Nauplius
The Journal of The Brazilian Crustacean Society

e-ISSN 2358-2936
www.scielo.br/nau
www.crustacea.org.br

Population structure of *Hepatus pudibundus* (Decapoda: Aethridae) off the coast of Sergipe State, northeastern Brazil

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Abstract

Shrimp trawling is an important socioeconomic activity but catches a large number of non-target species, including *Hepatus pudibundus*. This study aimed at assessing the population structure of *H. pudibundus*, analyzing its sex ratio, length distribution, size at first morphological maturity and biometric relationships, and identifying latitudinal patterns. Four samples of 6 kg (shrimps plus by-catch) were monthly collected in March/2015–May/2016 in Pirambu, Sergipe. Carapace width (CW) and length (LC), and total weight (TW, g) were measured. Sex and stage of morphological maturity were defined. A total of 240 individuals was collected from all samples and the sex ratio did not differ from 1:1. This was observed in low latitudes, but females dominated in higher latitudes. The carapace width was 20.8–60.1 mm for females and 19.1–60.8 mm CW for males. Larger sizes were observed in higher latitudes. The estimated carapace width-length relationships for females and males were not significantly different (CL=0.6764+0.7390·CW; sex grouped). The estimated weight-length

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SUBMITTED 19 June 2019
ACCEPTED 06 January 2020
PUBLISHED 23 March 2020

DOI 10.1590/2358-2936e2020008

relationship was $TW=0.0004 \cdot CW^{2.8568}$ for females and $TW=0.0001 \cdot CW^{3.1225}$ for males. When compared with previous studies carried out throughout the Brazilian coast, slope values (b) for weight-length relationships were higher for males. The length at first morphological maturity for females and males was 28.9 and 29.6 mm, respectively, the lowest ever recorded for this species, reflecting the occurrence of smaller sizes in lower latitudes. These results are the first obtained for northeastern Brazil.

Keywords

Brachyura, biometric relationships, allometric growth, morphological maturation, latitudinal variation

Introduction

Bottom shrimp trawling in Brazil is an important socio-economic activity, which was responsible for catches of approximately 38.7 thousand tonnes of marine shrimps in 2011 off Brazilian waters (MPA, 2011). In the state of Sergipe, shrimp catches amounted to approximately 1.3 thousand tonnes in 2014 (Araújo *et al.*, 2016). However, bottom shrimp trawlers are considered predatory, especially due to the low selectivity leading to high catches of non-target species that end up discarded. This causes a serious environmental problem, as many of these species may be ecologically important in the food chain (Muto *et al.*, 2014) or may be juveniles of commercially important species (Branco and Verani, 2006), even though they do not have economic importance (Crowder and Murawski, 1998; Hall *et al.*, 2000). FAO data indicate that 1,865 thousand tonnes of by-catch are discarded in relation to 1,126 thousand tonnes of shrimps landed in the world (1992–2001 period), with an average discard rate of 62% (Kelleher, 2005). Discarded by-catch includes several species of fish, crustaceans, mollusks, cnidarians, and echinoderms of no commercial importance (Branco *et al.*, 2015), which under continuous fishing pressure are subject to several environmental problems (Hall *et al.*, 2000; King, 2007; Freire and Pauly, 2010).

In surveys conducted along the Brazilian coast, many species are caught as by-catch in shrimp fisheries: 216 species off Santa Catarina (Branco *et al.*, 2015), 258 species off São Paulo (Graça-Lopes *et al.*, 2002), 77 species off Espírito Santo (Pinheiro and Martins, 2009), and 79 species of only crustaceans between Sergipe and Alagoas (Santos *et al.*, 2016). In these studies, the presence of brachyuran crabs is significant, indicating this group is widely distributed along the Brazilian coast and has been probably impacted by shrimp trawlers. One of the brachyurans with the highest catch rates is the flecked box crab *Hepatus pudibundus* (Herbst, 1785) (Severino-Rodrigues *et al.*, 2002; Costa *et al.*, 2016; Mantelatto *et al.*, 2016; Rodrigues-Filho *et al.*, 2016).

Hepatus pudibundus belongs to the Aethridae and occurs in the Western Atlantic Ocean, from Georgia (USA) to Rio Grande do Sul (Brazil), on muddy or sandy areas with biodetritus and up to 160 m depth (Melo, 1996). Some of the studies for this species off the southeastern-southern regions in Brazil reported its presence as by-catch and/or analysed the population structure and length at first maturity (Mantelatto *et al.*, 1995a; Fracasso and Branco, 2005; Bueno *et al.*, 2009; Klôh and Di Beneditto, 2010), population dynamics (Sardá *et al.*, 2013; Miazaki *et al.*, 2018), reproductive cycle (Reigada and Negreiros-Fransozo, 2000), natural feeding habits (Mantelatto and Petracco, 1997), distribution, abundance and reproductive biology (Mantelatto *et al.*, 1995b; Furlan *et al.*, 2013; Lima *et al.*, 2014a; 2014b), and morphological and morphometric analyses (Marochi and Masurani, 2016; Marochi *et al.*, 2016). Keunecke *et al.* (2007) assessed the mortality of *H. pudibundus* caused by shrimp trawlers and concluded this species is overexploited off Rio de Janeiro and São Paulo. These individuals are also subject to the effects of anthropogenic pollution, as evidenced by Magalhães *et al.* (2012). Their research observed the contamination and bioaccumulation of persistent organic pollutants in *H. pudibundus*. These studies are important for the assessment of the species caught, even as by-catch, and give support to management plans for local communities (King, 2007;

Pinheiro and Boss, 2016). All these studies were conducted along the coast of the southeastern and southern regions in Brazil and thus the absence of information for northeastern Brazil is evident.

Considering the absence of information for northeastern Brazil, this study was conducted aiming at analysing the population structure (sex ratio, length distribution and size at first morphological maturity) of *Hepatus pudibundus* caught as by-catch by shrimp trawlers off the state of Sergipe and its biometric relationships. Finally, the existence of latitudinal patterns in the population structure and biometric relationships was assessed based on the information available in the literature

Materials and Methods

Sampling and processing

Samples of approximately 6 kg each on average were collected monthly from March 2015 to May 2016 from four shrimp bottom trawlers (one sample per boat). All trawlers were 8.5 to 15 m long, operated with double nets, and were based in the municipality of Pirambu, in the state of Sergipe (10°44'16"S 36°51'22"W to 11°31'09"S 37°30'42"W), northeastern Brazil (Fig. 1). All samples were obtained before any sorting by fishermen and thus included both shrimps and by-catch (fish, crustaceans, mollusks, and others). Samples were stored in ice and later kept frozen in the Laboratório de Ecologia Pesqueira at the Universidade Federal de Sergipe (LEP/UFS) for future analysis.

All individuals of *Hepatus pudibundus* present in the samples were separated and identified according to Melo (1996). Each specimen was weighed (total weight, TW, g) using a BEL Engineering® scale (precision: 0.0001 g) and measured (carapace length-CL and width-CW, both in mm) with a Precision Gold® digital calliper (precision: 0.01 mm). All individuals were sexed based on the shape of the abdomen (oval for females and elongated or triangular for males) (Mantelatto *et al.*, 1995a; Melo, 1996). The definition of morphological maturity was based on the macroscopic observation of the adherence of the abdomen to the thoracic sternites: immature and mature individuals have attached and non-attached abdomens, respectively (Mantelatto *et al.*, 1995a; Melo, 1996).

Statistical analyses

A chi-square test (χ^2) with the Yates correction for continuity was applied to test if the overall sex ratio (M:F) differed from 1:1 (Zar, 2010). All individuals

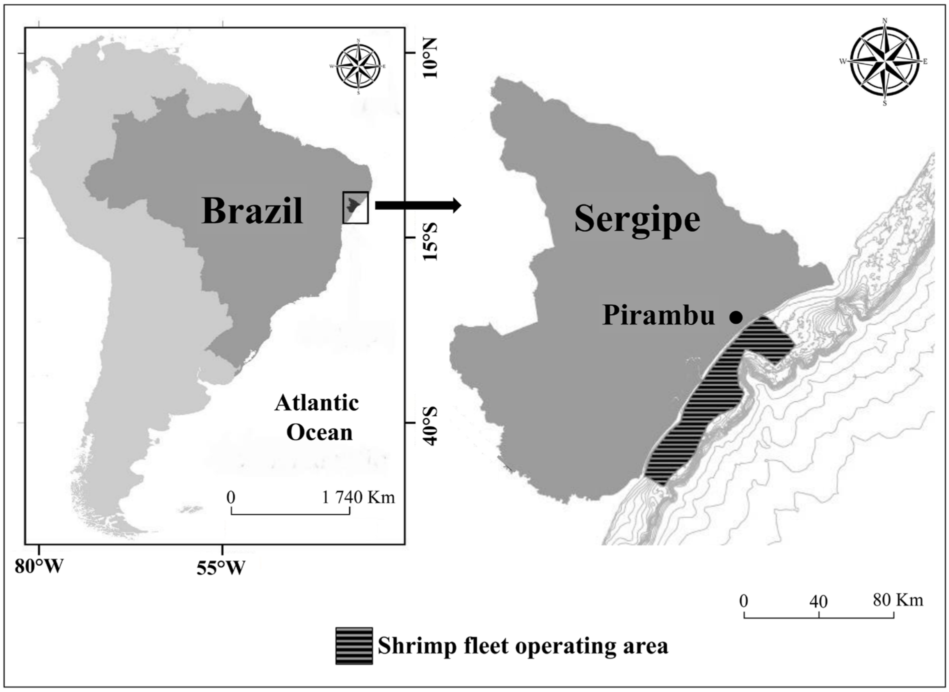

Figure 1. Study area off the state of Sergipe (northeastern Brazil), indicating the location of the municipality of Pirambu and the shrimp fleet operating area.

measured were divided into size classes of 5 mm CW, following Sturges (1926). The normality and homogeneity of the quantitative variables were tested by the Kolmogorov-Smirnov and Bartlet tests, respectively. A Student t-test with difference of variances was used to compare the mean carapace width (CW) and total weight (TW) between females and males (Zar, 2010). Maximum values of carapace width (CW_{max}) from different studies were obtained from the literature and compared to this study in order to test the hypothesis of increasing sizes in higher latitude using a linear regression. Relationships between carapace length and width were fitted using a linear model ($CL=a+b\cdot CW$), and relationships between total weight and carapace width using a power model ($TW=a\cdot CW^b$) for females and males, separately. The significance of the regressions was tested using an ANOVA for regression and differences between sexes were tested using the confidence intervals for the intercept (a) and slope (b) (Zar, 2010). The hypothesis of isometry was tested for the carapace length-width (b=1) and total weight-carapace length (b=3) relationships using a Student t-test (Froese, 2006; Zar, 2010). All tests were performed using a significance level of 5%.

Length at first morphological maturity (CW_m) was estimated using a logistic curve fitted to the percentage of mature individuals (% mature) and carapace width (CW) for females and males, separately: $\%mature=100/[1+\exp(a+b\cdot CW)]$ (Sparre and Venema, 1998). Parameters 'a' and 'b' were estimated using a non-linear method (SOLVER in Microsoft Excel).

Latitudinal pattern

All data related to population structure and biometric relationships were compared to the literature available, considering the latitude where each study was conducted. CW_{max} was plotted against latitude to verify changes with latitude. Finally, CW_m/CW_{max} for each study was calculated to check if it is constant or also varies with latitude.

Results

Population structure and biometric analysis

A total of 240 specimens of *Hepatus pudibundus* has collected and analysed: 128 females (11 immature and 117 mature) and 111 males (28 immature and 83 mature). The overall sex ratio was not statistically different from 1:1 (Chi-square test, χ^2=0.94, p=0.33). Quantitative variables were normal (Kolmogorov-Smirnov test, p>0.05) and with different variances between the sexes (Bartlet test, p<0.05). The carapace width ranged from 20.8 to 42.6 mm for immature females and from 25.0 to 60.1 mm for mature females (Fig. 2A). The carapace width ranged from 19.1 to 46.0 mm for immature males and from 25.8 to 60.9 mm for mature males (Fig. 2B). The mean carapace width for females (41.4±7.8 mm) was not statistically different from males (39.3±9.5 mm) (t-test, t=1.86, p=0.06). The total weight ranged from 2.5 to 17.6 g for immature females and from 3.8 to 47.8 g for mature females. The total weight ranged from 0.9 to 20.8 mm for immature males and from 3.9 to 57.6 mm for mature males. Similarly, the mean total weight for females (16.0±8.5 g) was not statistically different from males (15.3±11.0 g) (t=0.54, p=0.59).

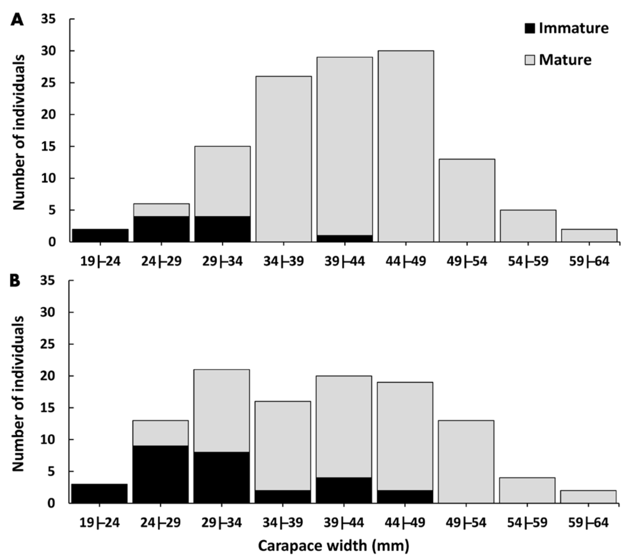

Figure 2. Number of individuals and morphological maturity stages for each carapace width (CW) class for females (A) and males (B) of *Hepatus pudibundus* off Sergipe (northeastern Brazil) in March/2015–May/2016.

The relationships estimated between carapace length and width for females and males were not statistically different (Tab. 1). Thus, a single relationship was estimated for both sexes: $CL=0.6764+0.7390\cdot CW$ (Fig. 3), indicating a negative allometry in the growth of the carapace length (b<1, t=43.45, p<0.05). The relationships between total weight and carapace width were TW=0.0004·$CW^{2.8568}$ and TW=0.0001·$CW^{3.1225}$ for females and males, respectively (Fig. 4). Significant difference was observed in the relationships estimated for females and males, indicating a negative allometry for females (b<3, t=3.23, p<0.05) and a positive allometry for males (b>3, t=2.44, p<0.05) (Tab. 1).

The length at first morphological maturity (CW_m) for females and males was 28.9 and 29.6 mm, respectively (Fig. 5).

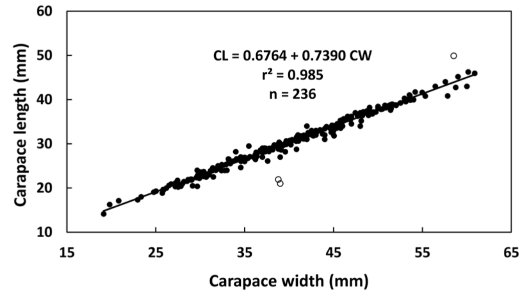

Figure 3. Relationship between carapace length (CL) and width (CW) for *Hepatus pudibundus* (both sexes) off Sergipe (northeastern Brazil) in March/2015–May/2016. White circles represent outliers.

Latitudinal pattern

The northernmost studies (Sergipe and Rio de Janeiro) indicated an equal proportion of females and males, and changed to predominance of females in higher latitudes. Table 2 presents the coefficients (a: intercept and b: slope) of the weight-width relationships for *Hepatus pudibundus* along the Brazilian coast. The weight-width relationships did not indicate any latitudinal pattern but higher values of b for males were evident throughout the Brazilian coast (Tab. 2). The maximum carapace width (CW_{max}) increases significantly with latitude: CW_{max}=1.1074·Lat+41.406 for females (r^2=0.676, F=16.7, p<0.01) and CW_{max}=1.1630·Lat+49.763 for males (r^2=0.738, F=22.6, p<0.01) (Fig. 6). CW_m was the smallest estimated for the Brazilian coast, but it is directly related to CW_{max}, as evidencied by the CW_m/CW_{max} (Tab. 3).

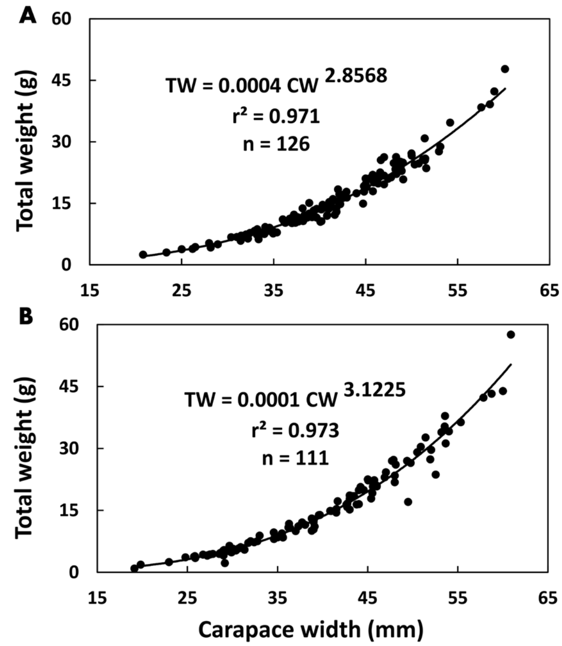

Figure 4. Relationship between total weight (TW) and carapace width (CW) for females (A) and males (B) of *Hepatus pudibundus* off Sergipe (northeastern Brazil) in March/2015–May/2016.

Table 1. Confidence intervals (0.95) for the parameters a and b from the biometric relationships of *Hepatus pudibundus* off Sergipe (northeastern Brazil) estimated for March/2015-May/2016.

Biometric relationships	Sex	a (CI)	b (CI)	r^2	n	F
	Female	0.5471 (-0.1047 - 1.1989)	0.7481 (0.7326 - 0.7636)	0.986	127	9 088.6*
CL=a+b·CW	Male	0.9033 (0.2437 - 1.5629)	0.7258 (0.7094 - 0.7421)	0.986	109	7 777.2*
	Mixed	0.6764 (0.1879 - 1.1647)	0.7390 (0.7271 - 0.7508)	0.985	236	15 130.7*
TW=a·CW^b	Female	0.0004 (0.0002 - 0.0005)	2.8568 (2.7691 - 2.9443)	0.971	128	4 164.7*
	Male	0.0001 (0.0000 - 0.0002)	3.1225 (3.0231 - 3.2218)	0.973	112	3 882.7*

CL = carapace length; CW = carapace width; TW = total weight; a = intercept; b = slope or power; CI = confidence interval; r^2 = coefficient of determination; n = sample size; F = Fisher's F for ANOVA regression; *indicates statistically significant results, p<0.05.

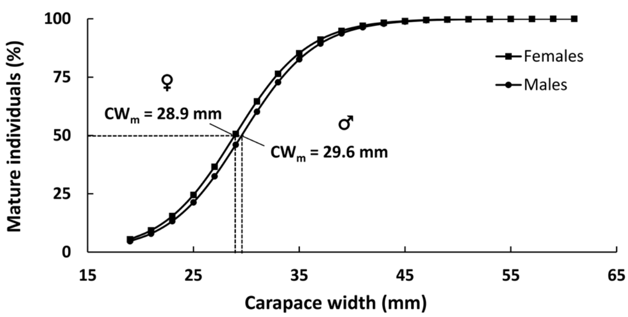

Figure 5. Length at first morphological maturity (CW_m) for females and males of *Hepatus pudibundus* off Sergipe (northeastern Brazil) in March/2015–May/2016.

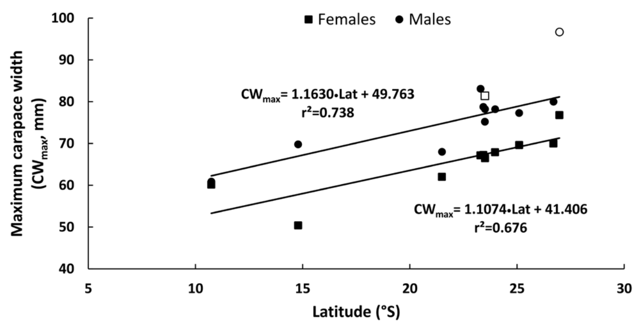

Figure 6. Relationships between maximum carapace width (CW_{max}) and latitude (Lat) for females and males of *Hepatus pudibundus* along the Brazilian coast. The white square corresponds to females off São Paulo (Lima *et al.*, 2014a) and the white circle to males off Santa Catarina (Sardá *et al.*, 2013).

Table 2. Intercept (*a*) and slope (*b*) of total weight-carapace width relationships ($TW=a{\cdot}CW^b$) for *Hepatus pudibundus* along the Brazilian coast. TW=total weight (g); CW=carapace width (mm); n=sample size; r^2=coefficient of determination.

State (latitude)	*a*		*b*		n		r^2		Source
	Females	Males	Females	Males	Females	Males	Females	Males	
Sergipe (10°44'-11°31'S)	0.0004	0.0001	2.8568	3.1225	128	112	0.971	0.973	This study
Rio de Janeiro (21°30'-21°50'S)	0.0003	0.0002	2.8734	3.0391	185	235	0.940	0.970	Klôh and Di Beneditto (2010)
Rio de Janeiro and São Paulo (23°18'-23°58'S)	$8.2{\times}10^{-5}$ *	$3.6{\times}10^{-5}$ *	3.1700	3.3800	524	408	0.850	0.920	Keunecke *et al.* (2007)
São Paulo (23°31'S)	0.0004	0.0002	2.8400	3.0100	380	244	—	—	Mantelatto and Fransozo (1992)
Santa Catarina (26°42'-26°46'S)	0.0003 **	0.0002 **	2.8312	2.9405	846	473	0.894	0.963	Fracasso and Branco (2005)
Santa Catarina (26°59'S)	0.0002	0.0002	2.9500	2.9400	946	907	0.960	0.990	Sardá *et al.* (2013)

*Values of *a* obtained using anti-log, as original references used log-transformed data.
**Values of *a* transformed as the original source estimated the weight-length relationship using width in cm.

Table 3. Length at first maturity (CW_m) and maximum carapace length (CW_{max}) for *Hepatus pudibundus*, and mean bottom water temperature along the Brazilian coast.

State (latitude)	CW_m (mm)		CW_{max} (mm)		CW_m/CW_{max} (%)		Mean bottom water temperature (°C)		Source
	Female	Male	Female	Male	Female	Male	Lowest	Highest	
Sergipe (10°44'- 11°31'S)	28.9	29.6	60.1	60.8	48.1	48.6	26.55 [a]	32.33 [a]	This study
São Paulo (23°30'S)	32.5	32.4	81.4	75.2	40.0	43.0	18.50 [b]	27.30 [b]	Lima *et al.* (2014b)
São Paulo (23°59'S)	35.0	38.0	67.9	78.2	51.5	48.6	—	—	Bueno *et al.* (2009)
São Paulo (25°06'S)	—	—	69.6	77.3	—	—	18.24	26.90	Miazaki *et al.* (2018)
Santa Catarina (26°42'-26°46'S)	36.0	35.0	70.0	80.0	50.6	43.8	17.86 [c]	25.30 [c]	Fracasso and Branco (2005)

Mean bottom water temperature values found for the same region in other studies: [a] Santos *et al.* (2017); [b] Lima *et al.* (2014a), approximate graphical values; [c] Sardá *et al.* (2013).

Discussion

The number of females and males of *Hepatus pudibundus* was not statistically different in Sergipe compared to what was observed in Rio de Janeiro (Kloh and Di Beneditto, 2010) and Santa Catarina (Sardá *et al.*, 2013). Nevertheless, several studies indicated predominance of females (Mantelatto *et al.*, 1995a; Reigada and Negreiros-Fransozo, 2000; Fracasso and Branco, 2005; Keunecke *et al.*, 2007; Bueno *et al.*, 2009; Lima *et al.*, 2014a; Miazaki *et al.*, 2018), all of them in high latitude. Fisher's theory (1930) postulates that a sex ratio of 1:1 is expected in dioecious species, as observed in this study. Differences in number of females and males of *H. pudibundus* along the Brazilian coast suggests that factors such as migration, growth and mortality exert differential control over each sex (Haley, 1979; Fracasso and Branco, 2005; Klôh and Di Beneditto, 2010).

Mean carapace width and mean total weight were not statistically different between females and males. Miazaki *et al.* (2018) also found no difference off São Paulo. However, studies conducted in Rio de Janeiro (Keunecke *et al.*, 2007; Klôh and Di Beneditto, 2010), São Paulo (Mantelatto *et al.*, 1995a; Keunecke *et al.*, 2007), and Santa Catarina (Sardá *et al.*, 2013) indicated larger mean carapace width for males than females. Overall, male brachyurans are larger than females (Hartnoll, 1978), which may be related to different foraging behaviour and reproductive strategies. Thus, the development process favours larger males with better reproductive success; on the other hand, females invest more in reproduction after first maturity, with less investment into growth (Mantelatto and Fransozo, 1994; Klôh and Di Beneditto, 2010; Marochi *et al.*, 2016).

In this study, no difference in mean size for males and females was observed, and factors such as different patterns of migration, food foraging, sexual behavior, and reproductive strategy may influence the dispersion of these individuals (Haley, 1979; Sardá *et al.*, 2013; Lima *et al.*, 2014a), and consequently the differential capture of size classes of specimens by fishing gear. The absence of crabs smaller than 19 mm CW may have been influenced by segregation and different spatial distribution between immature and mature crabs (Hines *et al.*, 1995; Watanabe *et al.*, 2014), and by the selectivity of the mesh size used (21 mm, JRJ and KMFF, personal observation).

Data compiled for maximum carapace width of *H. pudibundus* along the Brazilian coast showed an increase in width (and hence length) with latitude (Fig. 6). The largest individuals found in the literature were a male with 96.7 mm CW off Santa Catarina (Sardá *et al.*, 2013) and a female 81.4 mm CW long off São Paulo (Lima *et al.*, 2014a), in southern and southeastern Brazil, respectively. The smallest CW_{max} values found were 54.4 mm for females off Bahia (Almeida *et al.*, 2007) and 60.8 mm for males off Sergipe (present study), both in northeastern Brazil. Santos *et al.* (2016) found a CW_{max} of 62.6 mm for grouped sexes off the Alagoas-Sergipe states (original values of CL converted to CW using the linear equation CL×CW presented at Tab. 1), corroborating with the values found in the present study. This latitudinal variation of length is called Bergmann's Rule, which states that individuals of a certain species reaching larger corporal length tend to live in higher latitudes (Blackburn *et al.*, 1999).

One of the main factors affecting species body size is temperature, which controls metabolism and growth (Pauly and Cheung, 2018). Hines (1989) found latitudinal difference for crustaceans along the coast of North America and considered temperature as the main cause for this difference. Hirose *et al.* (2012) described a similar latitudinal pattern for *Leptuca uruguayensis* (Nobili, 1901), where the largest individuals were found in Argentina (36ºS) when compared with individuals from Brazil (23ºS). In fact, the southeastern and southern regions of Brazil are characterized by lower seawater temperature (Heileman and Gasalla, 2009) when compared with the northeastern region (Heileman, 2009) (see Tab. 3). Warmer waters have a lower amount of dissolved oxygen, and organisms have to adjust their metabolism to balance out oxygen availability and consumption. As a consequence, individuals reach smaller body size (Pauly, 2010). Conversely, invertebrates (crabs and others) inhabiting cold waters enjoy a larger amount of dissolved oxygen and if their enzymatic and metabolic systems are not affected by the low temperature, they will reach larger body size (Pauly, 2010). Other factors such as food availability and fishing pressure may also influence the maximum observed size (King, 2007).

The relationship between carapace width and length showed a pattern of negative allometry ($b<1$) for both sexes, indicating that carapace length grows relatively less than expected in relation to carapace width. Sardá *et al.* (2013) found a negative allometry for this relationship for *H. pudibundus* off Santa Catarina, even though there was significant difference between sexes. On the other hand, Bueno *et al.* (2009) found isometric growth ($b=1$) off São Paulo. The relationship between total weight and carapace length indicated differences in allometry between sexes: negative for females and positive for males. Thus, males grow more in weight than would be expected for their increase in length than females. Several other studies analysed this allometric difference in weight between sexes for *H. pudibundus*, and in general, males present larger *b* values (Tab. 2). Some authors attribute negative allometry on weight for females to reproductive factors, as females direct a large part of their energy to reproductive activities after maturity is reached, reducing investments in body growth (Klôh and Di Beneditto, 2010). Some authors, on the other hand, do not agree with this point of view (see, *e.g.*, Pauly, 2019). Positive allometry in males may be related to the need to maximize size and biomass to improve food search capabilities and territorial defence (Sardá *et al.*, 2013). Moreover, this may be related to much larger chelar propodus developed in males after maturity (Marochi *et al.*, 2016), common in brachyurans (Hartnoll, 1974; 1978).

Length at first morphological maturity was similar for females and males (around 29 mm CW), as found off other states in Brazil. In general, females begin to reproduce when reaching 40-62% of the maximum carapace length and males around 43-54% of CW_{max} (Tab. 3). The largest CW_m recorded along the Brazilian coast was found by Fracasso and Branco (2005) for females (36.0 mm CW, Santa Catarina, southern region) and by Bueno *et al.* (2009) for males (38.0 mm CW, São Paulo, southeastern region). The CW_m estimated in the present study for *H. pudibundus* were the smallest ever registered along the Brazilian coast (Tab. 3). Yet, this may also reflect the fact that individuals reach smaller sizes in lower latitudes, evidenced by the similarity in CW_m/CW_{max} observed along the coast (50% on average).

The population parameters estimated here for *H. pudibundus* for the first time in Sergipe, northeastern Brazil, differ, in some cases, from studies carried out off southeastern-southern Brazil, mainly due to latitudinal differences directly associated to temperature. We suggest that new studies are conducted along the Brazilian coast to better understand latitudinal patterns related to population structure and biometric relationships, especially in northeastern Brazil. As these communities are also impacted by high fishing effort, the information presented here represent an initial step towards sustainable management of the environment.

Acknowledgements

This study was supported by Projeto de Monitoramento Participativo de Desembarque Pesqueiro (PMPDP) and Fundação de Apoio à Pesquisa e Extensão de Sergipe (FAPESE) (Grant numbers 2600.0094374.14.4 and 2600.0099827.15.4). The authors are grateful to Maria Morais and fishermen from Pirambu (Sergipe) for the collection of samples used in this study, to Aline Alves dos Santos Dias and Ana Claudia Gaspar for helping with sample processing, to Robson Rosa for the map of the study area, and to two anonymous reviewers for their valuable comments on the first version of our manuscript.

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