi similar entre os sexos como uma consequência da similar constante de crescimento. A concha de gastrópode mais ocupada foi a espécie *Thaisella coronata* e a sobreposição no uso de conchas por ermitões de mesmo tamanho reflete suas interações competitivas. Ainda, foi observado diferença na ocupação de conchas entre os sexos, sugerindo que os machos podem ocupar conchas maiores e mais adequadas.

Palavras-chave: *Clibanarius symmetricus*, ecologia populacional, ocupação de conchas, Costa Amazônica.

Population ecology of *Clibanarius symmetricus* (Anomura: Diogenidae) on an exposed beach of the Brazilian Amazon Coast.

ABSTRACT

The hermit crab *Clibanarius symmetricus* has a wide geographical distribution along the Western Atlantic where is a conspicuous species in intertidal and shallow waters of several ecosystems as sandy beaches, tidal flats, mangroves and rocky shores. However, information on the life history traits of this species is in general limited to the subtropical regions. Here, we access the population structure and dynamics, and the shell occupation pattern of a C. symmetricus population inhabiting a rocky outcroup of an exposed sandy beach on the Amazon coast. For this purpose, monthly samplings were carried out from October 2015 to September 2016. Higher density of C. symmetricus occurred in the drier season and the frequent presence of ovigerous females suggests continuous reproduction. The overall sex-ratio was skewed toward females (0.6:1, M:F) and sexual dimorphism was recorded. Males and females had similar curvature, but smaller growth performance index than others subtropical populations. The turnover rate (P/B) was also similar between sexes as a consequence of similar growth constant. *Thaisella coronata* was the most occupied (97.1%) gastropod shell and the overlap in shell utilization by hermit crabs of same size may reflect competitive interactions. Also, some difference in occupation between sexes was documented, suggesting that males can occupy larger and more suitable shells.

Keywords: *Clibanarius symmetricus*, population ecology, shell occupation, Amazon Coast.

LISTA DE FIGURAS

LISTA DE TABELAS

SUMÁRIO

1. INTRODUCTION

Hermit crabs are conspicuous components of macrofauna from polar to tropical seas inhabiting mainly intertidal environments, where they became successful once the gastropod shell occupation allows them to respond effectively to desiccation, temperature variation and predation (HAZLETT, 1981; PRETTEREBNER et al., 2012; REESE, 1969). In a ecologic perspective, these organisms play an important role in marine trophic webs and nutrient cycling (FRANSOZO; MANTELATTO, 1998; NEGREIROS-FRANSOZO et al., 1997) acting as prominent scavengers and deposit feeders (LAIDRE; GREGGOR, 2015; TEOH; CHONG, 2014a). The hard mobile substratum provide by hermit crab-occupied shells are important islands of hard structures for the attachment of epifauna increasing its biodiversity mainly in soft bottom environments (BALAZY; KUKLINSKI, 2013; BROOKS; MARISCAL, 1986). Therefore, the knowledge of the population ecology of hermit crab is an important step for the understanding of the structure and functioning of coastal ecosystems.

The Diogenid hermit crab *Clibanarius symmetricus* (RANDALL, 1840), species previously confounded under the name *Clibanarius vittatus* (BOSC, 1802), has a wide geographical distribution along the Western Atlantic ranging from Caribbean Sea to southern Brazil where it lives in the intertidal zone of several environments as estuaries, mangroves, rocky shores, tidal flats and sandy beaches (MANTELATTO et al., 2010; NEGRI; LEMAITRE; MANTELATTO, 2014; SAMPAIO; MASUNARI; HASEYAMA, 2009; SANT'ANNA; REIGADA; PINHEIRO, 2009). Most of studies on *C. symmetricus* addressed population structure features and shell utilization pattern were carried out in subtropical environments (SAMPAIO; MASUNARI; HASEYAMA, 2009; SANT'ANNA; REIGADA; PINHEIRO, 2009; TURRA; LEITE, 2000), and only recently this species was studied in a equatorial region (MANTELATTO et al., 2010; RODRIGUES; MARTINELLI-LEMOS, 2016). According to these studies *C. symmetricus* shows larger males than females, sex ratio skewed towards females or males and size-frequency uni- and bimodal (RODRIGUES, 2016; SAMPAIO; MASUNARI; HASEYAMA, 2009; SANT'ANNA; REIGADA; PINHEIRO, 2009; TURRA; LEITE, 2000). The variable sext ratio between *C. symmetricus* population has been assigned to the absence/scarcity of mature females, that can migrate to higher salinity sites, while the frequent scarcity/ absence of juveniles can be result of this migration or as a form to habitat partition (TURRA; LEITE, 2000).

Regarding the reproduction period, a shifting from seasonal to continuous reproduction from subtropical to tropical populations was verified for *C. symmetricus* (MANTELATTO et al., 2010; RODRIGUES, 2016; TURRA; LEITE, 2000). Moreover, as predicted, for crustaceans species (DEFEO; MCLACHLAN, 2005; PETRACCO; CARDOSO; CORBISIER, 2010), smaller individuals (including smaller ovigerous females) were verified in an equatorial estuary when compared to subtropical populations of *C. symmetricus* (RODRIGUES, 2016), despite this trend not be so clear for ovigerous females. On the other hand, an opposite pattern was verified between tropical and subtropical *C. symmetricus* populations, probably due to local factors as differential availability of adequate shells between sites which can overcomes the latitude effect as hypothesized by Mantelatto et al. (2010). This fact shows the importance of the gastropod shells as a major limiting resource for hermit crabs (HAZLETT, 1981; VANCE, 1972). The use of inadequate shells can influence the size structure, reproductive period, growth and mortality rates between sexes, mainly considering that females and males frequently have different preferences for shell species (MANTELATTO et al., 2010; REESE, 1968; SPIGHT, 1977; TURRA; LEITE, 2000).

In contrast with the substantial knowledge regarding populations structure, data on dynamic population of *C. symmetricus* as growth and mortality, mainly those discriminated by sexes are scarse and do not contemplate tropical populations(SANT'ANNA; REIGADA; PINHEIRO, 2009; TURRA; LEITE, 2000). These information are relevant both to understand other life history traits as size structure, sex ratio, life span and the response of the population to the environment features, frequently reported for sandy beach crustaceans (DEFEO; MCLACHLAN, 2005). Therefore, simultaneous assessment on population structure and dynamics, and the pattern of shell occupation allows better understanding of population ecology of hermit crabs. Another important gap in knowledge about population ecology refers to the scarcity on density data, although *C. symmetricus* populations have been frequently denominated as abundant in intertidal of different environments (e.g. MANTELATTO et al., 2010; RODRIGUES; MARTINELLI-LEMOS, 2016; SANT'ANNA; REIGADA; PINHEIRO, 2009). Furthermore, data on density temporal variation and the factor that regulates this variation are still poorly know for *C. symmetricus* (but see Rodrigues, 2016).

Studies on *C. symmetricus* were carried out mostly in environments with low hydrodynamics as tidal flats, sheltered sandy beaches and estuaries (MANTELATTO et al., 2010; RODRIGUES; MARTINELLI-LEMOS, 2016; SANT'ANNA; REIGADA; PINHEIRO, 2009; TURRA; LEITE, 2000) and there is no information on population ecology in exposed sandy beaches, one of the harsher marine environments (MCLACHLAN; BROWN, 2006). Population studies in environments with different features and latitudes are fundamental to comprehend differences among populations and their adaptive mechanisms of establishment (MANTELATTO et al. 2010). In this context, lower length, higher growth and mortality rates, and shorter lifespan are expected in populations of *C. symmetricus* that live both at tropical when compared to subtropical regions, as well as in milder hydrodynamic conditions (tidal flats and sheltered sandy beaches) than those inhabitants of more hydrodynamic environments (e.g. exposed sandy beaches). These predictions are sustained by recurrent trends in these life history traits of crustacean species from lower towards higher latitudes as well as from harsh reflective beaches towards more benign conditions of exposed dissipative beaches (DEFEO; MCLACHLAN, 2005).

The Amazon coast has peculiar environmental characteristics as high river discharge, macrotidal and precipitation regimes, the latter characterized by two contrasting periods, which lead to marked salinity variation in coastal environments. High salinity has been suggested important for larval development of this species as evidenced to congeneric *C. vittatus* (YOUNG; HAZLETT, 1978), and low salinity has been described as a limiting factor for spatial distribution and can trigger the migration of ovigerous females of *C. symmetricus* to higher salinity areas (RODRIGUES, 2016; SANT'ANNA et al., 2006b). Therefore, the marked salinity variation in the study area provides an opportunity to assess a possible effect of the salinity on the temporal density of this hermit crab. The presence of a large population of *C. symmetricus* in a rocky outcrop of a macrotidal exposed sandy beach located in Brazilian Amazon coast still allows carry out a comprehensive study on population structure and dynamic of *C. symmetricus* in this unique equatorial environment, and to compare it to those studied in other environments and latitudes. Specifically we access the density temporal variation, sex ratio, size structure, reproductive pattern, individual growth, mortality rate, secondary production, and the occupation pattern of shells by *C. symmetricus.*

2. MATERIALS AND METHODS

2.1 Study Area

The study was conducted at Farol Velho beach (0°35'30.4"S and 47°19'20.9"W), located on Salinópolis, Pará state, in the Brazilian Amazon Coast (Figure 1). In this region the climate is tropical wet with total annual rainfall between 2400 e 3330 mm (MORAES et al., 2005) and mean annual temperature of 27°C (EL-ROBRINI et al., 2006). Two different seasons are established based on the rainfall: a rainy season (from December to May) and a drier season (from June to November) (Moraes et al. 2005).

Farol Velho is a macrotidal (4 to 5.3 m) dissipative exposed sandy beach, with a gentle slope (1 - 1.40°), sediment composed predominantly by fine sands (2.6 to 2.8 phi) and waves heights below 0.90 m (RANIERI; EL-ROBRINI, 2016). Rocky outcrops are exposed on the lower beach face during low tides generating tide pools inhabited by the hermit *Clibanarius symmetricus*, gastropods, among others macrofauna representatives.

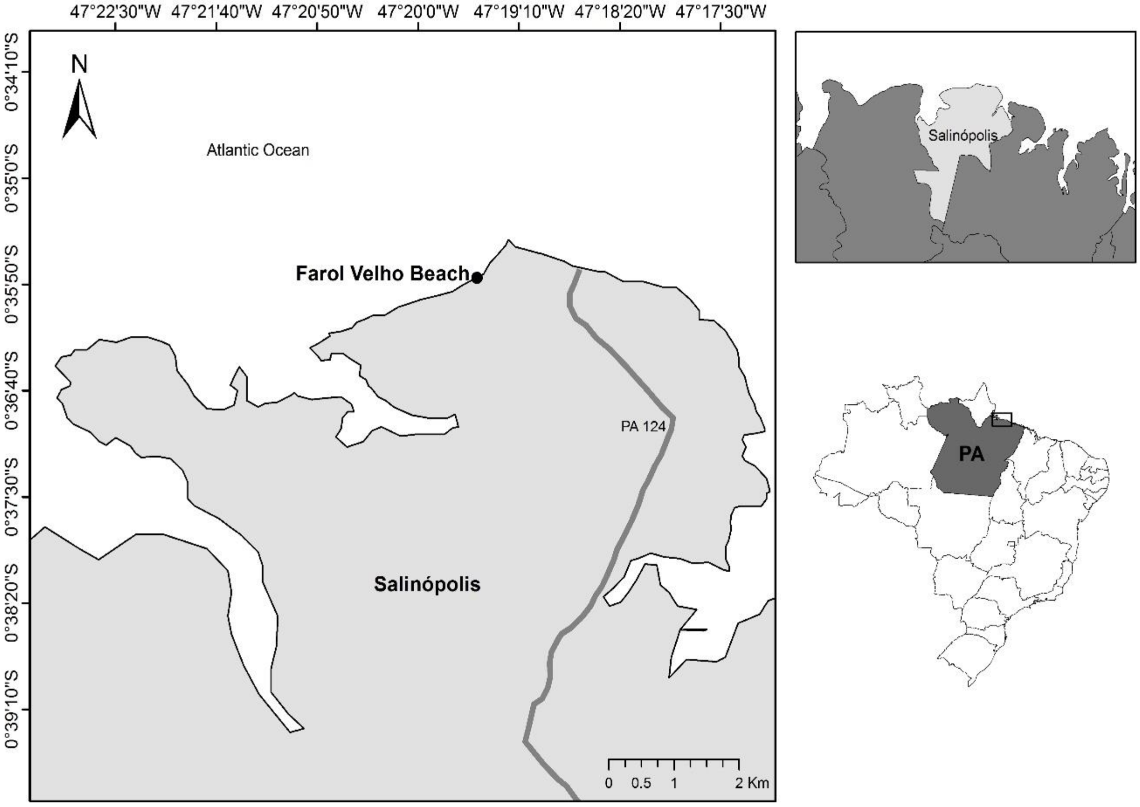


Figure 1 - Localization of Farol Velho Beach on the Amazon Coast, Brazil.

2.2 Sampling and laboratory procedures

Sampling was carried out monthly from October 2015 to September 2016, in spring low tide periods. Three transects perpendicular to the waterline were established randomly within a homogeneous segment of 30 m (parallel to the waterline) in the lower zone of the rocky outcrop. Along each transect, five equidistant levels were established six meters apart. At each level samples were obtained inside five contiguous quadrats (0.5 m of size: 0.25 m² of area) (totaling 1.25 m² of area per level/transect). Water temperature and salinity were measured monthly using a thermometer and an optical refractometer, respectively. Monthly precipitation was gathered online at INMET portal (*Instituto Nacional de Meteorologia* - http://www.inmet.gov.br)

The hermit crabs were manually removed from shells and sexed according the following characteristics: i) juveniles: individuals smaller than the smallest ovigerous female (2.6 mm of cephalothoracic shield length, CSL); ii) females: individuals with gonopores on the coxae of the third pair of pereiopods; iii) males: individuals with gonopores on the coxae of the fifth pair and iv) intersex individuals: gonopores on the coxae of both third and fifth pereiopods. The CSL was measured from the tip of the rostrum to the midpoint of the cervical groove, using a vernier caliper.

To obtain the ash-free dry mass, used in the mass-length relationship, individuals were dried at 70°C for 48 hours, to measure the dry mass (DM). Ash mass (AM) was obtained after burning the dried individuals in a muffle furnace for 4 h at 500 °C. Ash-free dry mass (AFDM) was calculated by subtracting the ash mass from the dry mass. To assess the pattern of occupation of gastropod shells by *C. symmetricus*, the shells were measured (total length and aperture length and width, mm) using a vernier caliper, weighed, and identified at species level.

2.3 Data analysis

The temporal variation of water temperature between seasons was assessed using Mann Whitney U-test, since the data did not satisfy the assumption of normality according to the Kolmogorov–Smirnov test. To compare salinity between dry and rainy seasons the Student's t-test was performed. To assess a possible effect of environmental variables on the density, correlation analysis were performed between monthly density and the physical factors considered (temperature, salinity and precipitation). Density of C. *symmetricus* was compared between seasons and among months using a two-way nested ANOVA with months nested in seasons, using the transects as replicates. The Tukey test a posteriori was used to identify differences among months. To compare size (CSL) between sexes the Mann Whitney U-test was performed, because the assumption of normality was not met, using transects as replicates. The monthly and overall sex ratio were tested with Chi-Square (χ^2) test, intersexes were not considered.

The relationship between ash-free dry mass (AFDM) and length (CSL) used in the estimate of biomass and secondary production was estimated by the power function $M=aL^b$, where M is AFDM per individual (g), L is the cephalothoracic shield length of the size class (mm), and a and b are constants. An analysis of covariance (ANCOVA) was employed to compare the length-mass relationship between sexes, using cephalothoracic shield length (CSL) as covariate. To this purpose, the data were log-transformed to fulfill the ANCOVA assumptions.

The individual growth analyzes of *C. symmetricus* were performed separately for males and females due to sexual dimorphism. Juveniles were divided equally between sexes and monthly length-frequency distributions of females and males were grouped in 0.5 mm. Initially we tried to build age-length key for males and females using the Bhattacharya method to perform the growth analysis as suggested by Gómez & Defeo (1999). However, as data did not allow building satisfactory age-length keys we used the ELEFAN I (Electronic Length Frequency Analysis) routine of the FISAT II package (FAO-ICLARM Stock Assessment Tools) (GAYANILO; SPARRE; PAULY, 2005). ELEFAN assumes that growth is described by the Von Bertalanffy growth function (VBGF) (GARCÍA-BERTHOU et al., 2012; SOMERS, 1988) for seasonality as:

$Lt = L_\infty (1 - \exp(- K(t - t_0) - St + St_0))$; with $S(t) = (CK/2\pi)\sin(2\pi(t - ts))$; and $St_0 = (CK/2\pi)\sin(t_0 - ts))$, where Lt is length (mm) at time t; L_∞ is the asymptotic length; K is the curvature parameter; C is the seasonal growth oscillation constant; t_0 is the theoretical age at zero length; ts is the beginning of the sinusoid growth oscillation; and WP (winter-point) is the period of growth reduction (WP = ts + 0.5), expressed in year fraction. The Rn index is used for evaluating the goodness of fit of the estimated VBGF.

To estimate the VBGF parameters in ELEFAN, the males and females to growth curves were fixed in two main cohorts presents in the study period. The growth index phi prime (Φ'), calculated as $\Phi' = 2\log_{10} (L_\infty) + \log_{10}K$ (PAULY; MUNRO, 1984), was employed to compare growth performance between males and females, and between *C. symmetricus* population of Farol Velho beach and other populations of this species.

The instantaneous mortality rate (Z) represented by the slope of the single negative exponential relationship between number of individuals per size classes and age was calculated using the length-converted catch curve method (PAULY; MOREAU; ABAD, 1995) of the FISAT program (GAYANILO; SPARRE; PAULY, 2005). To compare Z between sexes a *t-test of difference of slope* was performed. Life span (t_{max}) was estimated using the length representing the 99th percentile of the population ($L_{99\%}$) (SPARRE; URSIN; VENEMA, 1989).

The annual somatic production (P) of population (males and females separately) was estimated by the mass-specific growth rate method (BREY, 2001; CRISP, 1984). In this method, the production is calculated from the length-frequency distribution obtained from all pooled samples, the length-mass relationship, and the von Bertalanffy growth function parameters. The production is given by the equation: $P = \Sigma\Sigma f_i . m_i . G_i$, where f_i is the annual mean number of individuals in length-class *i*, m_i is the mean individual mass in length-class *i*, calculated from the mean length in length-class *i*. G_i is the mass-specific growth rate in length-class *i* obtained through the equation: $G_i = b.K. [(L_\infty/L_i) - 1]$, where *b* is the exponent of the length-mass relationship, K and L_∞ are VBGF parameters, and L_i is the mean length in length-class *i*. The P/B ratio was calculated by the ratio between somatic production (P) and mean biomass (B).

Regressions analyses were employed to determine relationships between hermit crab size (CSL) and shell parameters of the most occupied species and for all the species together, according to Scully (1983) low values of the determination coefficients of the regressions indicate low shell adequacy for the hermit crabs. All analyses were conducted at 0.05 significance level.

3. RESULTS

3.1 Physical factors and Population Structure

The monthly precipitation varied between 0 (November) and 571.8 mm (April) (*Instituto Nacional de Meteorologia* - http://www.inmet.gov.br), from what we defined two seasons: the rainy (January to June) and the drier period (July to December). The salinity differed between seasons ($t=3.80$, $p<0.001$) with lower salinity in April (17) and higher salinity in November and December (40), respectively, agreeing with the rainy and drier seasons (Figure 2). The seawater temperature did not differ between seasons and was almost constant during all study period (29°C – 31°C).

The annual mean density of *C. symmetricus* was estimated in 11.39 ± 5.70 ind.m^{-2} (mean ± SD). The nested ANOVA detected differences in density between seasons (F=29.71, d.f.= 1, 24, $p<0.001$), with higher values in the drier season, and among months (F=7.77, d.f.=10, 24, $p<0.001$) with a density peak in December (Figure 3). There was no correlation between density and temperature or salinity or precipitation, although the relationship between density and salinity was close (0.06) to the significant value of p (0.05).

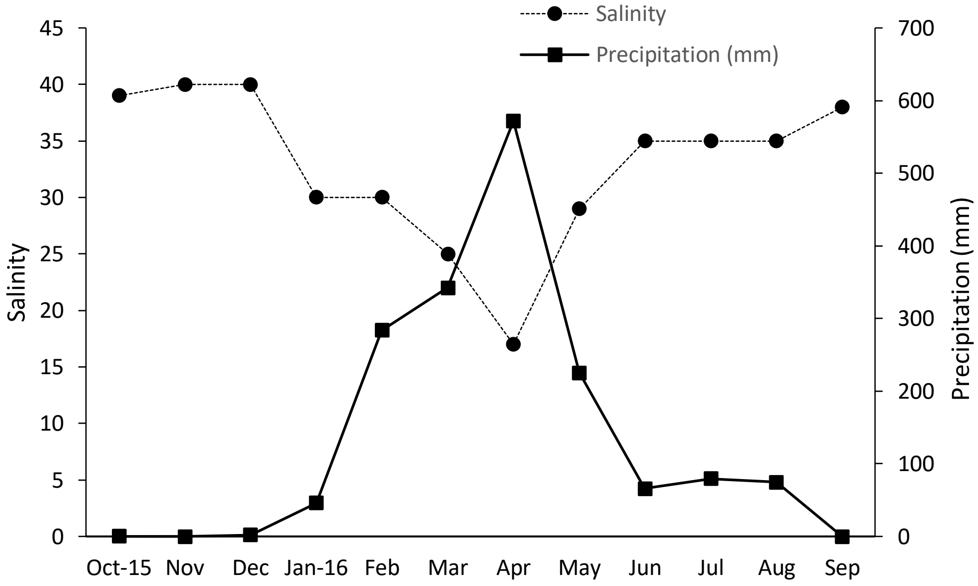


Figure 2 - Temporal variation of salinity at Farol Velho Beach and precipitation in Salinópolis, Amazon Coast.

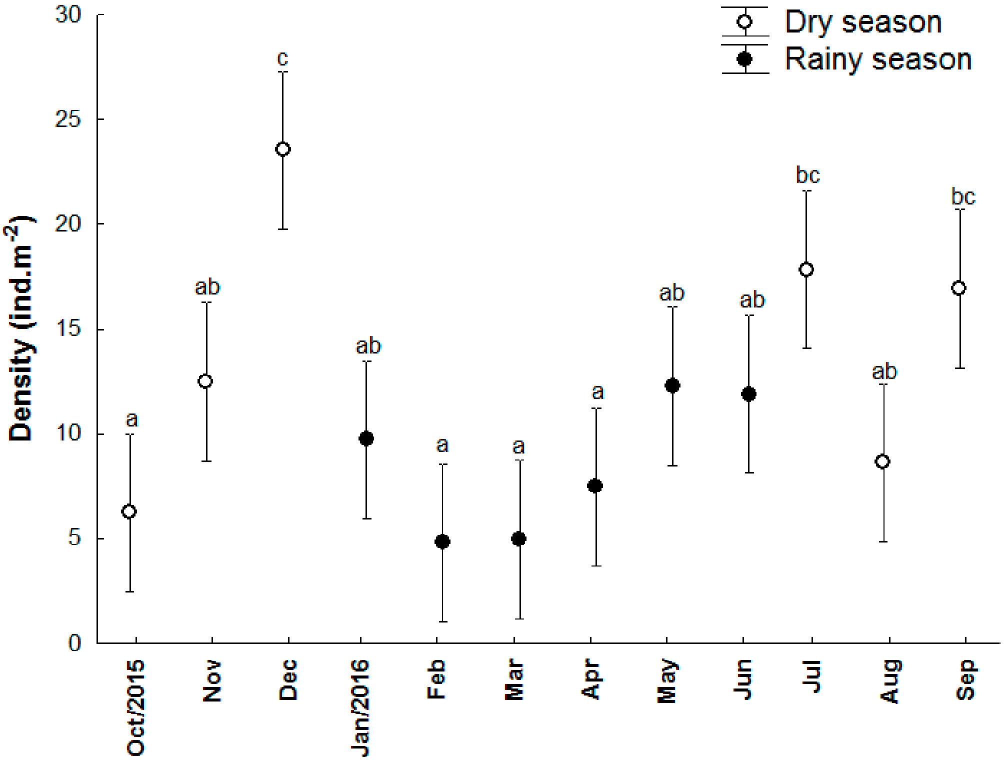


Figure 3 - *Clibanarius symmetricus*. Monthly mean density. The letters discriminate results of post-hoc Tukey Test. Vertical bars are standard deviation.

A total of 2486 individuals were sampled - juveniles (29.04%), males (27.23%), non-ovigerous females (38.50%), ovigerous females (4.02%), and intersexes (1.20%). Females (ovigerous and non-ovigerous) had significant higher proportion than males om most of the months (Figure 4). Similarly, the overall sex ratio (M:F) was significantly skewed toward females (0.6:1, χ^2 = 83.28, $p<0.001$). Regarding the presence of population categories over the study period, juveniles and ovigerous females were sampled throughout all year, except on October for ovigerous females (Figure 4). Similarly, intersex individuals were present in most of the months, being absent in August.

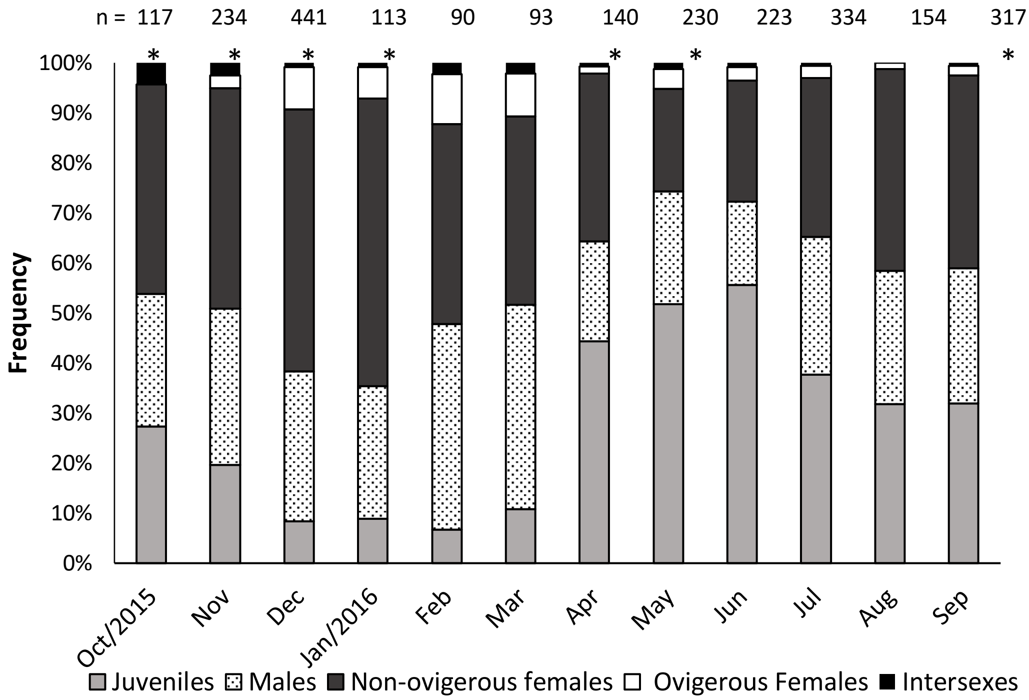


Figure 4 - *Clibanarius symmetricus*. Monthly frequency distribution of juveniles, males, non-ovigerous females, ovigerous females and intersexes. Asterisks indicate significant sex ratio.

Concerning the size-frequency distribution, the cephalothoracic shield length (CSL) of the smallest and the largest individuals measured 0.6 (juvenile) and 12.0 mm (male), respectively (Table 1). The smallest ovigerous female was 2.6 mm. The first size class was dominated for juveniles, and the intermediate classes (3|-4 and 4|-5 mm) were composed mainly of females while the males were more abundant in the larger classes (Figure 5). Ovigerous females were represented from 2|-3 mm to 6|-7mm size classes, and intersexes individuals from 1|-2 mm to 3|-4 mm classes. Males were significant larger than females (Mann Whitney U test, $p<0.001$).

Table 1 - *Clibanarius symmetricus*. Number, size range and mean size of cephalothoracic shield length (mm) for the population categories.

Categories	**N**	**Min**	**Max**	**Mean ±SD**
Juveniles	722	0.6	2.5	2.04 ± 0.30
Males	677	2.6	12	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
Intersexes	30	1.9	4.0	2.93 ± 0.45
Total	**2486**	**0.6**	**12**	**3.20 ± 0.80**

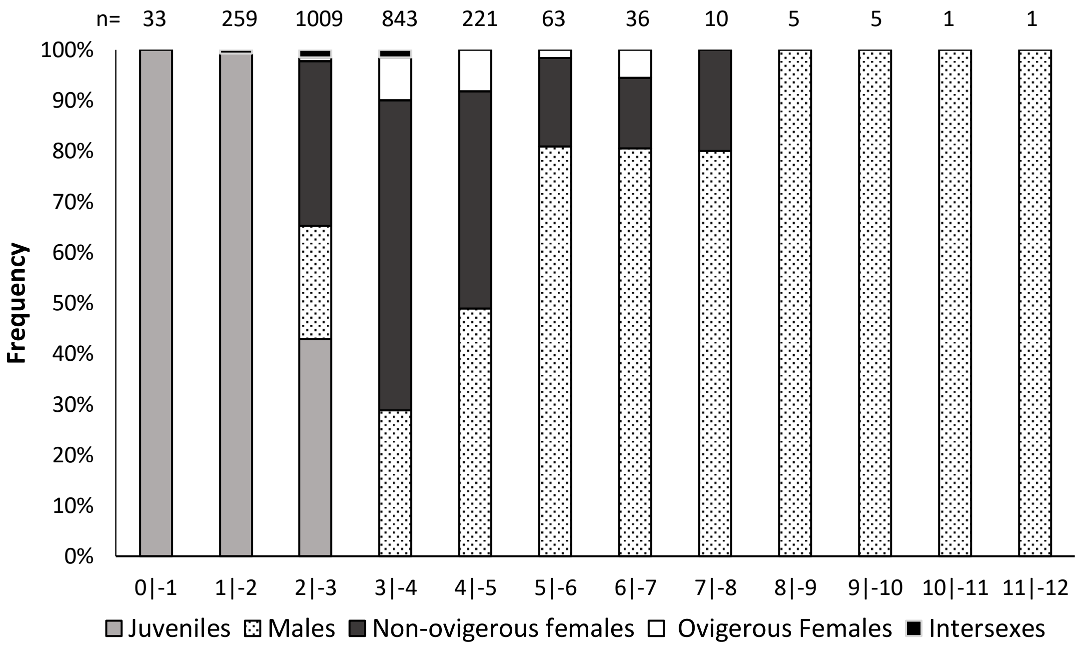
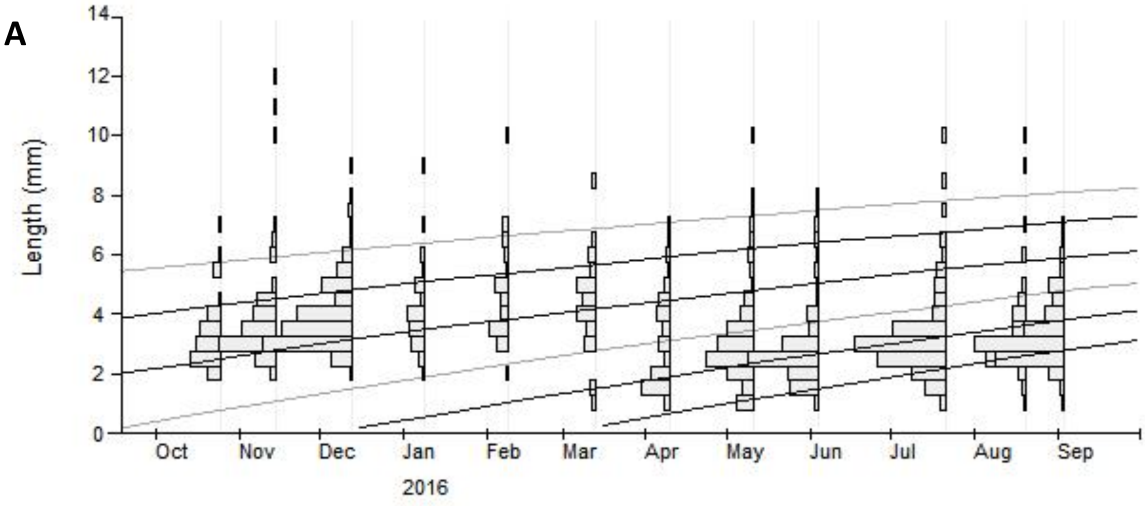


Figure 5 - *Clibanarius symmetricus*. Annual size-frequency distribution (cephalothoracic shield length, mm) of juveniles, males, non-ovigerous females, ovigerous females and intersexes.

3.2 Population Dynamics

The asymptotic length (L_∞) of the von Bertalanffy growth function (VBGF) was greater for males (12.6 mm) than females (9.3 mm) and they had similar curvature parameter (*K*) (0.48 and 0.47 year^{-1}, respectively) (Figure 7). No seasonal oscillation in growth was observed in this population; i.e. C= 0. The growth index phi prime (*Φ')* of males (1.88) was higher than females (1.61). The instantaneous mortality Z of males (1.76 year^{-1}) was smaller than females (3.26 year^{-1}) (*t* = - 3.93, df= 21, p <0.05*)* *(*Figure 8), and, conversely, the life span of males (2.51 years) was longer than females (1.61 years).



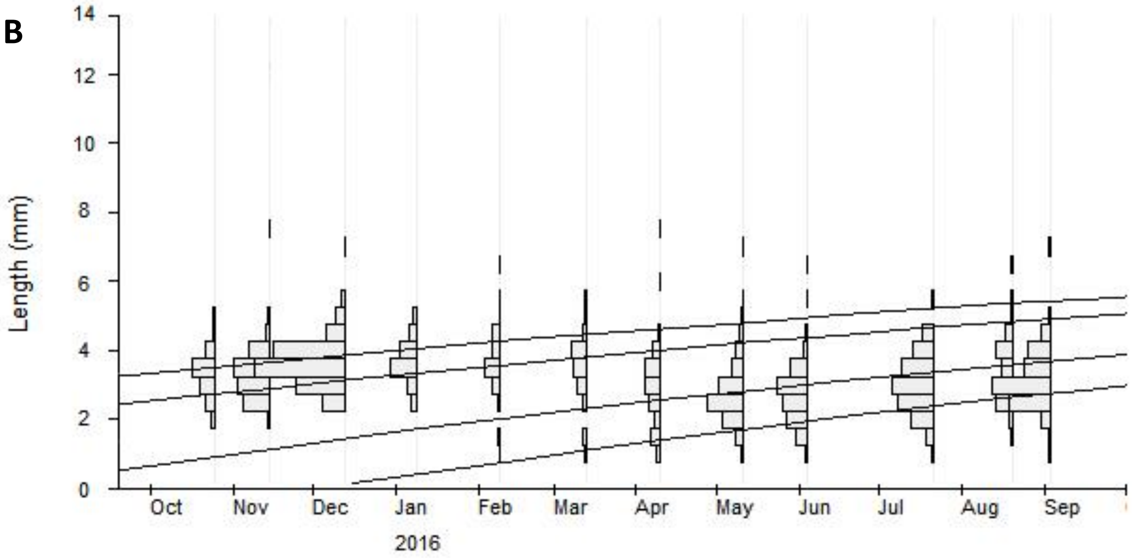


Figure 6 - *Clibanarius symmetricus*. Frequency distribution of cephalothoracic shield length and the von Bertalanffy growth function (VBGF) for males (A) and females (B).

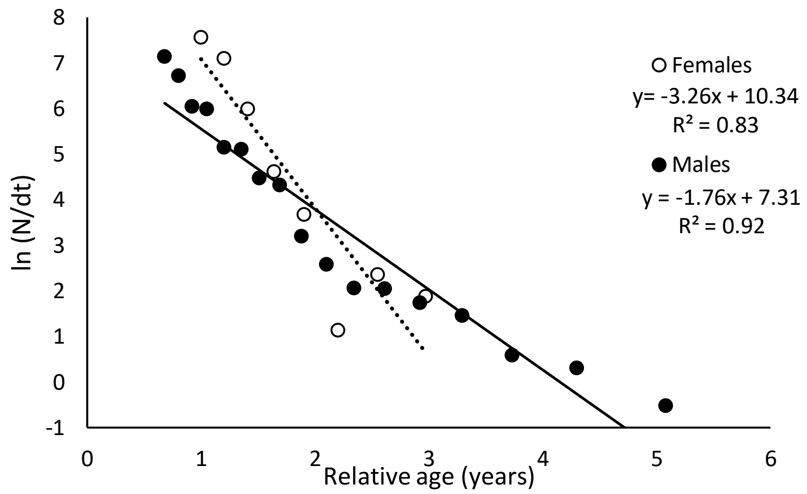


Figure 7- *Clibanarius symmetricus*. Length-converted catch curve used to estimate the mortality rate of males and females.

3.3 Mass-length relationship and secondary production

The length explained more than 97% the variance of the mass for both sexes (Figure 6). The relationship between cephalothoracic shield length (CSL) and ash-free dry mass (AFDM) did not differ between males and females (ANCOVA, F= 1.84, d.f.= 1, 84, $p > 0.05$)

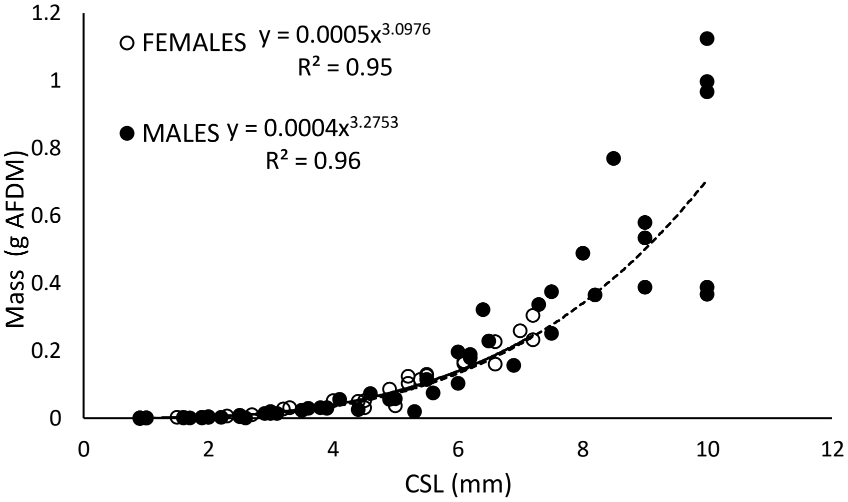
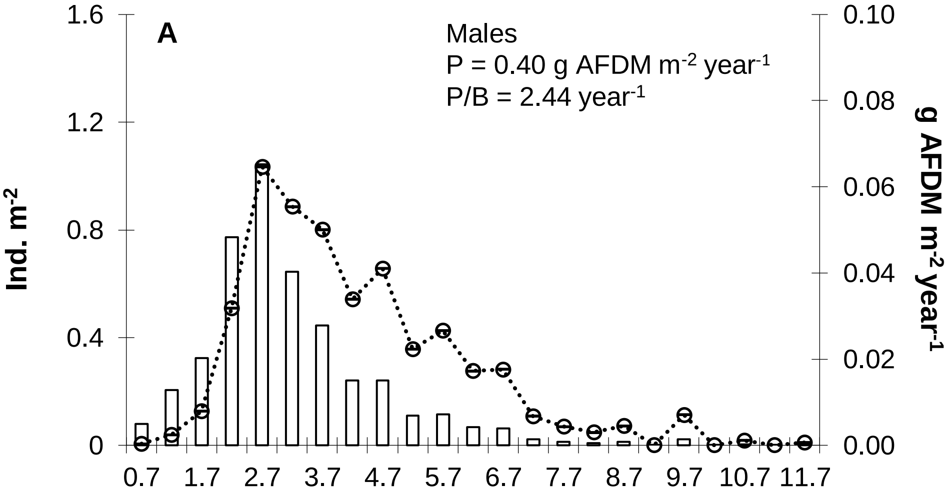


Figure 8 - *Clibanarius symmetricus*. Length-mass relationship for males and females.

The annual population production was estimated in 0.70 g AFDM m^{-2} $year^{-1}$ with higher value for males (0.40 g AFDM m^{-2} $year^{-1}$) than females (0.30 g AFDM m^{-2} $year^{-1}$). Males and females had similar P/B ratio, 2.44 $year^{-1}$ and 2.43 $year^{-1}$, respectively. For both sexes, the highest peak of production occurred around the 2.7 and 3.2 mm size classes. For males, the individuals between 1 and 3.7 mm contributed more than 50% to the production while for females these length classes contributed more than 80%. The higher values for production followed the peaks of density. (Figure 9).



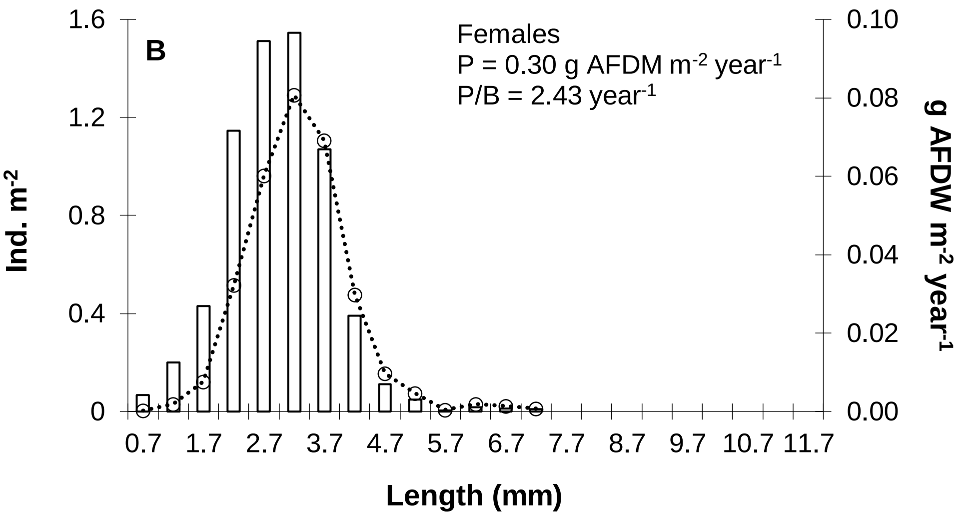


Figure 9 - *Clibanarius symmetricus*. Annual distribution of production (circles) and density (bars) of males (A) and females (B) for different length classes from October 2015 to September 2016.

3.4 Shell Utilization

The hermit crabs occupied nine different species of gastropods shells with predominance of *Thaisella coronata* (97.10%) (Figure 10). The species *T. coronata* was the only one occupied by all population categories, and ovigerous females and intersexes occupied it exclusively. Almost all size classes of hermit crabs occupied *T. coronata*, except the largest ones dominated by *P. tupiniquim (*Figure 11).

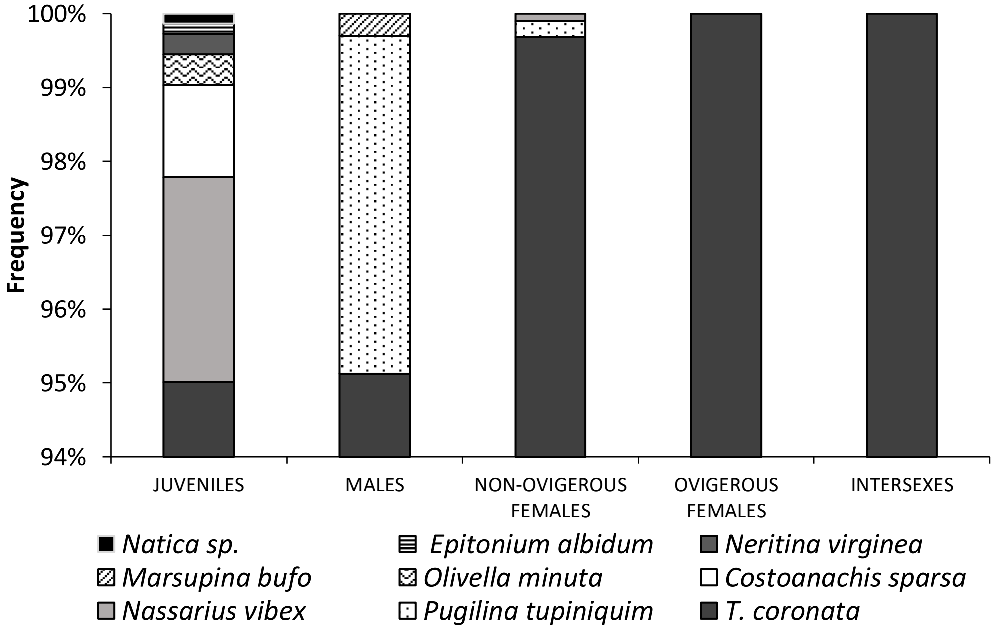


Figure 10 - *Clibanarius symmetricus*. Annual frequency distribution of shells species occupied by population categories of hermit crabs. (Y-axis values from 94%)

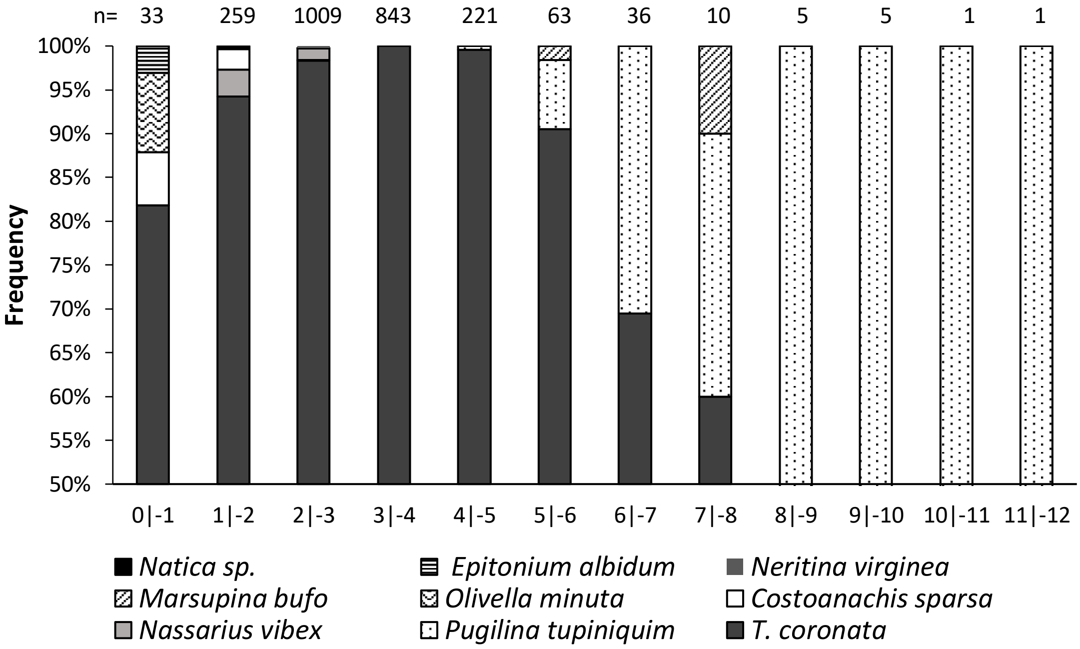
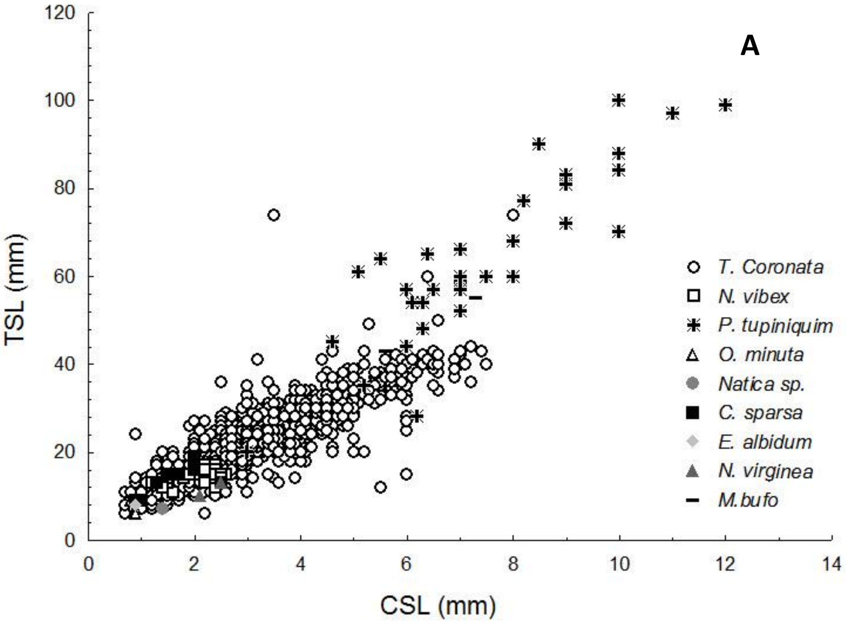


Figure 11 - *Clibanarius symmetricus*. Frequency distribution of shell species in relation to its cephalatoracic shield length (CSL). (Y-axis values from 50%).

The regressions between shell dimensions of *T. coronata* and hermit crab size were significant, and had relatively higher values (r^2) when all population categories were analyzed together (Table 2). In general, males had higher determination coefficients (r^2) than females for all shell parameters. When all shell species are considered, the smaller hermit crabs occupied a greater variety of small/lighter shells while in the largest ones, composed usually by males, was observed the occupation of the species *P. tupiniquim*, which appears to reach larger sizes than *T. coronata*. It is also possible to observe that individuals of same size occupied different species, sizes and weights of shells (Figure 12).

Table 2 - Clibanarius symmetricus. Linear regressions between cephalothoracic shield length (CSL) and shell parameters of Thaisella coronata. (TSL= total shell length; SAL= Shell Aperture Length; SAW= Shell aperture width; SW= shell weight). Asterisks indicate significant differences.

Relation	**Group**	**Equation**	r^2
CSL X TSL	Juveniles	$y = 4.41 + 5.71x$	0.42*
	Males	$y = 5.08 + 5.38\ x$	0.70*
	Non-ovigerous females	$y = 6.80 + 4.89x$	0.50*
	Ovigerous females	$y = 5.18 + 5.51x$	0.57*
	All categories	$y = 5.27 + 5.34x$	**0.73***
CSL X SAL	Juveniles	$y = 1.70 + 3.73x$	0.40*
	Males	$y = 3.25 + 2.98x$	0.59*
	Non-ovigerous females	$y = 4.65 + 2.62x$	0.43*
	Ovigerous females	$y = 6.10 + 2.39x$	0.28*
	All categories	$y = 3.33 + 2.98x$	**0.66***
CSL X SAW	Juveniles	$y = 1.46 + 1.14x$	0.26*
	Males	$y = 0.17+ 1.49x$	0.58*
	Non-ovigerous females	$y = 1.03 + 1.24x$	0.46*
	Ovigerous females	$y = 0.19 + 1.63x$	0.33*
	All categories	$y = 1.04 + 1.27x$	**0.60***
CSL X SW	Juveniles	$y = 0.1854x^{1.7279}$	0.45
	Males	$y = 0.1025x^{2.323}$	0.74*
	Non-ovigerous females	$y = 0.1384x^{2.0815}$	0.51
	Ovigerous females	$y = 0.1185x^{2.2669}$	0.74
	All categories	$y = 0.1493x^{2.0287}$	**0.78**



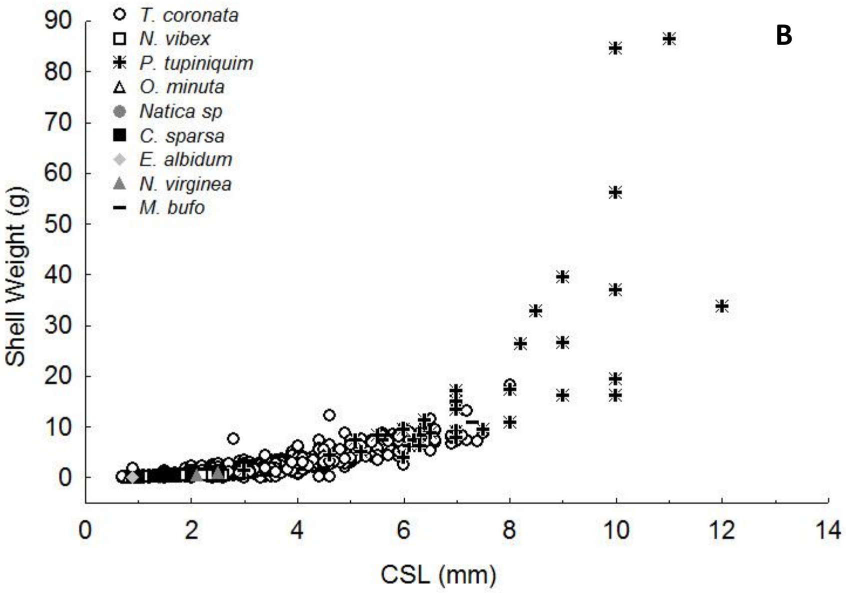


Figure 12 - *Clibanarius symmetricus*. Regression analyses between the biometric variables of gastropod shells (A, Total shell length and B, Shell weight) and hermit crab size (Cephalothoracic shield length, CSL).

4. DISCUSSION

The moderate wash climate typical of dissipative exposed beaches as Farol Velho contributed to the presence of *C. symmetricus* in the lower intertidal, since the occurrence of this species has been more frequently related to tidal flats and sheltered sandy beaches (e.g. SAMPAIO; MASUNARI; HASEYAMA, 2009; SANT'ANNA et al., 2008; TURRA; LEITE, 2000). Furthermore, the high density of *C. symmetricus* in this beach, with peak close to 25 ind.m^{-2}, reflects the relevant role that the rocky outcrop plays, conferring microhabitats that provide shelter, food and protection against desiccation and wave action to the macrofauna (KOSTYLEV et al., 2005). The higher mean density in an Amazon estuary (21 ind.m^{-2}) (RODRIGUES, 2016) compared to Farol Velho (11 ind.m^{-2}) can be a result of the lower hydrodynamic of the former environment. Even dissipative sandy beaches, the more benign morphodynamic state among sandy beaches, are physical stressful environments.

The high *C. symmetricus* mean density in the drier season than in the rainy one can be assigned to higher salinity when the decrease of riverine freshwater discharge contributes for the increase of salinity. The Amazonian estuarine population studied by Rodrigues (2016) didn't show correlation with the salinity, as in our study, but the author observed high density of *C. symmetricus* in the region near the mouth of the estuary where the salinity is higher. Young and Hazlett (1978) demonstrated that for *C. vittatus* larvae the survival and ratio of development to juvenile crabs is optimal at higher salinities. In this context, Sant'Anna et al. (2009) attributed low abundance of juveniles and ovigerous females in a subtropical estuarine sheltered sandy beach to the wide salinity variation in their study area (20 to 35) (SANT'ANNA et al. 2009). Here we also observed a wide variation of salinity (17 to 40) but the high abundance of juveniles during all year suggests better salinity conditions to their development in this tropical beach. In addition, the presence of juveniles in the Farol Velho population demonstrates that the recruitment area is the same as occupied by the adults, in opposition to what was reported by some studies that suggests that ovigerous females might migrate to the entrance of the estuary to access optimum salinity for their larvae (RODRIGUES, 2016; SAMPAIO; MASUNARI; HASEYAMA, 2009; SANT'ANNA; REIGADA; PINHEIRO, 2009). Therefore the importance of salinity as an important regulator of population biology.

The presence of ovigerous females during almost all year indicates a continuous reproductive pattern, as observed for other tropical hermit crab populations including two tropical populations of *C. symmetricus* (e.g. LITULO, 2005; MANTELATTO et al., 2010; REESE, 1968b; RODRIGUES, 2016; TEOH; CHONG, 2014b; TURRA; LEITE, 2000). On the other hand, subtropical *C. symmetricus* populations have discontinuous reproduction (MANTELATTO et al., 2010; SANT'ANNA; REIGADA; PINHEIRO, 2009; TURRA; LEITE, 2000), reinforcing the reproductive pattern according to latitude (temperature) of sandy beach crustaceans. (DEFEO; MCLACHLAN, 2005). Overall sex ratio skewed towards females has already been found for *C. symmetricus* (MANTELATTO et al., 2010; SANT'ANNA; REIGADA; PINHEIRO, 2009; TURRA; LEITE, 2000), this trend has also been identified for other species of hermit crabs (BENVENUTO; GHERARDI, 2001; LOWERY; NELSON, 1988; MANJÓN-CABEZA; GARCÍA-RASO, 1998; MANTELATTO et al., 2007). According to Turra and Leite (2000) sex ratio skewed towards females may be a result of higher mortality acting on males, habitat partitioning, differential feeding or differential spatial patterns, however our results don't support the first hypothesis since here females showed higher mortality than males as well as smaller life span.

Here we recorded the smallest ovigerous female registered for this species (2.6 mm CSL) , which indicates an earlier sexual maturity reached by tropical populations, once high temperatures allow premature maturity (DEFEO; MCLACHLAN, 2005). The higher length attained by males allied to its great abundance in the larger size-classes support the idea of sexual size dimorphism, which is widely reported in hermit crabs (e.g. BERTNESS, 1981; LITULO, 2005; MANJÓN-CABEZA; GARCÍA-RASO, 1998; MANTELATTO et al., 2010; SAMPAIO; MASUNARI; HASEYAMA, 2009; SANT'ANNA; REIGADA; PINHEIRO, 2009; TURRA; LEITE, 2000). Among possible reasons for sexual dimorphism in hermit crabs are the differential availability of energy for growth, since the females direct more energy to reproduction while the males channel it into somatic growth, and the sexual selection, since larger males have higher chances to find potential mates and succeed intrasexual fights over possession of females (ABRAMS, 1988). These hypotheses are supported by our growth analysis, which revealed higher growth performance index, despite similar k values, lower mortality and longer life span for males, enabling them to reach larger sizes than females. On the other hand, the higher reproductive effort of females, mainly in a population with continuous recruitment may increase their mortality compared to males. In addition, larger males can reduce intraspecific competition since they can make available the smaller shells for females (SANT'ANNA et al., 2008), causing differential shell occupation between sexes.

Few studies assessed *C. symmetricus* growth parameters and most of them were carried out on subtropical latitudes. In our study, the asymptotic length (L_∞) of males and females was smaller than the other two subtropical *C. symmetricus* populations studied, therefore according with the smaller size attained by tropical populations (DEFEO; MCLACHLAN, 2005). The growth constant (K) of Farol Velho *C. symmetricus* population was slightly similar to Sant'Anna et al. (2008) and smaller than Turra and Leite (2000) (Table 3). These two subtropical populations have similar growth performance index due to their opposite asymptotic length and growth constant. Consequently, the growth performance index of the Farol Velho population was smaller than those in southeastern Brazil (SANT'ANNA et al., 2008; TURRA; LEITE, 2000). The shorter life span of the *C. symmetricus* population of Farol Velho than the subtropical populations of this species, reinforces that the life cycle of tropical populations is faster than in higher latitudes.

The estimated production for males and females of *C. symmetricus* is close to the median estimated by Petracco et al. (2013) for sandy-beach Crustacea. However, in the same study, when only Decapoda are considered our values of production revealed to be much lower, the authors suggested that this happen because the presence of *Emerita brasiliensis* in their dataset, a decapod species with high biomass and rapid growth (PETRACCO; VELOSO; CARDOSO, 2003). In addition, the lower abundance but larger size and higher biomass of males than females may explain the higher estimated production for the former.

The P/B ratio is a measure of a species biomass turnover rate (DOLBETH et al., 2012) and is often correlated to several biotic factors such as growth, life span, mortality and reproductive period (ALLEN, 1971; CUSSON; BOURGET, 2005; ROBERTSON, 1979; WATERS, 1977). The similar P/B values estimated here for males and females reflect their also similar growth constant (K) and are close to the median values of sandy beach crustaceans (2.33 $year^{-1}$) estimated by Petracco et al. (2013). According to Allen (1971) the P/B ratio is equal to the mortality rate, although this relationship between Z (1.76 - 3.26 $year^{-1}$) and P/B (2.44 – 2.43 $year^{-1}$) was not observed here. Differences between Z and P/B ratio have been already described for others sandy beach macrofauna populations (PETRACCO et al., 2012, 2014; PETRACCO; CARDOSO; TURRA, 2013).

Table 3 - Parameters of the von Bertalanffy growth function ($L\infty$: mm; K: year^{-1}; C and WP), phi prime (Ø), mortality rate (Z: year^{-1}) and life span (LS: months) for the genus Clibanarius.

Species	Local/Latitude	L_∞	K	C	WP	Rn	Ø	Z	LS	Authors
Clibanarius symmetricus	**Farol Velho Beach, Brazil 0°35'30.4"S 47°19'20.9"W**	**Males: 12.6**	**0.48**	**0**	**----**	**0.124**	**1.88**	**1.76**	**30.1**	**This study**
		Females: 9.3	**0.47**	**0**	**----**	**0.342**	**1.61**	**3.26**	**19.3**	
Clibanarius antillensis	Pernambuco Islet, Brazil 23º 49'S 45º24' W	7.39	0.60	1.0	0.9	0.228	1,51	----	48	TURRA; LEITE, 2000
Clibanarius sclopetarius		12.70	0.65	0.9	0.78	0.208	2.02	----	47	
Clibanarius symmetricus (as C. vittatus)		10.67	0.96	1.0	0.7	0.232	2.04	----	42	
Clibanarius symmetricus *(as C. vittatus)*	Pescadores Beach Brazil 23º 58' 21'' S 46º 23' 35'' W	Males: 14.92	0.51	0.98	0.23	----	2,05	----	60	SANT'ANNA et al., 2008
		Females: 13.85	0.40	0.77	0.57		1,88	----.	66	

Clibanarius symmetricus occupied nine species of gastropods shells, although the shells of the muricid *Thaisella coronata was* occupied with a much higher frequency (97%) when compared to the other species. The synonymised species *T. trinitatensis* was also the preferred (93%) by the population of *C. symmetricus* in an Amazon estuary (RODRIGUES; MARTINELLI-LEMOS 2016). According to Reese (1969) hermit crabs commonly utilize shells of the more abundant gastropod, therefore this suggests the high availability of empty shells of *T. coronata* in the region.. On subtropical shores, *C. symmetricus* was found occupying mainly *Stramonita haemastoma* shells (MANTELATTO et al., 2010; SAMPAIO; MASUNARI, 2010; SANT'ANNA et al., 2006a). This muricid gastropod species has similar architecture to *T. trinitatensis,* declining the possibility of random choice of shells (RODRIGUES; MARTINELLI-LEMOS, 2016).

As well as in the Amazon estuary studied by Rodrigues & Martinelli-Lemos (2016) juveniles hermit crabs occupied a greater diversity of shells than adults, indicating changes in preference of shell type along its growth (RODRIGUES; MARTINELLI-LEMOS, 2016; STRAUGHAN; GOSSELIN, 2014). In addition, for juveniles the relationship between hermit crab size and *T. coronata* shell parameters had low determination coefficients (r^2) that may indicates inadequacy, reinforcing their necessity of use others shells at this life stage. Analogously, males had a slightly better shell adequacy (higher determination coefficients) than other population categories, such as recorded for other Diogenidae by Garcia and Mantelatto (2001), Turra and Leite (2001) and Frameschi et al. (2015). This indicate that males have the capacity to occupy the "best shells" since their larger size allow them to win agonistic encounters for suitable shells, increasing their shells fitness more than females (ASAKURA, 1995).

When considered the shell parameters for all population categories together, the shell total length and weight had the highest determination coefficients. Weight was also an important factor for the estuarine population studied by Rodrigues and Martinelli-Lemos (2016). This is an essential parameter in the process of selection because a heavy shell can protect against predators or from being washed away by the waves (REESE, 1969). On the other side the locomotion and foraging may be compromised by the use of heavier shells (FOTHERINGHAM, 1976). However, despite we have not made the shell adequacy analysis, the slightly smaller coefficients for aperture length and width may indicate shell inadequacy since these parameters are more related to shell architecture and they limit hermit crab morphology more than shell length or weight (TURRA; LEITE, 2002, 2004).

There was overlap of shell utilization when all shell species were analyzed together, with individuals of same size occupying different shell lengths, weights and species. Overlap in shell utilization demonstrates that individuals may experience intraspecific competitive interactions (TURRA; LEITE, 2002). Factors as high shell availability and shell species partitioning between sexes may contribute to the reduction of competition (TURRA; LEITE, 2001). Therefore, in this population same size hermit crabs are competing for shells of better adequacy.

5. CONCLUSION

The lesser harshness of physical factors faced by the macrofauna in exposed dissipative beaches is reflected in the high abundance of hermit crabs observed in this study. The presence of juveniles and ovigerous females in the population reinforces the importance of local scale factors, such salinity, and the continuous reproductive pattern of tropical latitudes. The growth analysis revealed that the population studied, in general, has smaller asymptotic length and growth constant than subtropical *C. symmetricus* populations, which results in smaller growth performance. Here we also, achieved the first estimates of secondary production for this species, where the similarity of turnover rate (P/B) between sexes is a consequence of their also similar growth. Shell utilization in this tropical beach is dominated by high availability of *T. coronata,* and the intraspecific competition for shells may favor males due to their large size. Our work is among the first performed with the *C. symmetricus* populations on the Amazon Coast, highlighting the importance of further studies in such peculiar region for better understanding of the ecology of tropical sandy beach macrofauna populations.

6. REFERENCES

ABRAMS, P. A. Sexual difference in resource use in hermit crabs; consequences and causes. In: CHELAZZI, G.; VANNINI, M. (Eds.). . **Behavioral adaptation to intertidal life**. New York: Plenum Press, 1988. p. 283–296.

ALLEN, K. R. Relation Between Production and Biomass K. **Journal of the Fisheries Research Board of Canada**, v. 28, p. 1573–1581, 1971.

ASAKURA, A. Sexual Differences in Life History and Resource Utilization by the Hermit Crab. **Ecology**, v. 76, n. 7, p. 2295–2313, out. 1995.

BALAZY, P.; KUKLINSKI, P. Mobile hard substrata - An additional biodiversity source in a high latitude shallow subtidal system. **Estuarine, Coastal and Shelf Science**, v. 119, p. 153–161, 2013.

BENVENUTO, C.; GHERARDI, F. Population structure and shell use in the hermit crab, Clibanarius erythropus: a comparison between Mediterranean and Atlantic shores. **Journal of the Marine Biological Association of the UK**, v. 81, n. 1, p. 77–84, 2001.

BERTNESS, M. D. Pattern and plasticity in tropical hermit crab growth and reproduction. **The American Naturalist**, v. 117, n. 5, p. 754–773, 1981.

BREY, T. **Population Dynamics in Benthic Invertebrates. A Virtual Handbook. Version 1.2.** Disponível em: <http://www.thomas-brey.de/science/virtualhandbook/>.

BROOKS, W. R.; MARISCAL, R. N. Population variation and behavioral changes in two pagurids in association with the sea anemone Calliactistricolor (Lesueur). **Journal of experimental marine biology and ecology**, v. 103, n. 1–3, p. 275–289, 1986.

CRISP, D. J. Energy flow measurements. In: HOLME, N. A.; MCINTYRE, A. D. (Eds.). . **Methods for the Study of Marine Benthos, IBP Handbook, vol. 16.** Oxford: Blackwell Scientific Publications, 1984. p. 284–372.

CUSSON, M.; BOURGET, E. Global patterns of macroinvertebrate production in marine benthic habitats. **Marine Ecology Progress Series**, v. 297, p. 1–14, 2005.

DEFEO, O.; MCLACHLAN, A. Patterns, processes and regulatory mechanisms in sandy beach macrofauna: a multi-scale analysis. **Marine Ecology Progress Series**, v. 295, p. 1–20, 2005.

DOLBETH, M. et al. Secondary production as a tool for better understanding of aquatic ecosystems. **Canadian Journal of Fisheries and Aquatic Sciences**, v. 69, n. 7, p. 1230–1253, 2012.

EL-ROBRINI, M. et al. Erosão e Progradação do Litoral Brasileiro: Pará. In: MUEHE, D. (Ed.). . **EROSÃO E PROGRADAÇÃO DO LITORAL BRASILEIRO**. Brasília: Ministério do Meio Ambiente, 2006. p. 1–46.

FOTHERINGHAM, N. Population Consequences of Shell Utilization by Hermit Crabs. **Ecology**, v. 57, n. 3, p. 570–578, 1976.

FRAMESCHI, I. F. et al. Shell occupation by the hermit crab Dardanus insignis (Decapoda, Diogenidae) from the north Coast of Sao Paulo state, Brazil. **Brazilian Journal of Biology**, v. 75, n. 4 Suppl S, p. S35--S44, 2015.

FRANSOZO, A.; MANTELATTO, F. L. M. Population structure and reproductive period of the tropical hermit crab Calcinus tibicen (Decapoda : Diogenidae) in the region of Ubatuba, Sao Paulo, Brazil. **Journal of Crustacean Biology**, v. 18, n. 4, p. 738–745, 1998.

GARCÍA-BERTHOU, E. et al. A technical note on seasonal growth models. **Reviews in Fish**

Biology and Fisheries, v. 22, n. 3, p. 635–640, 13 set. 2012.

GARCIA, R. B.; MANTELATTO, F. L. M. Shell selection by the tropical hermit crab Calcinus tibicen (Herbst, 1791) (anomura, diogenidae) from southern Brazil. **Journal of Experimental Marine Biology and Ecology**, v. 265, n. 1, p. 1–14, 2001.

GAYANILO, F. C.; SPARRE, F.; PAULY, D. FAO-ICLARM Stock Assessment Tools II (FiSAT II). Revised version. User's guide. **FAO Computerized Information Series (Fisheries)**, n. 8, p. 168, 2005.

GÓMEZ, J.; DEFEO, O. Life history of the sandhopper Pseudorchestoidea brasiliensis (Amphipoda) in sandy beaches with contrasting morphodynamics. **Marine Ecology Progress Series**, v. 182, p. 209–220, 1999.

HAZLETT, B. A. The Behavioral Ecology of Hermit Crabs. **Annual Review of Ecology and Systematics**, v. 12, n. 1, p. 1–22, nov. 1981.

KOSTYLEV, V. E. et al. The relative importance of habitat complexity and surface area in assessing biodiversity: Fractal application on rocky shores. **Ecological Complexity**, v. 2, n. 3, p. 272–286, set. 2005.

LAIDRE, M. E.; GREGGOR, A. L. Swarms of swift scavengers: ecological role of marine intertidal hermit crabs in California. **Marine Biology**, v. 162, n. 5, p. 969–977, 10 maio 2015.

LITULO, C. Population structure and reproduction of the hermit crab *Dardanus deformis* (Anomura: Diogenidae) in the Indian Ocean. **Journal of the Marine Biological Association of the United Kingdom**, v. 85, n. 4, p. 883–887, 2005.

LOWERY, W. A.; NELSON, W. G. Population Ecology of the Hermit Crab Clibanarius vittatus (Decapoda: Diogenidae) at Sebastian Inlet, Florida. **Journal of Crustacean Biology**, v. 8, n. 4, p. 548, nov. 1988.

MANJÓN-CABEZA, M. E.; GARCÍA-RASO, J. E. Population Structure and Growth of the Hermit Crab Diogenes pugilator (Decapoda: Anomura: Diogenidae) from the Northeastern Atlantic. **Journal of Crustacean Biology**, v. 18, n. 4, p. 753, nov. 1998.

MANTELATTO, F. L. et al. Population features of the Western Atlantic hermit crab Pagurus exilis (Anomura, Paguridae) in Brazil. **Atlantica**, v. 29, n. 2, p. 107–114, 2007.

MANTELATTO, F. L. et al. A comparative study of population traits between two South American populations of the striped-legged hermit crab Clibanarius vittatus. **Acta Oecologica**, v. 36, n. 1, p. 10–15, jan. 2010.

MCLACHLAN, A.; BROWN, A. C. **The Ecology of Sandy Shores**. 2. ed. [s.l.] Elsevier, 2006.

MORAES, B. C. DE et al. Variação espacial e temporal da precipitação no Estado do Pará. **Acta Amazonica**, v. 35, n. 2, p. 207–214, jun. 2005.

NEGREIROS-FRANSOZO, M. L. et al. Anomuran species (Crustacea, Decapoda) and their ecological distribution at Fortaleza Bay sublitoral Ubatuba, São Paulo, Brazil. **Iheringia Serie Zoologia**, v. 83, p. 187–194, 1997.

NEGRI, M.; LEMAITRE, R.; MANTELATTO, F. L. 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). **Journal of Crustacean Biology**, v. 34, n. 6, p. 848–861, 4 nov. 2014.

PAULY, D.; MOREAU, J.; ABAD, N. Comparison of age-structured and length-converted catch curves of brown trout Salmo trutta in two French rivers. **Fisheries Research**, v. 22, n. 3–4, p. 197–

204, 1995.

PAULY, D.; MUNRO, J. L. **Once More on The Comparison of Growth in Fish and InvertebratesFishbyte**, 1984.

PETRACCO, M. et al. Production of Excirolana armata (Dana, 1853) (Isopoda, Cirolanidae) on an exposed sandy beach in southeastern Brazil. **Helgoland Marine Research**, v. 66, n. 3, p. 265–274, 30 set. 2012.

PETRACCO, M. et al. Population biology of the gastropod Olivella minuta (Gastropoda, Olividae) on two sheltered beaches in southeastern Brazil. **Estuarine, Coastal and Shelf Science**, v. 150, p. 149–156, out. 2014.

PETRACCO, M.; CARDOSO, R. S.; CORBISIER, T. N. Population biology of Excirolana armata (Dana, 1853) (Isopoda, Cirolanidae) on an exposed sandy beach in Southeastern Brazil. **Marine Ecology**, v. 31, n. 2, p. 330–340, 30 jun. 2010.

PETRACCO, M.; CARDOSO, R. S.; TURRA, A. Patterns of sandy-beach macrofauna production. **Journal of the Marine Biological Association of the United Kingdom**, v. 93, n. 07, p. 1717–1725, 8 nov. 2013.

PETRACCO, M.; VELOSO, V. G.; CARDOSO, R. S. Population dynamics and secondary production of Emerita brasiliensis (Crustacea: Hippidae) at Prainha Beach, Brazil. **Marine Ecology**, v. 24, n. 3, p. 231–245, 2003.

PRETTEREBNER, K. et al. Hermit crabs and their symbionts: Reactions to artificially induced anoxia on a sublittoral sediment bottom. **Journal of Experimental Marine Biology and Ecology**, v. 411, p. 23–33, 2012.

RANIERI, L. A.; EL-ROBRINI, M. Condição Oceanográfica, Uso e Ocupação da Costa de Salinópolis (Setor Corvina – Atalaia), Nordeste do Pará, Brasil. **Revista de Gestão Costeira Integrada**, v. 16, p. 133–146, 2016.

REESE, E. S. Shell Use: An Adaptation for Emigration from the Sea by the Coconut Crab. **Science**, v. 161, n. 3839, p. 385–386, 26 jul. 1968.

REESE, E. S. Behavioral adaptations of intertidal hermit crabs. **Integrative and Comparative Biology**, v. 9, n. 2, p. 343–355, 1969.

ROBERTSON, A. I. The relationship between annual production: Biomass ratios and lifespans for marine macrobenthos. **Oecologia**, v. 38, n. 2, p. 193–202, 1979.

RODRIGUES, A. C. M. **Distribuição espaço temporal, estrutura populacional e padrão de ocupação de conchas do ermitão Clibanarius symmetricus (Randal, 1840) (Crutacea: Diogenidae) em um estuário Amazônico Equatorial**. Dissertação de Mestrado. Universidade Federal do Pará, 2016.

RODRIGUES, A. C. M.; MARTINELLI-LEMOS, J. M. Gastropod shell utilisation pattern by the hermit crab Clibanarius symmetricus (Anomura: Diogenidae) in an Equatorial Amazon estuary. **Journal of Natural History**, v. 50, n. 41–42, p. 2657–2671, 9 nov. 2016.

SAMPAIO, S. R.; MASUNARI, S. Characterization of the occupied shells by the hermit crab Clibanarius vittatus (Decapoda, Diogenidae) at Baixio Mirim tideflat, Guaratuba Bay, southern Brazil. **Anais da Academia Brasileira de Ciências**, v. 82, n. 4, p. 833–842, dez. 2010.

SAMPAIO, S. R.; MASUNARI, S.; HASEYAMA, K. L. F. Distribuição temporal do ermitão Clibanarius vittatus (Anomura, Diogenidae) no litoral do Paraná. **Iheringia. Série Zoologia**, v. 99, n. 3, p. 276–280, set. 2009.

SANT’ANNA, B. S. et al. Shell utilization pattern of the hermit crab Clibanarius vittatus (Crustacea, Anomura) in an estuary at São Vicente, State of São Paulo, Brazil. **Iheringia. Série Zoologia**, v. 96, n. 2, p. 261–266, jun. 2006a.

SANT’ANNA, B. S. et al. Spatial distribution and shell utilization in three sympatric hermit crabs at non-consolidated sublittoral of estuarine-bay complex in São Vicente, São Paulo, Brazil. **Revista de Biología Marina y Oceanografía**, v. 41, n. 2, p. 141–146, dez. 2006b.

SANT’ANNA, B. S. et al. Growth of the hermit crab Clibanarius vittatus (Bosc, 1802) (Crustacea, Anomura, Diogenidae) at São Vicente, São Paulo, Brazil. **Brazilian Archives of Biology and Technology**, v. 51, n. 3, p. 547–550, jun. 2008.

SANT’ANNA, B. S.; REIGADA, Á. L. D.; PINHEIRO, M. A. A. Population biology and reproduction of the hermit crab Clibanarius vittatus (Decapoda: Anomura) in an estuarine region of southern Brazil. **Journal of the Marine Biological Association of the United Kingdom**, v. 89, n. 04, p. 761, 27 jun. 2009.

SOMERS, I. F. **On A Seasonally Oscillating Growth FunctionFishbyte**, 1988.

SPARRE, P.; URSIN, E.; VENEMA, S. C. **Introduction to Tropical Fish Assessment: Manual. FAO Fisheries Technical Papers (306/1).** Rome: FAO, 1989.

SPIGHT, T. M. Availability and use of shells by intertidal hermit crabs. **Biology bulletin**, v. 152, p. 120–133, 1977.

STRAUGHAN, N. A.; GOSSELIN, L. A. Ontogenetic changes in shell preferences and resource partitioning by the hermit crabs Pagurus hirsutiusculus and P. granosimanus. **Journal of Experimental Marine Biology and Ecology**, v. 451, p. 1–8, 2014.

TEOH, H. W.; CHONG, V. C. Shell use and partitioning of two sympatric species of hermit crabs on a tropical mudflat. **Journal of Sea Research**, v. 86, p. 13–22, 2014a.

TEOH, H. W.; CHONG, V. C. Reproduction strategies and population dynamics of two Diogenes hermit crabs (Superfamily: Paguroidea) in a tropical mangrove estuary. **Hydrobiologia**, v. 724, n. 1, p. 255–265, 8 fev. 2014b.

TURRA, A.; LEITE, F. P. P. Population biology and growth of three sympatric species of intertidal hermit crabs in south-eastern Brazil. **Journal of the Marine Biological Association of the UK**, v. 80, n. 6, p. 1061–1069, dez. 2000.

TURRA, A.; LEITE, F. P. P. Shell Utilization Patterns of a Tropical Rocky Intertidal Hermit Crab Assemblage : I . the Case of Grande Beach. **Journal of Crustacean Biology**, v. 21, n. 2, p. 393–406, 2001.

TURRA, A.; LEITE, F. P. P. Shell utilization patterns of a tropical intertidal hermit crab assemblage. **Journal of the Marine Biological Association of the UK**, v. 82, p. 97–107, maio 2002.

TURRA, A.; LEITE, F. P. P. Shell-size selection by intertidal sympatric hermit crabs. **Marine Biology**, v. 145, n. 2, p. 251–257, 2004.

VANCE, R. R. The Role of Shell Adequacy in Behavioral Interactions Involving Hermit Crabs. **Ecology**, v. 53, n. 6, p. 1075–1083, nov. 1972.

WATERS, T. F. Secondary Production in Inland Waters. In: **Advances in Ecological Research**. v. 10p. 91–164.

YOUNG, A. M.; HAZLETT, T. L. The effect of salinity and temperature on the larval development of clibanarius vittatus (Bosc) (crustacea: decapoda: diogenidae). **Journal of Experimental Marine**

Biology and Ecology, v. 34, n. 2, p. 131–141, jan. 1978.