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POPULATION BIOLOGY OF *Panopeus lacustris* DESBONNE 1867 (BRACHYURA: PANOPEIDAE) IN PIAUÍ COASTAL, BRAZIL

Biologia populacional de *Panopeus lacustris* Desbonne 1867 (Brachyura: Panopeidae) na Costa do Piauí, Brasil

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ABSTRACT

Specimens of Panopeus lacustris *were identified, sexed, and measured to obtain the following dimensions: carapace width, carapace length, body height, the propodus major length, the propodus major wide, the propodus major height, abdomen width and gonopodium length. The average carapace width (CW) and the average weight differed significantly between the sexes. The proportion of right-handed crabs was significantly higher than the left-handed. Males were more frequent in classes 22.41|--25.75 mm, and females in class 19.06|--22.41 mm. Biometric data were subjected to regression using a power function. The morphological sexual maturity width of the carapace showed an average of 12.32 mm on males and 12.00 mm on females. However, it was observed that 50% of physiologically mature crabs presented 11.35 mm of CW for males and 10.61 mm for females. The sex ratio of all crabs analyzed was 1:1.15 (males:females). The data collected during this study suggest that the reproductive period of this species is continuous. The results of this study are common to populations of Brachyura, and indicate that the population of* P. lacustris *is stable in the environment.*

Key words*: population structure; relative growth; sex ratio; sexual maturity.*

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RESUMO

Os espécimes de *Panopeus lacustris* foram identificados, separados quanto ao sexo e mensurados para obtenção das seguintes dimensões: largura da carapaça, comprimento da carapaça, altura do corpo, comprimento do maior quelípodo, largura do maior quelípodo, altura do maior quelípodo, largura do abdômen, e comprimento do gonopódio. O tamanho médio da largura de carapaça e o peso médio diferiram estatisticamente entre os sexos. Os machos foram mais frequentes na classe 22,41 |-- 25,75, e as fêmeas na classe 19,06 |-- 22,41. Os dados biométricos foram submetidos a uma regressão, utilizando-se uma função do tipo potência ($y=ax^b$). A LC com a qual ocorre a maturação sexual morfológica é de 12,32 mm em machos e de 12,00 mm em fêmeas. Constatou-se que 50% dos machos apresentam-se maduros fisiologicamente com 11,35 mm de LC e as fêmeas com 10,61 mm. A razão sexual para o total de caranguejos examinados foi 1:1,15 (machos:fêmeas). Os dados coletados sugerem que o período reprodutivo dessa espécie é contínuo. Os resultados encontrados no presente estudo são comuns para populações de Brachyura, e indicam que a população de *P. lacustris* se encontra estável no ambiente.

Palavras-Chave: estrutura populacional; crescimento relativo; razão sexual; maturidade sexual.

INTRODUCTION

The crabs of Panopeidae family are common organisms of marine intertidal zone and shallow habitats, along temperate and tropical coastline of American continent (Souza *et al.*, 2013). They can be found in freshwater environments, and marine estuaries (Schubart *et al.*, 2000).

According to Melo (1996), seven species of *Panopeus* can be found on the Brazilian coastline. The species *P. lacustris* Desbonne, 1867 (Figure 1) is widely distributed on the west coast of the Atlantic (Florida, Bermuda, Caribbean region, Colombia, Brazil) and Eastern Pacific (Hawaii). This crab species lives under rocks, in estuaries and bays, and can be also found in polluted regions, under rotting branches and associated with oysters (Melo, 1996).

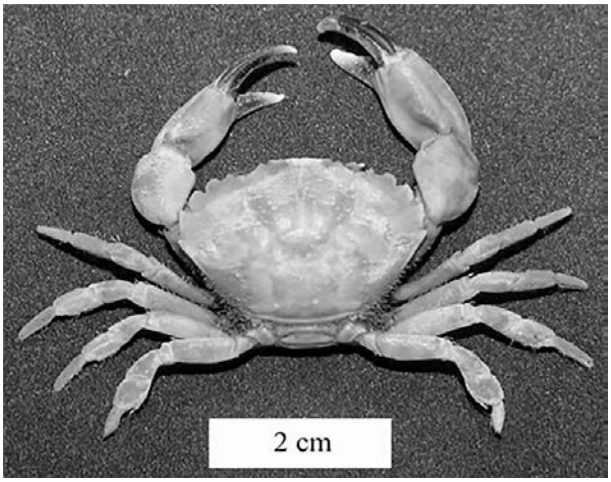

Figure 1 - Photography *Panopeus lacustris*.
Source: Private author.

The structural characterization of populations constitutes fundamental information for measures aimed at the maintenance of natural resources (Di Benedetto & Masunari, 2009). Natural populations are generally subjected to specific environmental pressures, which lead them to evolve independently of one another. These populations, therefore, reflect the limitations of the environment to which they are subject. Thus, studies that allow comparisons between populations are performed to understand the functioning and influence of different environments (Turra & Leite, 2000).

Studies related to the population characteristics of crustaceans are focused on collection of information about the distribution of individuals in different size classes, the comparison of males and females body size (sexual dimorphism), the sex ratio, the reproductive period, among other data (Castiglioni *et al.*, 2011). This collection of data contributes to the knowledge of the ecological balance of the animals in a given habitat, as well as it leads to a better understanding of its biology (Araújo *et al.*, 2012).

The aspects related to the growth of crabs direct to studies about the understanding of sexual differentiation between species, as well as the highlight of the transition from juvenile to adult, during the pubertal molting (Góes & Fransozo, 1997).

The size at which the crab sexual maturity occurs is the primary information needed for management of crustacean species (Somerton, 1980). The estimate of sexual maturity body size of crabs is the most important parameter for the assessment and management of natural population (Marochi *et al.*, 2013). Also, it is important to ensure the sustainability of populations. Based on this feature, it is common to establish the minimum size capture, to ensure adequate reproduction and subsequent recruitment. (Shinozaki-Mendes *et al.*, 2013).

The present study aims to investigate the population biology of *P. lacustris* of Piauí coast, analyzing the relative growth, morphological and physiological sexual maturity, frequency distribution in size classes, sex ratio and reproductive period.

MATERIAL AND METHODS

Description of the study area

The population biology study of the crab *Panopeus lacustris* was performed in the area delimited by the Coqueiro Beach in the municipality of Luís Correia, State of Piauí,

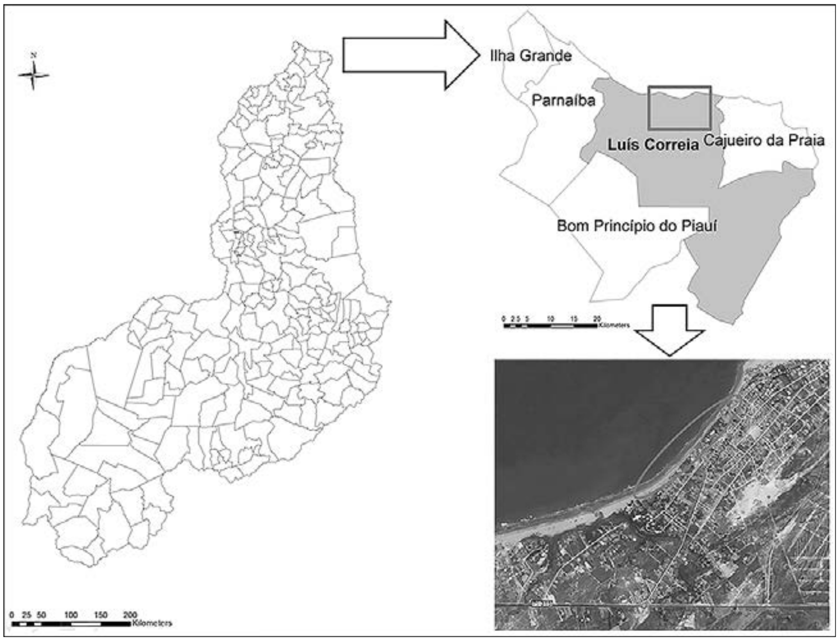

Figure 2 - Collection area. State of Piaui, Brazil. Highlighted, municipality of Luís Correia and Coqueiro Beach, respectively. Source: Google Earth.

Brazil (02° 54′ 20″ S e 041° 34′ 32″ W) (Figure 2). This beach has a significant number of sandstone outcrops, with an important biota composition, an abundant marine macroalgae and animals. The easy access to this beach and the population living in this area generate a strong anthropogenic impact in this environment, and arising the problems related to the coastal hydrodynamic changes (Lima Júnior *et al.*, 2010).

Data collect

Crabs were collected monthly from June/2004 to May/2005, under low tide condition. The capture was performed manually and randomly, without area delimitation. After capture, the animals were placed in individual plastic bags and transported to the Zoology Laboratory of the Universidade Federal do Piauí (UFPI), Parnaíba (PI). They were maintained frozen until the analysis of their structural characteristics.

Prior to data analysis, the animals were thawed at room temperature. The crabs were separated according to sex, and the following dimensions were measured using a caliper (0.05mm accuracy): carapace width (CW), carapace length (CL), body height (BH), propodus major length (PML), propodus major width (PMW), propodus major height (PMH), abdomen width in the fourth somite (AW) and gonopod length (GL). All individuals not injured (with all appendices) had their humid weight (HW) measured in Grams.

Data analysis

CW and HW showed normal distribution, as detected by the Shapiro-Wilk test ($\alpha = 0.05$) (Zar, 2010). The average size comparison of males and females CW, which can indicates sexual dimorphism, was performed using the *Student t* test for independent samples ($\alpha=0.05$) (Zar, 2010). To compare the weight mean of males and females, it was used the Mann-Whitney test for independent samples ($\alpha=0,05$), since the Shapiro-Wilk test ($\alpha = 0.05$) did not detect normal distribution (Zar, 2010).

The population structure was analyzed by plotting, on histograms, the number of individuals of each population group (male and female) according to the CW size classes. The number of classes obtained from CW size was calculated according to the equation of Sturges (1926), $I = 1 + 3.32 \log N$, in which "I" represents the number of classes, and "N" the sample size. Crabs were grouped into sexual demographic categories (male and female) to verify the temporal variations of the frequency distributions. The frequency distribution of the total sampled crabs was calculated using the Shapiro-Wilk test ($\alpha=0.05$) (Zar, 2010), to verify the normality of the distributions, according to Castiglioni *et al.* (2006).

To study the relative growth the biometric data obtained were plotted in scatter plots, using the power function $y=ax^b$. The CW was considered as an independent variable (x) and the other dimensions as dependent variables (y). The significance of the values assumed by "b" in the equation ($y = ax^b$) was tested using *Student's t* test ($\alpha=0.05$) (Zar, 2010). If b = 0, isometry was considered; b > 1, positive allometric growth; and b <1, negative allometric growth (Fonteles-Filho, 2011). The equations obtained were then linearized using the logarithmic transformation ($\log y = \log a + b \log x$).

The determination of the inflection point on the scatter plot, to establish the morphological sexual maturity, was performed using the software REGRANS (Pezzuto, 1993). Females AW females and males PML were used as dependent variables. The inflection point determined for each sex was tested comparing multiple regressions (α=0.05) (Zar, 2010).

The physiological sexual maturity was verified by adjusting the Galton ogive curve, according to Fonteles-Filho (2011), for each sex. In this study, we have also analyzed the gonadal development stage of the animals. They were dissected for a macroscopic analysis and classification of their gonads according to the color and size, which were compared to hepatopancreas, as recommended by Kyomo (1988). Therefore, four stages of maturation were established for each sex: immature, rudimentary, in developing and developed, according to Góes (2000). The organisms were divided into size classes with 2 mm amplitude. Individuals with rudimentary, developing and developed gonads were considered mature. The proportion of mature individuals was considered as a dependent variable (y) and carapace width as independent variable (x) according to equation: $y = 1 - e^{-AX^{b}}$, whose linearized equation is: $ln\ [-ln\ (1-Y)] = ln\ A + b\ ln\ X$. To estimate the physiological sexual maturity carapace width it was used the equation "$L_{50} = exp^{\,ln[-\ln(1-0{,}50]-lnA}$", according to Fonteles-Filho (2011).

Sex ratio was determined on each month of collection for each CW class. It was noted that the sex ratio follows the theory of natural proportion (1 male : 1 female), proposed by Fisher (1930), by using the goodness of fit test (chi-square) (α=0.05). The same procedure was repeated with the total number of individuals collected.

The population reproductive period was determined based on the frequency of ovigerous females, and adults of both sexes with mature gonads (considering the developing and developed stages).

RESULTS

Were collected a total of 704 crabs, 327 males (46.45%), 302 female non-ovigerous (42.90%) and 75 ovigerous females (10.65%). The CW of the males varied from 6.00 to 42.45 mm (mean ± standard deviation: 24.21 ± 7.38 mm), and the females from 5.70 to 37.60 mm (22.86 ± 5.82 mm). Data for male and female CW values exhibited a normal distribution ($P>0.05$). The CW mean value of males was significantly higher than females ($t = 2.83$;DF = 702; $p<0.05$).

The humid weight (HW) varied from 0.110 to 24.866g (5.57 ± 4.76g) for males, and from 0.038 to 15.822g (4.13 ± 2.72g) for females. The weight data of both sexes did not show a normal distribution ($p<0.05$). The males exhibited humid weight mean higher than females ($p<0.05$).

All crabs analyzed were divided into eleven CW size classes, according to the equation: $I = 1 + log_2 N$, with class interval of 3.34 mm. Males were more frequent on the class 22.41|--25.75 mm, and females on class 19.06|--22.41mm. The frequency distribution of the population into size classes was unimodal for both males and females ($p>0.05$) (Figure 3).

Figure 4A and 4B showed the males and females frequency distribution during each month of capture. Throughout the year the male frequency into size classes was unimodal (April/2005), bimodal (October/2004, December/2004) and polymodal (June/2004, July/2004, August/2004, September/2004, November/2004, January/2005, February/2005, March/2005, May/2005). The monthly female frequency into size classes was bimodal (June/2004, July/2004, August/2004, October/2004, November/2004, January/2005,

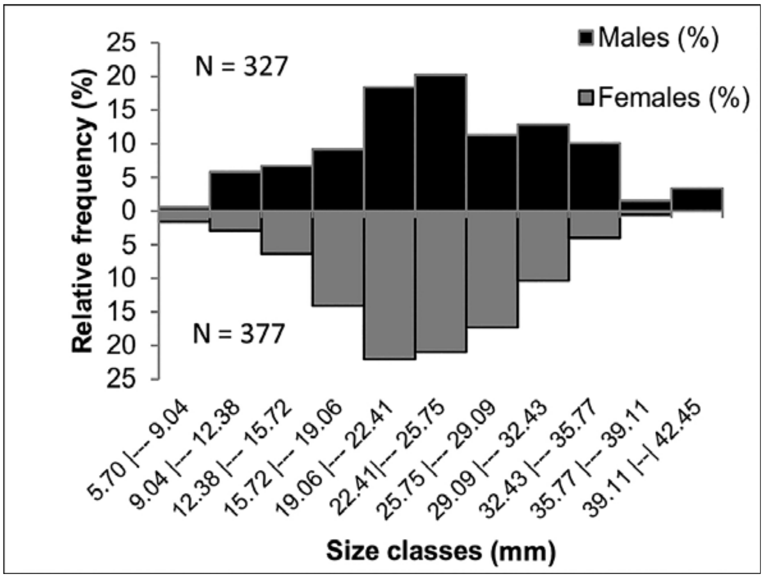

Figure 3 - Relative frequency (%) distribution in carapace width size classes (CW) of *Panopeus lacustris* collected at Coqueiro Beach, Luís Correia-PI, Brazil, from June 2004 to May 2005. N = total number of individuals.

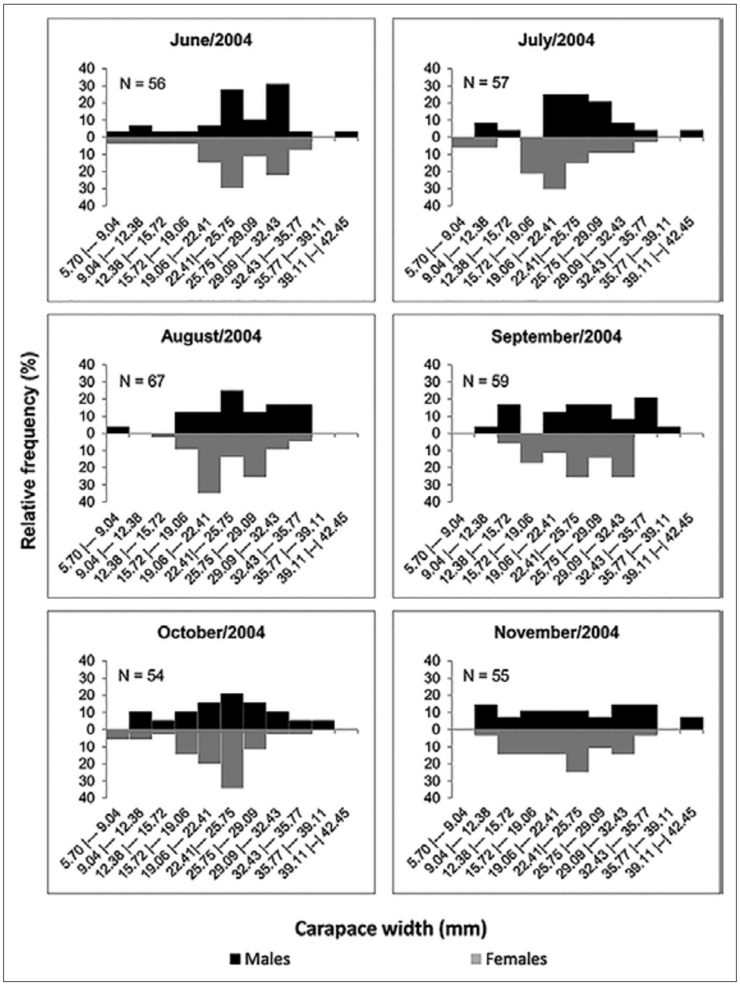

Figure 4A - Monthly distribution of the relative frequency (%) of males and females of *Panopeus lacustris* in carapace width size classes (CW), the Coqueiro Beach, Luís Correia-PI, Brazil. N = total number of individuals.

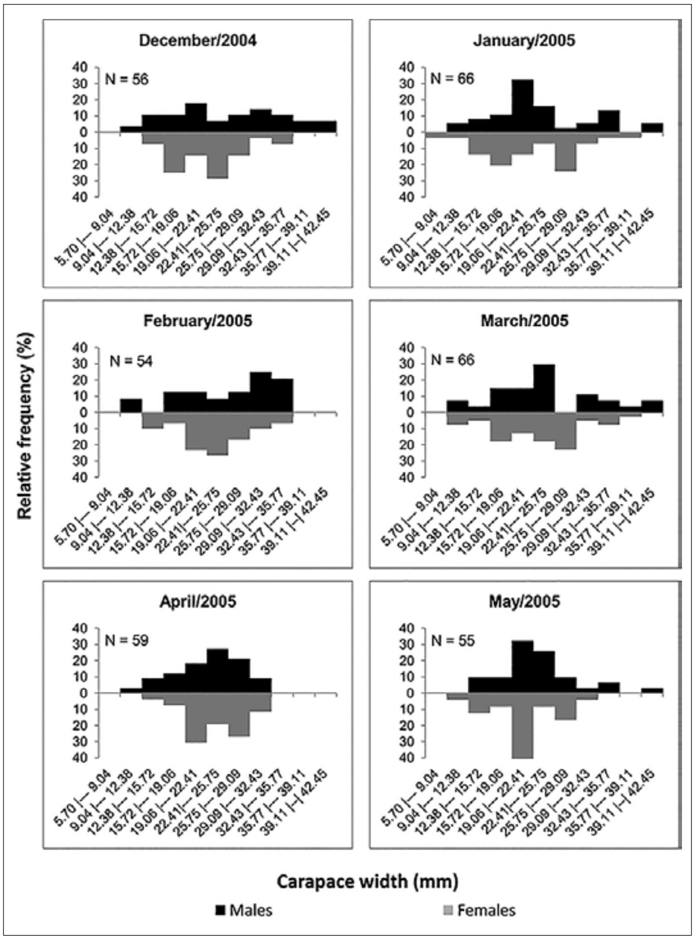

Figure 4B - Monthly distribution of the relative frequency (%) of males and females of *Panopeus lacustris* in carapace width size classes (CW), the Coqueiro Beach, Luís Correia-PI, Brazil. N = total number of individuals.

February/2005, April/2005) and polymodal (March/2004, September/2004, December/2004, May/2005).

Based on regression analysis, where male CW and PML were compared, and female CW vs. AW were compared, it was determined that the morphological sexual maturation of males is achieved with CW of 12.32 mm and females with 12.00 mm ($p<0.05$). The smallest ovigerous female found showed a CW of 16mm (figures 5 and 6).

The relative growth analysis of *Panopeus lacustris* males and females are presented in Table 1. In this analysis the morphological sexual CW was considered to separate young and adults crabs. It was verified that the males showed a positive allometry (*t*-test; $P<0.05$) on comparison between CW vs. AW (young b = 1.775), CW vs. PML (young b = 1.160), CW vs. PMW (adults b = 1.140; total of individuals b = 1.101), and CW vs. PMH (adults b = 1.145; total of individuals b = 1.091). A positive allometric relationship in females was observed for CW vs. AW (adult b = 1.300; total of individuals b = 1.204), CW vs. PMW (adults b = 1.015; total of individuals b = 1.042), and CW vs. PMH (adults b = 1.071; total of individuals b = 1.048). The weight had a positive relative

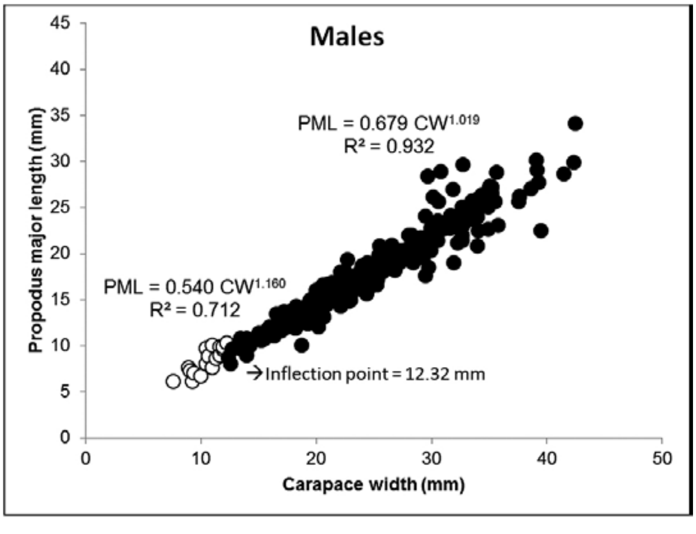

Figure 5 - Points of dispersion for the CW vs. PML of the males of *Panopeus lacustris*. White circles = juveniles; Black circles = adults; CW = Carapace width; PML = Propodus major length; R^2 = coefficient of determination.

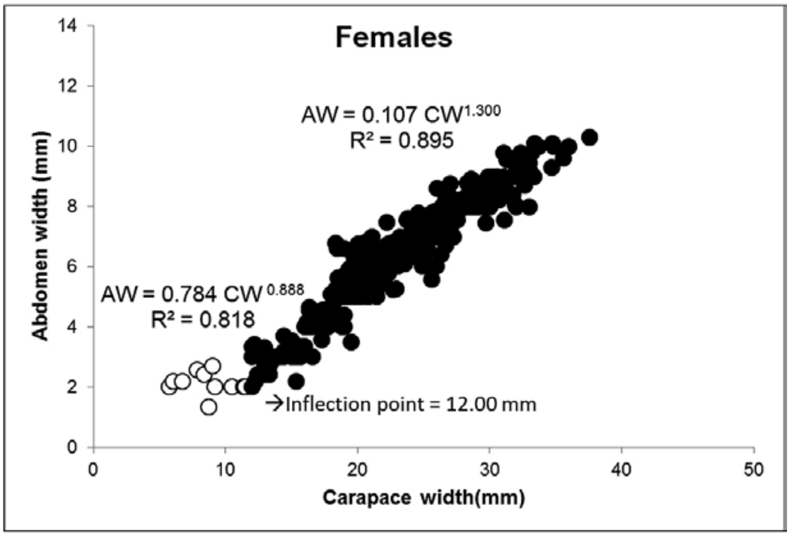

Figure 6 - Points of dispersion for the CW vs. AW of the females of *Panopeus lacustris*. White circles = juveniles; Black circles = adults; CW = Carapace width; AW = Abdomen width R² = coefficient of determination.

Table 1. Results of regressions obtained for the population of *Panopeus lacustris* of Coqueiro Beach, Luís Correia-PI, Brazil. The carapace width (CW) was used as an independent variable. Notes: M = male; F = female; A = adult; Y = young; T = total number of individuals; a and b = constant power equation; BH = body height; CL = carapace length; AW = abdomen width; PML = propodus major length; PMW = propodus major width; PMH = propodus major height; GL = gonopod length; HW = humid weight; allometry = test for slope b; R² = coefficient of determination; 0 = isometrics; - = Negative allometry; + = Positive allometry.

Relationship	Sex	N	Power equation $y = ax^b$	R²	Allometry
BH	F Y	10	$BH = 0.376\ CW^{1.055}$	0.817	0
	F A	355	$BH = 0.471\ CW^{0.964}$	0.961	-
	FT	365	$BH = 0.453\ CW^{0.976}$	0.969	-
	M Y	20	$BH = 0.470\ CW^{0.972}$	0.668	0
	M A	300	$BH = 0.402\ CW^{1.022}$	0.983	0
	M T	320	$AC = 0.426\ CW^{1.004}$	0.975	0
CL	F Y	12	$CL = 0.614\ CW^{1.055}$	0.875	0
	F A	354	$CL = 0.821\ CW^{0.946}$	0.968	-
	F T	366	$CL = 0.965\ CW^{0.968}$	0.975	-
	M Y	21	$CL = 0.694\ CW^{1.013}$	0.884	0
	M A	300	$CL = 0.787\ CW^{0.963}$	0.972	-
	M T	321	$CL = 0.776\ CW^{0.968}$	0.982	-
AW	F Y	12	$AW = 0.784\ CW^{0.888}$	0818	0
	F A	358	$AW = 0.107\ CW^{1.300}$	0.895	+
	F T	370	$AW = 0.143\ CW^{1.204}$	0.888	+
	M Y	19	$AW = 0.043\ CW^{1.775}$	0.722	+
	M A	299	$AW = 0.478\ CW^{0.805}$	0.883	-
	M T	318	$AW = 0.380\ CW^{0.877}$	0.911	-
PML	FJ	10	$PML = 1.332\ CW^{0.722}$	0.690	0
	FA	333	$PML = 0.905\ CW^{0.914}$	0.905	-
	FT	343	$PML = 0.875\ CW^{0.925}$	0.930	-
	MJ	17	$PML = 0.540\ CW^{1.160}$	0.712	+
	MA	263	$PML = 0.679\ CW^{1.019}$	0.932	0
	MT	280	$PML = 0.789\ CW^{0.973}$	0.945	0
PMW	F Y	10	$PMW = 0.220\ CW^{0.986}$	0.916	0
	F A	327	$PMW = 0.213\ CW^{1.025}$	0.855	+
	F T	337	$PMW = 0.202\ CW^{1.042}$	0.897	+
	M Y	16	$PMW = 0.199\ CW^{1.071}$	0.423	0
	M A	258	$PMW = 0.156\ CW^{1.140}$	0.914	+
	M T	274	$PMW = 0.177\ CW^{1.101}$	0.930	+
PMH	F Y	10	$PMH = 0.277\ CW^{1.134}$	0.752	0
	F A	328	$PMH = 0.296\ CW^{1.071}$	0.913	+
	F T	338	$PMH = 0.318\ CW^{1.048}$	0.929	+
	M Y	16	$PMH = 0.661\ CW^{0.769}$	0.416	0
	M A	256	$PMH = 0.245\ CW^{1.145}$	0.940	+
	M T	272	$PMH = 0.292\ CW^{1.091}$	0.949	+
GL	M Y	18	$GL = 1.843\ CW^{0.322}$	0.053	0
	M A	296	$GL = 0.644\ CW^{0.824}$	0.764	-
	M T	314	$GL = 0.540\ CW^{0.878}$	0.834	-
HW	F Y	11	$HW = 2.85x10^{-9}\ CW^{3.078}$	0.964	0
	F A	334	$HW = 8.08x10^{-9}\ CW^{2.974}$	0.976	0
	F T	345	$HW = 4.50x10^{-9}\ CW^{3.054}$	0.983	0
	M Y	21	$HW = 1.94x10^{-4}\ CW^{3.111}$	0.799	0
	M A	291	$HW = 2.34x10^{-4}\ CW^{3.071}$	0.976	+
	M T	312	$HW = 2.02x10^{-4}\ CW^{3.116}$	0.982	+

growth only for males (adults b = 3.071; total of individuals b = 3.116).

The frequency of mature males and females in relation to CW size class, were adjusted to the physiological maturation using Galton's ogive curves, which indicated that 50% of males are physiologically mature at 11.35 mm CW and females with 10.61 mm (Figure 7 and 8).

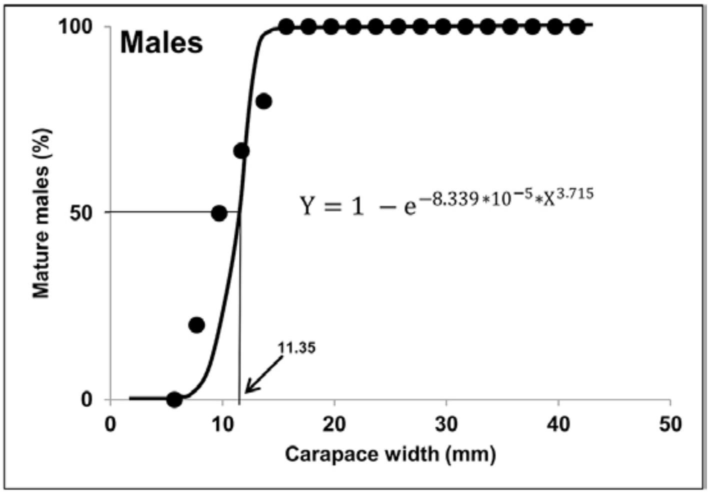

Figure 7 - Cumulative frequency of physiological maturity of males *Panopeus lacustris*.

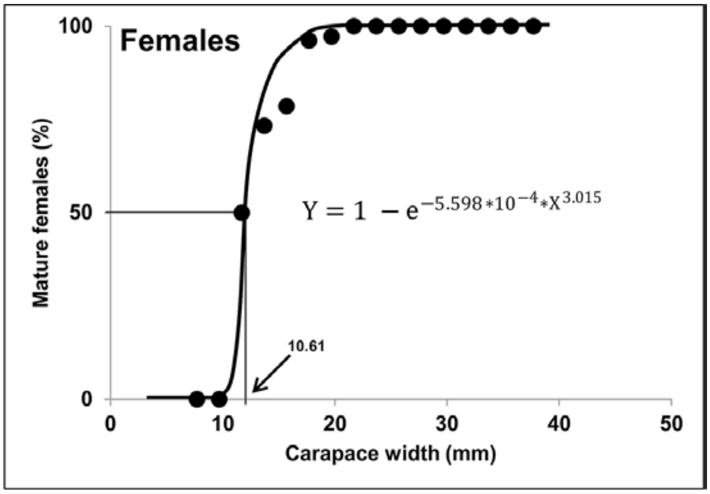

Figure 8 - Cumulative frequency of physiological maturity of females *Panopeus lacustris*.

The sex ratio of all crabs examined was 1: 1.15 (males: females), which it was statistically equal to the expected 1: 1 ratio (P>0.05). Note, in Figure 9, in four size classes LC has had significant difference in the ratio between males and females (P <0.05). Two of these class showed that females are predominant (15.72|--19,06 and 25.75|--29.09), and on other classes males are predominant (32.43|--35.77 and 39.11|--|42.45). The last class analyzed showed a population of 100% males. The analysis of sex ratio in relation to the months of capture demonstrated that females were significantly more numerous than males (P<0.05) in August and October of 2004 (Figure 10).

Ovigerous females were observed in every month of collection (Figure 11) with a lower frequency between the months of November/2004 and February/2005.

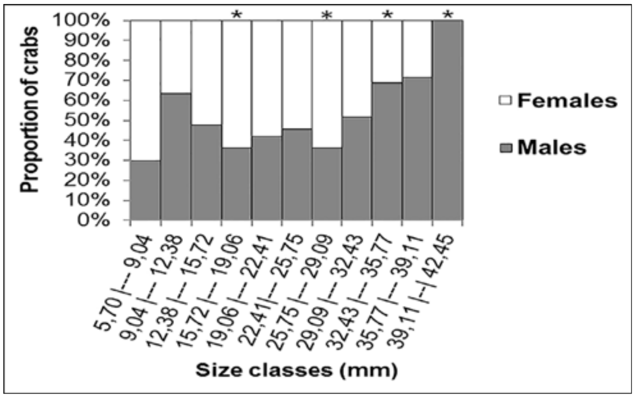

Figure 9 - Sex ratio of *Panopeus lacustris* by carapace width size class (mm). (*) Significant difference between the proportions of males and females (chi-square: P<0.05).

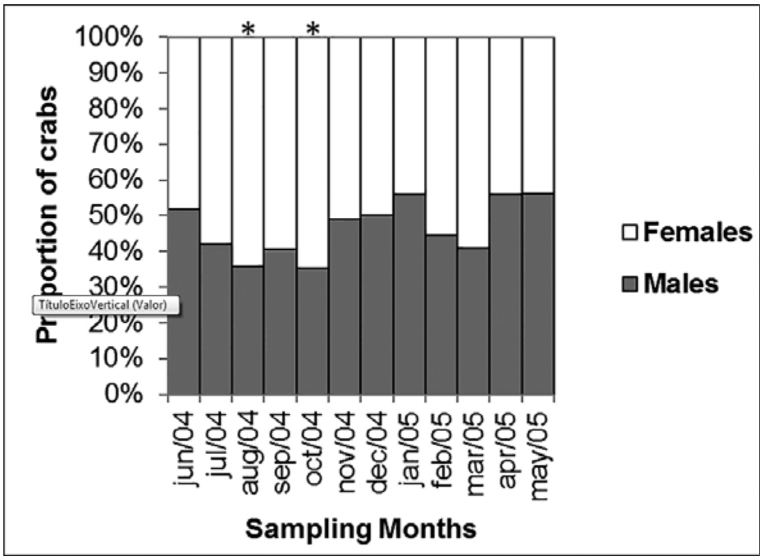

Figure 10 - Monthly Sex ratio of *Panopeus lacustris*. (*) Significant difference between the proportions of males and females (chi-square: P<0.05).

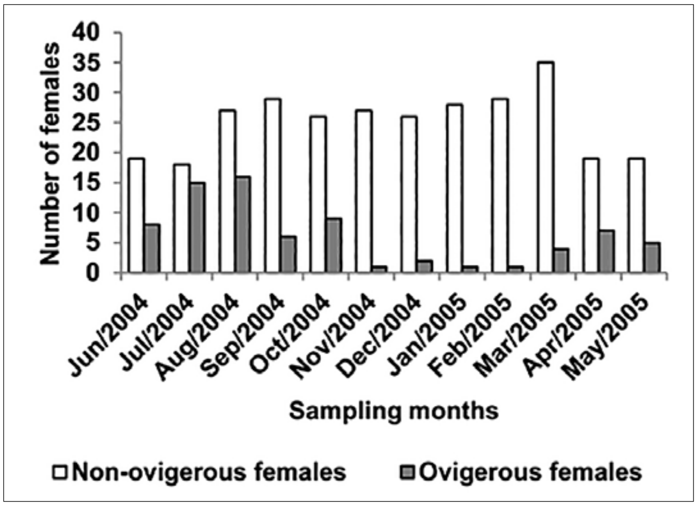

Figure 11 - Monthly distribution of the ovigerous and non-ovigerous females of *Panopeus lacustris* on the Coqueiro beach, Luís Correia-PI, Brazil.

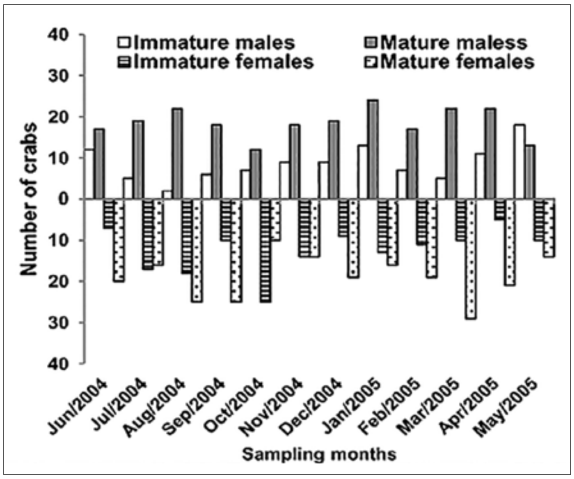

Figure 12 - Monthly distribution of mature and immature individuals *Panopeus lacustris*, on the Coqueiro beach, Luís Correia-PI, Brazil.

Mature females and males (with developing or developed gonads) were also observed in every month of sampling (Figure 12). Only in July and October of 2004, the number of mature females was lower than immature ones. The number of mature males was lower only in May 2005.

DISCUSSION

According to Hartnoll (1985), the differential growth between sexes after the pubertal moult, where males show more significant development in size than females, is a result of the metabolic energy that males use for the somatic growth, while females direct this energy to the production of oocytes. Therefore, males reach larger sizes than females. After reaching sexual maturity, females direct its energy resources to reproduction and release of eggs, resulting in less investment to the growth process of females compared to males (Mokhtari *et al.*, 2008; Tudesco *et al.*, 2012). According Stearns (1989) the growth and reproductive processes are mediated by hormones, and can occur simultaneously. However the patterns of this trade-off may vary depending on the concentration of hormones and the sensitivity of the different cell types to the hormones.

The fact that males of the species *P. lacustris* reach higher CW size than females, showing sexual dimorphism, can also be reflected on their weight pattern, once this is directly proportional to the size of the animals. *Hepatus pudibundus* (Mantelatto & Fransozo, 1994) and *Dilocarcinus pagei* (Pinheiro & Taddei, 2005) have showed the same pattern of sexual dimorphism relative to the weight. The authors reinforce the hypotheses that the lowest weight presented by females is due to directing nutrients to reproductive metabolism and gonad maturation, after they reaching their sexual maturity. The biological significance of the largest weight recorded in males may be the result of selection pressure in the reproductive context; larger males are more likely to have offspring than smaller males, as they have advantages on the defense of territory, manipulation of females and mating. (Mantelatto & Fransozo, 1994; Botelho *et al.*, 1999).

The size class distribution of population individuals is a dynamic characteristic that can vary throughout the year as a result of rapid reproduction and recruitment of larvae and juveniles, and also because of individual deaths (Thurman, 1985). The unimodal distribution observed in the population of *Panopeus lacustris* is a common feature for tropical decapod (Castiglioni *et al.*, 2011; Oliveira *et al.*, 2013). The unimodality is considered characteristic of a stable population, that show continuous recruitment and constant mortality rates throughout the life cycle (Castiglioni *et al.*, 2011; Araújo *et al.*, 2012). According to Díaz & Conde (1989) and Litulo (2005b) the bimodality or polymodality of the distribution of crabs size frequency generally reflects recruitment pulses, differential or catastrophic mortality, what was seen in some months sampling in the population of *P. lacustris* in this study**.**

Data distribution of population size of *P. lacustris*, with a predominance of males in the last class size, and difference in male growth pattern relative to females, can reinforce the hypotheses of energy allocation for reproductive purposes by females (Díaz & Conde, 1989).

Litulo (2005a) considered that in populations of *Uca annulipes* in East Africa mangrove, size frequency distributions presenting unimodal and bimodal distribution throughout the study period, may indicate the existence of two different age groups in the population studied. Therefore, monthly distributions of *P. lacustris* presenting unimodal, bimodal and polymodal structure, may suggest the existence of several age groups in the study area.

Generally, when two dimensions of the shell are correlated in Brachyura (such as CW vs. CL), there are no clear changes during ontogeny, because growth tends to be isometric (Hartnoll, 1985), as observed in *Arenaeus cribrarius* (Pinheiro & Fransozo, 1993), *Eriphia gonagra* (Góes & Fransozo, 1997), and *Sesarma rectum* (Silva *et al.*, 2007). In *Mithrax tortugae* (Cobo & Alves, 2009) and *Uca thayeri* (Araújo *et al.*, 2012) there were also no variations during ontogeny. However, the presented pattern and allometric growth was negative. In *Hexapanopeus schmitti*, as verified by Fumis *et al.* (2007), there was differential growth between the juvenile and adult stages of both sexes. Similarly, in this study, *Panopeus lacustris* showed growth differences between youth and adulthood, comparing CW vs. CL in both sexes.

The comparison between CW vs. BH showed difference in growth rate between immature and mature females. In males the standard for all ontogenesis was isometric. The differential growth between juvenile and adult stages is probably related to the accommodation of the gonads, due to its development, after sexual maturity (Fumis *et al.*, 2007). Therefore, it is suggested that the changes observed in *P. lacustris* in the CL growth rate in both sexes, and BH of females, are reflex adaptations to accommodate gonadal mass after sexual maturity. Benetti & Negreiros-Fransozo (2004) also consider that differences in the growth process related to puberty molt can be evidenced in the dimensions of the carapace as a result of the development of the gonads.

In adult crabs, the male abdomen is narrow, triangular or in "T" shape, while the female abdomen is broad and round covering most of the thoracic sternum (Yeo *et al.*, 2008). The main function of the abdomen in females is related to the protection and incubation of eggs (Cobo & Fransozo, 1998; Masunari & Swiech-Ayoub, 2003). The abdomen and the sternum form an enclosed cavity that facilitates egg attachment and protection during incubation. According Hartnoll (1982), immature females showed positive allometric growth in the abdomen compared to the width of the carapace, and the allometry degree decreases after pubertal molt. In the present study, this growth pattern has not been registered (young: isometrics; adults: positive allometry). Unlike males, females have four pairs of pleopods that need to grow during maturity phase to hold the eggs (Masunari & Swiech-Ayoub, 2003; Freire *et al.*, 2011). Therefore, it can be suggested that the positive allometry observed in mature *P. lacustris* females, can be associated with the pleopod growth needed for the attachment of the eggs.

The male abdomen slightly changed during the immature and mature stages, and usually has isometric growth (Hartnoll, 1982). Almeida *et al.* (2013) studied three species of the genus *Persephona* and observed that male's abdomen growth ranged between isometric and negative allometric during the immature and mature stages. There was a reduction in growth rate between immature and mature stages. Likewise, the AW of the males had a decrease in growth rate after maturity (positive allometric in young and negative allometry in adults).

Isometry has been observed in the length of the major cheliped of the adult males, along with the positive allometric height and width. These observations suggest that the growth of this structure is not proportional, since it is not too long, but it is thick and robust (the cheliped grows more slowly in length in relation to its height and width). The negative allometric observed in the length of the major cheliped of adult females, with the positive height and width allometry, may indicate that this structure grows similarly to the cheliped of the males, but smaller in length.

The brachyurans growth is generally similar between genders until maturity, when it becomes slower in females due to an extension of the intermoult period, induced by the production and incubation of the eggs (Hartnoll, 1985). This is related to the fact that the length of the greater cheliped of *P. lacustris* females grows to a lesser extent compared to males. This growth pattern was observed by Hartnoll (1982) in Crustacea Brachyura, which show mildly allometric in the juvenile phase and strongly allometric in adulthood, in both males and females.

The use of chelipeds can also determine hierarchical dominance in adult males. Hence, in juvenile of *P. lacustris* allometric growth is observed in smaller proportions compared to adults. These appendices are used in the adult stage to territorial defense, combat, display or control over the female, protecting it before, during and after copulation (Castiglioni *et al.*, 2006; Fumis *et al.*, 2007). This fact reinforces the largest growing of the length of the major cheliped of adult male.

The growth of gonopodium showed isometry in the juvenile phase and negative allometry after sexual maturity. In *Eriphia gonagra* (Góes & Fransozo, 1997), *Uca rapax* (Castiglioni & Negreiros-Fransozo, 2004), *Mithrax tortugae* (Cobo & Alves, 2009), *Uca mordax* (Fransozo *et al.*, 2009), *Uca thayeri* (Araújo *et al.*, 2012), juvenile also showed allometric growth in a higher proportion as compared to adults. The greater growth in the juvenile phase, observed in *P. lacustris*, may reflect the need for pre-adults to reach sexual maturity, to change the size of characters that allow mating (Fonteles-Filho, 2011).

Positive allometry verified by CW and HW comparison in male of the species may indicate that the biomass gain increases along the maturity of the animal. This fact can be explained by a greater investment in somatic growth by males (Masunari *et al.*, 2005; Hartnoll, 2006). In females, the isometric relation between CW and HW indicates proportional increase of these variables with the development of the individual. Females direct many of the reserved energy accumulated in the hepatopancreas to the gonad development and supply of egg mass during the laying period (Díaz & Conde, 1989), which can probably explain the difference in weight growth between the sexes.

The smallest ovigerous female collected showed 16 mm of CW, and contributed to validate the size of morphological sexual maturity determined for females. Differences between sexes in the size of sexual maturity are common and often found in Brachyura (Fumis *et al.*, 2007), which can be considered as a consequence of alteration in male growth rate (Benetti & Negreiros-Fransozo, 2004). The positive allometric growth registered for some dimensions could be related to its biological significance, especially in terms of reproductive activity.

In *P. lacustris* species, morphological and physiological sexual maturity are not synchronously occurring. According to Hartnoll (1978 and 1982), some morphological changes can be observed in the beginning of sexual maturity, such as the variations occurring in male chelipeds and in the abdomen of females. These changes may or may not occur synchronously with the maturation of the gonads (Hartnoll, 1982; Sastry, 1983). The synchrony between the physiological and morphological maturity is a reproductive strategy that can provide more adults able to copulate, optimizing the reproductive effort of the population (Cobo & Fransozo, 2005). However, the morphological maturity not always coincides with the gonadal maturity of individuals. Some Brachyura can display external adult characteristics but without mature gonads or vice versa (Sastry, 1983). This could be occurring in *P. lacustris* crabs, since the males presented their mature gonads with 11.35 mm of CW and displayed external morphologic features that characterize them as mature individuals with 12.32 mm. Females have also demonstrated the same pattern, gonads maturation with 10.61 mm of CW, and sexual morphologic maturity reached later with 12.00 mm of CW.

The proportion of males and females in the population is a feature that reflects the balance of this population (Silva *et al.,* 2007). However, during ontogenesis, a number of factors can affect this relation, leading to widespread of only one sex (Leigh, 1970). Johnson (2003) showed that the sex ratio is strongly influenced by species, period of year, use and location of the habitat. The same author suggests that local factors such as food supply and predation level are probably the main determinants of changes in the sex ratio of the adult population. Bedê *et al.* (2008) affirmed that differences in the sex ratio in some size classes may occur as a result of greater or lesser difficulty in capturing individuals due to behavioral factors of the species.

Sex ratio different of 1:1 is widespread among crustaceans, which may be the result of differences in their life cycle, migration, differential mortality between males and females, increased mobility of males causing greater dispersion, growth rate, sex reversal and behavioral differences (Leite *et al.,* 2003). Deviations in the ratio 1: 1 can directly affect the reproduction of the population and its size (Díaz & Conde, 1989).

Seed (1980) studied a population of *Panopeus herbstii* and observed that the sex ratio for the species was 1:0.70 (males:females), with a predominance of males over females. Unlike this species, the population of *P. lacustris* of this study follows the ratio of 1:1, showing stable during most months of capture and most of the size classes.

The classes on the edges, represented by only one sex, may indicate growth rate differentiated between sexes, differences in recruitment rates and mortality (Shinozaki-Mendes *et al.*, 2013). Our results suggested that there are no distinctions in recruitment rates and mortality of the species *P. lacustris* because only the last size class is represented by a single sex, and in the other classes there is a prevalence of both sexes.

The reproductive frequency has been studied in several species of Brachyura, with species with females reproducing throughout the year, others with reproduction occurring in each one in one or more seasons, and still others in which the reproductive period occurs every two years in one season, so that all these patterns correlate with favorable local environmental conditions (Negreiros-Fransozo *et al.*, 2002; Gebauer *et al.*, 2007). The pattern of continuous reproduction can be commonly observed in Brachyura crabs of tropical and subtropical regions (Costa & Negreiros-Fransozo, 1998; Litulo, 2006). Some species of tropical and subtropical crabs have continuous reproduction, such as: *Aratus pisonii* (Warner, 1967; Díaz & Conde, 1989), *Hepatus pudibundus* (Reigada & Negreiros-Fransozo, 2000), *Goniopsis cruentata* (Silva & Oshiro, 2002), *Sesarma rectum* (Castiglioni *et al.,* 2011), among others.

The species that live in tropical environments reproduce continuously due to the relatively stable environmental conditions of temperature and food (Gebauer *et al.*, 2007). According to Wenner *et al.* (1974), tropical crustaceans have continuous reproduction due to the constant water temperatures, enabling reproduction throughout the year.

Araújo *et al.* (2011), found in a population of *Callinectes danae*, that the presence of adult males and females in all months of the year, and ovigerous females in almost all of them indicated that the reproductive activity occurred continuously. Males and females of *P. lacustris* also presented reproductive activity throughout the study period, therefore, it is suggested that the species reproduces continuously in Coqueiro beach, Piauí, Brazil.

Rodríguez *et al.* (1997) observed that the crab *Panopeus africanus*, has pattern of seasonal reproduction with females presenting gonads developed in the spring. Unlike, the females and males of *P. lacustris* showed developed gonads during the whole study period, which can also indicates a continuous reproduction.

CONCLUSIONS

In this study, it was observed that the crab *Panopeus lacustris* from Coqueiro beach, Luís Correia-PI, Brazil, presents sexual dimorphism on the carapace width and weight. This population showed environmental stability, which is reflected in its frequency distribution in size classes and sex ratio.

The continuous reproduction contributes to characterize the environment as appropriate for the reproductive development of the species, which follows the usual patterns of tropical crustaceans.

The chelipeds of males as well as the abdomen of females are crucial in the reproductive process of the species, and also the different growth rates shown in the other dimensions, which are most evident after puberty molt.

Overall, the results showed that the Coqueiro Beach (Piauí, Brazil) provides a favorable environment for colonization of *P. lacustris.*

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