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Research Article

Population biology and morphometric sexual maturity of the fiddler crab *Uca* (*Uca*) *maracoani* (Latreille, 1802) (Crustacea: Decapoda: Ocypodidae) in a semi-arid tropical estuary of northeastern Brazil

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ABSTRACT. The population biology and size at sexual maturity of *Uca* (*Uca*) *maracoani* were studied for the first time in a semi-arid tropical estuary of northeastern Brazil. A catch-per-unit-effort (CPUE) technique was used to sample the crabs, on the surface and inside burrows, for 60-min sampling periods by one person on a monthly basis during spring low tide periods from June 2013 to June 2014 in an estuary area of Baixa Grande Beach. A total of 406 crabs were obtained, of which 317 were males, 87 non-ovigerous females, and two ovigerous females. Males were larger than non-ovigerous females. The *U.* (*U.*) *maracoani* population presented unimodal size frequency distribution, which may reflect a continuous recruitment, with no disruption of classes and constant mortality rates, indicating a stable population. The overall sex ratio (3.5 males: 1 female) differed significantly from the expected 1:1 proportion. The major cheliped was on the right side in 45.1% of the males, as reported for other fiddler crabs populations. A total of 294 males and 89 females were used in the allometric study. The specimens were measured at carapace width (CW), the major propodus length (MPL) of males, and abdomen width (AW) of females. In males, the relationship between CW and MPL was 22.3 mm CW, which is considered the functional value at maturity. In females, the size at sexual maturity was 19.3 mm CW based on the relationship between CW and AW. The CPUE method is discussed as one of the reasons of the high sex ratio skewed towards males. This is the first account regarding population structure of *U.* (*U.*) *maracoani* in semi-arid tropical areas.

Keywords: *Uca* (*Uca*) *maracoani*, population structure, sex ratio, sexual maturity, CPUE technique.

Estructura poblacional y madurez sexual del cangrejo *Uca* (*Uca*) *maracoani* (Latreille, 1802) (Crustacea: Decapoda: Ocypodidae) en un manglar semiárido tropical en el noreste de Brasil

RESUMEN. La estructura poblacional y la madurez sexual morfométrica del cangrejo *Uca* (*Uca*) *maracoani* fueron estudiadas en un manglar tropical en el noreste de Brasil. Los cangrejos fueron colectados mensualmente durante los periodos de marea baja de junio 2013 a junio 2014. Se utilizó la técnica de captura por unidad de esfuerzo (CPUE) con períodos de una hora de captura realizada por una persona. Se obtuvo un total de 406 cangrejos: 317 machos, 87 hembras no-ovígeras y dos hembras ovígeras. El tamaño de los machos fue significativamente mayor que el de las hembras no-ovígeras. La población mostró una distribución unimodal de frecuencias de tamaños, lo que puede reflejar un reclutamiento continuo, sin interrupción de las clases y las tasas de mortalidad constantes, lo que indica una población estable. La proporción sexual (3.5 machos: 1 hembras) se alejó significativamente de la proporción esperada 1:1. El quelípodo mayor estaba en el lado derecho en el 45,1% de los machos, según lo informado por otras poblaciones. Se realizaron mediciones del ancho del caparazón

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(CW) y longitud del propodio mayor (MPL) de 294 machos, y del ancho del caparazón (CW) y ancho del abdomen (AW) de 89 hembras. En los machos, el punto de inflexión se determinó en 22,3 mm CW, considerado el tamaño morfológico al inicio de la madurez. En las hembras, el tamaño de madurez sexual fue de 19,3 mm CW basado en la relación entre CW y AW. El método CPUE se discute como una de las razones que explican el elevada proporción sexual sesgada hacia los machos. Este es el primer estudio relacionado con la estructura poblacional de *U.* (*U.*) *maracoani* en zonas semiáridas tropicales.

Palabras clave: *Uca* (*Uca*) *maracoani*, biología poblacional, proporción sexual, madurez sexual, técnica de CPUE.

INTRODUCTION

Fiddler crabs, species of *Uca* Leach, 1814, are one of the most familiar and abundant inhabitants of mangrove forests and estuaries in the tropical, subtropical and temperate areas of the world (Crane, 1975; Thurman *et al.*, 2013). They are characterized by a great sexual dimorphism in chelae size. The males develop their chelae into a major claw that is used in ritualized agonistic interaction and in mate attraction, while females have small isomorphic claws (Crane, 1975). The presence of the larger claw has been shown to be energetically unfavorable and males exhibit roughly 17% higher metabolic rates than females (Matsumasa & Murai, 2004).

These crabs excavate burrows in the substrate to protect themselves from predators and harsh environmental conditions, and for physiological needs. Burrows are also sites for molting, courtship, and reproduction (Crane, 1975; Genoni, 1991). This burrowing behavior, together with the foraging activities, improves the aeration of the substrate, increases the decomposition rate of plant debris within sediments and enhances the growth of micro-organisms in the substrate (Genoni, 1985; Colpo & Negreiros-Fransozo, 2004; Lim & Heng, 2007). Moreover, fiddler crabs are an important link to higher trophic levels in intertidal and shallow-water food webs (Koch *et al*., 2005).

Several studies regarding population and reproduction and allometric growth of *Uca* spp. have been conducted in recent years, revealing information on density, size frequency distribution, sex ratio, handedness, reproductive period, fecundity and size at sexual maturity, especially along the coast of Brazil (for a review, see Ribeiro & Bezerra, 2014). Some studies related to spatial distribution, handedness, behavioral, systematics, phylogenetic or growth of *U.* (*U.*) *maracoani* are known to date (Crane, 1958, 1975; Rosenberg, 2001; Masunari *et al.*, 2005; Bezerra *et al.*, 2006; Hirose & Negreiros-Fransozo, 2007; Thurman *et al.*, 2013). However, although it is a large and common species, there are only three known studies on its population and reproductive aspects, one in the Amazon region (Koch *et al*., 2005) and two of which were conducted in the subtropical coast of southeastern Brazil by Hirose & Negreiros-Fransozo (2008) and by Benedetto & Masunari (2009).

Around 97 species of fiddler crabs are currently known worldwide (Beinlich & Von Hagen, 2006; Landstofer & Schubart, 2009; Shih *et al.,* 2009, 2010; Naderloo *et al.*, 2010). In Brazil, ten species comprising three subgenera (*Uca*, *Minuca* and *Leptuca*) are known to inhabit estuaries and mangrove forests along the coast (Bezerra, 2012). *Uca* (*Uca*) *maracoani* (Latreille, 1802; Ocypodidae) is the only species of the subgenus *Uca* that lives in the coast of South America, occurring from Venezuela to southern Brazil (State of Paraná) (Bezerra, 2012). It lives near the mouths of rivers, in open mudflats without vegetation, in very soft silt, sandy silt or mud with a high content of organic matter, and in meso or euryhaline salinities (Bezerra *et al.*, 2006; Thurman *et al.,* 2013).

Only one study has been published on the population structure of *U.* (*U.*) *maracoani* in tropical areas (Koch *et al*., 2005). Few studies have been conducted on the tropical fiddler crab population (Litulo, 2005a, 2005b; Bezerra & Matthews-Cascon, 2006, 2007; Castiglioni *et al*., 2010; Araujo *et al*., 2012; Farias *et al*., 2014). Comparisons can be an important strategy to verify differences between these populations, and to understand the environment and biological constraints that are shaping them (Oshiro, 1999; Litulo, 2005b).

Thus, this study analyses abundance, size structure, sex ratio, handedness, and size at sexual maturity of *U.* (*U.*) *maracoani* in a tropical estuary of northeastern Brazil.

MATERIALS AND METHODS

Site description and sampling technique

The fieldwork was conducted at the Baixa Grande Estuary, State of Rio Grande do Norte, northeast of Brazil (4°55’90”S, 37°04’51”W) (Fig. 1). The climate is tropical with a maximum temperature of 35°C and minimum of 22°C, with an average yearly temperature of 28ºC. The rainy season is concentrated within a few months of the year (February to June) with an annual

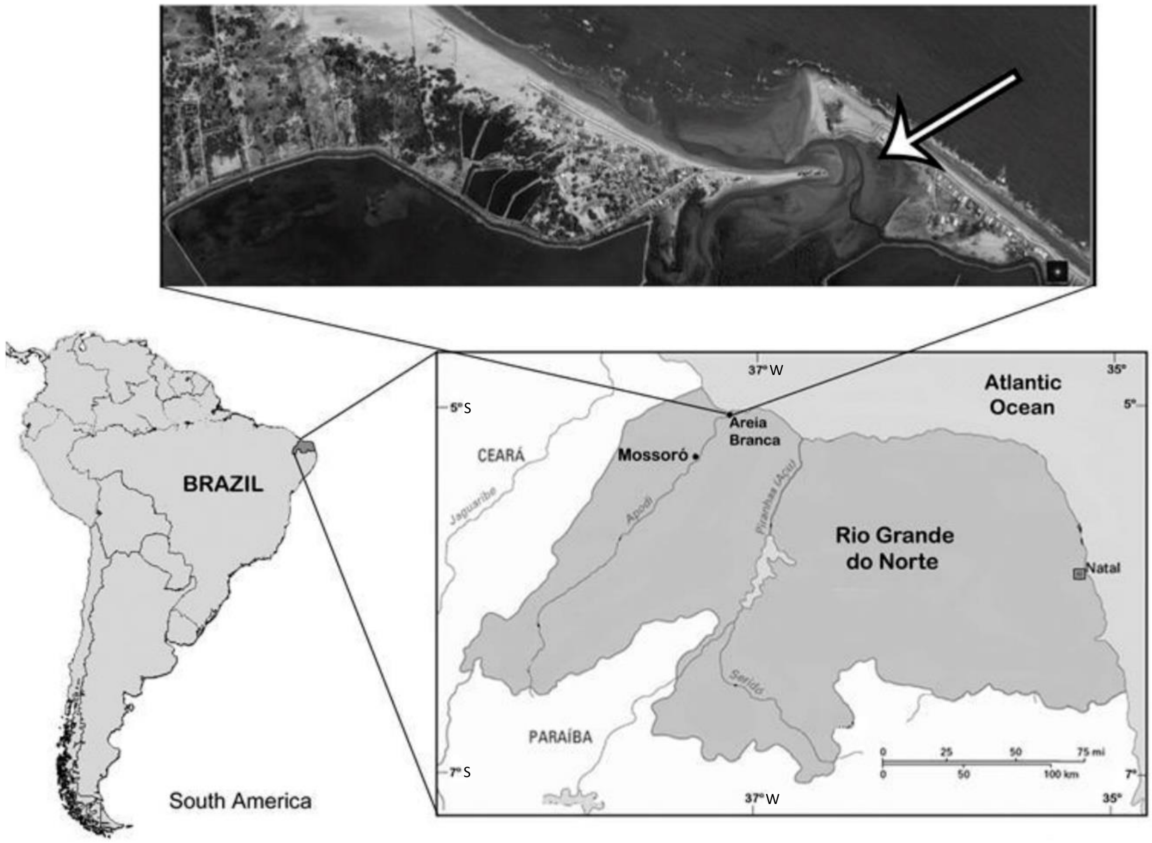

Figure 1. Map indicating the sampling area (arrow) at the Baixa Grande Estuary, northeast Brazil.

average rainfall of 600-1000 mm. Tides are semidiurnal with maximum tidal amplitude of about 3.1 m and a minimum of 0.9 m. This portion of the littoral of State of Rio Grande do Norte is known as "white coast" due to the salt production, which is the biggest salt production in Brazil. Estuaries in this region are hypersaline, due to the construction of tanks to keep the sea water to obtain salt by evaporation (EMPARN). Specimens of *U.* (*U.*) *maracoani* were present in open mud flats exposed during spring low tides.

Monthly sampling (CPUE, 1 person for 1 hour) took place during spring low-tide periods from June 2013 through June 2014, within a sampling area of approximately 450 m^2, which is the total area of occurrence of *U.* (*U.*) *maracoani* in the estuary. Specimens were obtained manually, some exposed on the surface of substrate, and others captured by digging until approximately a depth of 30 cm. All fiddler crabs were bagged, labeled and preserved in 70% ethanol until further analysis.

The pluviometric indices from June 2013 to June 2014 were gathered by the Empresa de Pesquisa Agripecuária do Rio Grande do Norte (EMPARN).

Laboratory analysis

In the laboratory, specimens were identified and sexed. Female pleopods were checked for the presence of eggs and cheliped handedness for each male was registered. The carapace width (CW), the major cheliped propodus length (MPL) of males, and in the case of females, the abdomen width (AW) (measured between the fourth and fifth somites) were measured using a digital vernier caliper (±0.05 mm accuracy). Crabs with damaged carapace or incomplete chelipeds were not considered in the analyses.

The population size structure was analyzed to determine the size frequency distribution of all individuals collected during the study period. Specimens were grouped in 2-mm size classes, from 12.0 to 38.0 mm CW.

The morphometric relationships CW/MPL for males and CW/AW for females were tested to estimate the size at sexual maturity, based in changes of these structures. The carapace width (CW) was used as the independent variable *x*, because this is the most representative dimension of the overall size of crustaceans, according to Hartnoll (1982). The choice of dependent variables MPL and AW was based on the importance of these structures to reproductive process in males and females respectively (Hartnoll, 1982).

Statistical procedures

We used a Chi-square test for goodness of fit (χ^2; α = 0.05) to test for significant deviation from the hypothesized 1:1 ratio, Fisher's test (*z*) to evaluate the sex ratio in each month, and Kolmogorov-Smirnov (KS) test for normality of overall size-frequency distributions (α = 0.05; Zar, 2010), and the mean sizes of males and ovigerous and non-ovigerous females were compared using Student's *t*-test (α = 0.05).

Aiming to investigate allometry occurrence, between morphometric variables, their values were logarithmized (log y = log a + b log x). The function $y = a\,x^b$, where *x* is the independent variable (CW), *y* is the dependent variable, *a* is the intercept (value of *y* when *x* = 0), and *b* the slope of the regression line, was adjusted to the empirical points. The *b* value indicates the growth patterns of the analyzed variables, considering three possibilities: *b* = 1 (isometry), *b* < 1 (negative allometry), *b* > 1 (positive allometry) (Hartnoll, 1982).

To determine the juveniles and adults groups, a K-means clustering analysis was performed accor-ding to Sampedro *et al*. (1999). Log-transformed biometric data is used in multivariate analysis of K-means clustering, followed by a bivariate discriminant analysis. After the separation of groups, each category was divided into size classes of 1.5 mm of CW and the proportion of juveniles and adults were calculated in each class, with the proportion of adults being fitted with a logistic equation [$y = a/(1 + be^{-cx})$] according to Vazzoler (1996). After this, data was interpolated to estimate the $CW_{50\%}$, the size at which 50% of individuals were already matures and adults.

The statistical significance of *b* was tested by Student's *t*-test. The slopes and the intercept of the regression lines among juveniles and adults were compared by an analysis of covariance (ANCOVA) of $\log_{10}$-transformed data (α = 0.05) (Zar, 2010).

RESULTS

Population structure

During the study period, it was sampled a total of 406 crabs, being 317 males (78.1%), 87 non-ovigerous females (21.4%) and 2 ovigerous females (0.5%) (Table 1). The mean size of CW of males was 27.1 ± 5.47 mm (mean ± SD), ranging from 12.4 to 38.0 mm CW. The CW of non-ovigerous females ranged from 15.7 to 36.7 mm CW (23.4 ± 4.2 mm). The two specimens of ovigerous females collected in August 2013 and in November 2013 were 24.2 and 30.9 mm CW, respectively. Males were significantly larger than non-ovigerous females (t = 6.6352; P < 0.0001). Due to the small number of ovigerous females collected, it was not possible make comparisons. Figure 2 shows the mean size of all sampled crabs.

The yearly size frequency distributions for males and ovigerous and non-ovigerous females during the sampling period are in Figures 3a and 3b, respectively. There was a conspicuous size distribution, with a unimodal, normal distribution for males (KS = 0.0767, P > 0.01) and a unimodal, non-normal distribution for females (KS = 0.2632; P < 0.01). Males were more abundant in the mid to largest size classes (24-26 mm, 26-28 mm, 28-30 mm, 32-34 mm) while females were more abundant in the smallest size classes (18-20 mm, 20-22 mm, 22-24 mm, 24-26 mm).

The number of crabs sampled monthly throughout the year is listed in Table 1. The overall sex ratio was 3.56 (number of male: number of female), which differs significantly from the expected 1:1 proportion (χ^2 = 129.6; P < 0.0001). Monthly sex ratio was skewed towards males in all months sampled (Table 1). The proportion of males with the right-handed (143 individuals) or left-handed (174 individuals) chelae hypertrophied did not differ significantly from the expected 1:1 proportion (1:0.82; χ^2 = 3.032; P < 0.0001). Furthermore, no adult male with either two giant chelipeds or two small chelipeds was collected (Table 1).

Sexual maturity

Three hundred and eighty three fiddler crabs, being 294 males and 89 females, were intact enough to be used for data acquisition for allometric analyses. In males, the size of $CW_{50\%}$ at morphological sexual maturity was estimated at 22.3 mm (Fig. 4a), with the smaller adult with 21.7 mm and largest juvenile with 23.6 mm (Fig. 5a).

Regarding females, the size of $CW_{50\%}$ at morphological sexual maturity was estimated at 19.3 mm CW (F = 1500.6496; P < 0.05) (Fig. 4b), with the smaller adult with 20.3 mm and largest juvenile with 19.9 mm (Fig. 5b).

Relative growth of the *U.* (*U.*) *maracoani* showed a positive allometry in males to the dimension MPL (Fig. 5a). In females, the positive allometric growth was observed only for the abdominal width in juveniles (Fig. 5b) (Table 2). The lines of relative growth between juveniles and adults showed significant statistical differences in males (F = 10.7199; P < 0.05) and females (F = 1500.6496; P < 0.05).

Table 1. Total number, handedness and sex ratio of *Uca* (*Uca*) *maracoani* collected monthly at Baixa Grande Estuary, northeast Brazil. *Significant deviations from the 1:1 proportion to sex ratio (χ^2, $P < 0.0001$).

Months	Males					Non-ovigerous females		Ovigerous females		Proportion
	Right-handed (a)	Left-handed (b)	Total (a+b)	%	Proportion (b/a)	Total (c)	%	Total (d)	%	M:F (a+b/c+d)
June/13	11	18	29	90.6	1:0.61	3	9.4	-	-	9.67:1*
July/13	8	10	18	66.7	1:0.80	9	33.3	-	-	2:1*
August/13	6	17	23	82.1	1:0.35	4	14.3	1	3.6	4.6:1*
September/13	8	17	25	83.3	1:0.47	5	16.6	-	-	5:1*
October/13	12	14	26	81.3	1:0.86	6	18.8	-	-	4.33:1*
November/13	12	9	21	72.5	1:1.33	7	24.1	1	3.4	2.6:1*
December/13	15	11	26	72.2	1:1.36	10	27.8	-	-	2.6:1*
January/14	10	13	23	65.7	1:0.77	12	34.3	-	-	1.91:1*
February/14	9	16	25	83.3	1:0.56	5	16.7	-	-	5:1*
March/14	8	13	21	70.0	1:0.62	9	30.0	-	-	2.33:1*
April/14	16	15	31	88.6	1:1.07	4	11.4	-	-	7.75:1*
May/14	14	11	25	83.3	1:1.27	5	16.7	-	-	5:1*
June/14	14	10	24	80.0	1:1.40	6	20.0	-	-	4:1*
Total	143	174	317	78.1	1:0.82	87	21.4	2	0.5	3.56:1*

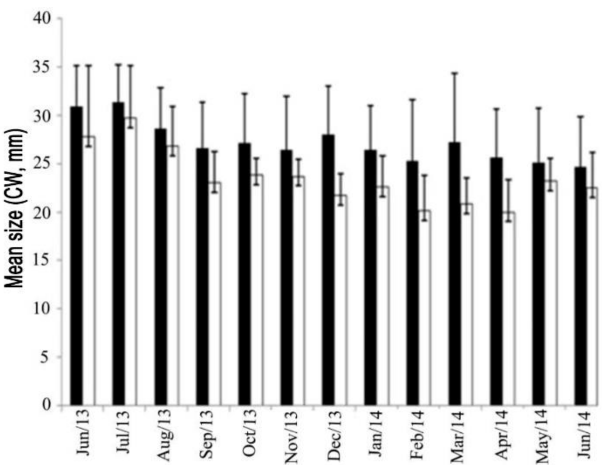

Figure 2. *Uca* (*Uca*) *maracoani* (Latreille, 1802). Mean size of individuals collected at Baixa Grande Estuary, northeast Brazil, between June 2013 and June 2014. Black bars: males; white bars: females.

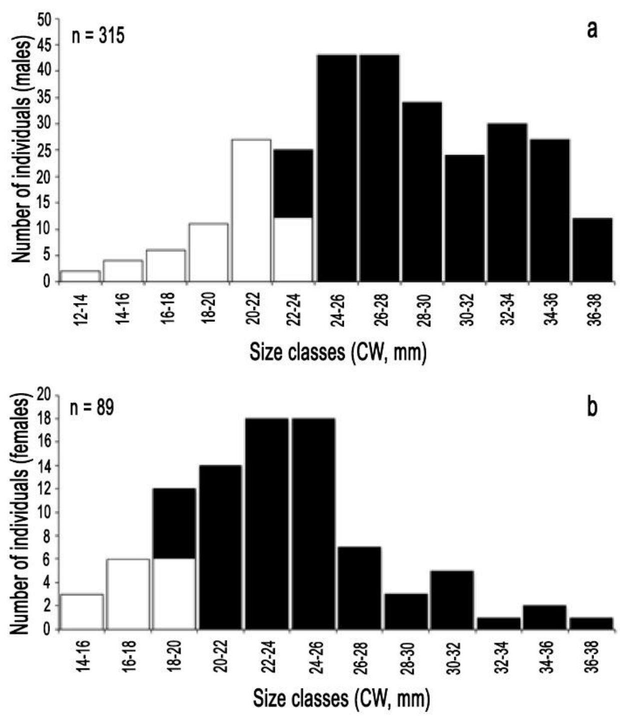

Figure 3. Overall size frequency distribution of *Uca* (*Uca*) *maracoani*, collected at Baixa Grande Estuary, northeast Brazil, from June 2013 to June 2014. a) males, b) females. White bars: juveniles (<22.3 mm CW for males; <19.3 mm CW for females); black bars: adults.

DISCUSSION

The amount of crabs collected in the present contribution (404 individuals) was small when compared to other *U.* (*U.*) *maracoani* population studied in Brazil (Table 3). In fact, subtropical populations are known to be more numerous than tropical ones (Brown, 2014). However, it is important to keep in mind that that the number of collectors and the sampled area are not the same among the previous studies, which can generate bias in the comparisons. Koch *et al.* (2005) conducted the only study of *U.* (*U.*) *maracoani* tropical population, in Pará. In this case, however, the methodology used was by transects, and comparisons with the present study are not reliable.

Table 3 summarizes the results found with other *U.* (*U.*) *maracoani* populations regarding capture method, sampling regime, mean size, sex ratio, reproductive period, and age at sexual maturity. Females are usually smaller than males, about equal in some species, but

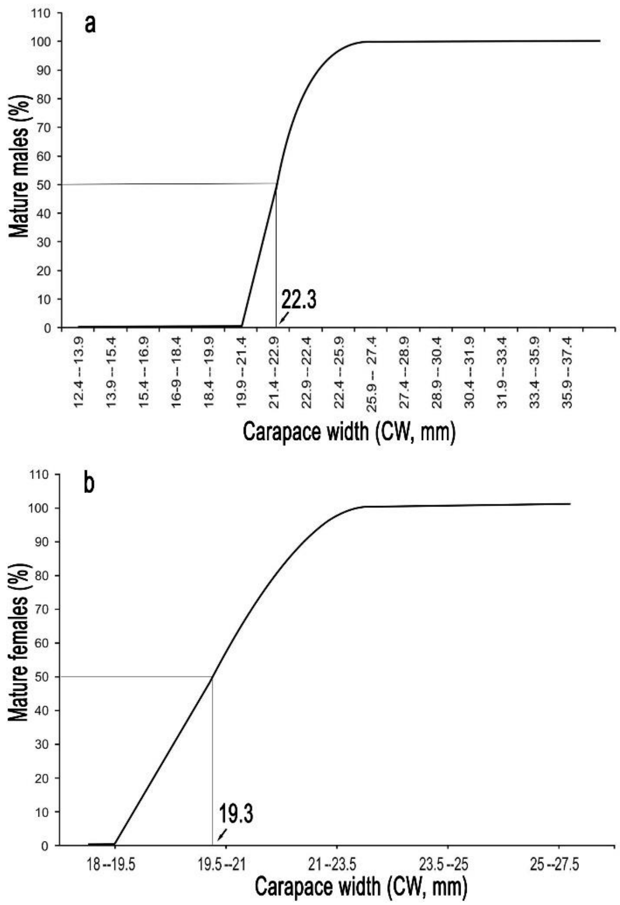

Figure 4. *Uca* (*Uca*) *maracoani* a) L50% maturity males, b) L50% maturity females.

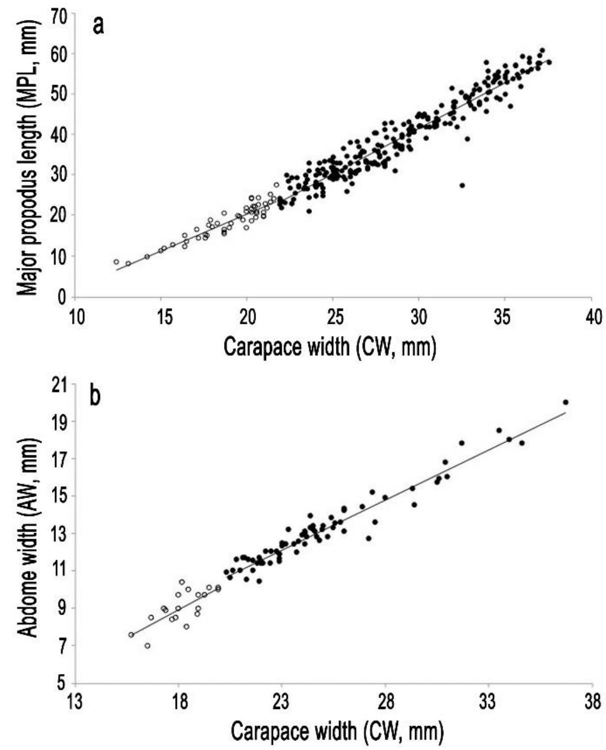

Figure 5. *Uca* (*Uca*) *maracoani*. a) Dispersion points, and adjusted curve for males relationship MPL x CW, b) dispersion points and adjusted curve for female relationship AW x CW.

never attaining greater lengths than their males (Crane, 1975; Ribeiro & Bezerra, 2014). In general, females specimens of *Uca* spp. may have reduced growth rates to concentrate their budget on gonad development (Johnson, 2003), and larger males have greater chances of obtaining females for copulation and of winning intra-specific fights (Christy & Salmon, 1984).

Differences between male and female sizes among populations may be due to the organic content of the sediment that can promote better nutritional conditions, which results in different growth rates of specimens in different areas (Benetti *et al*., 2004).

The frequency size distribution of *U.* (*U.*) *maracoani* population from Baixa Grande Estuary was unimodal, which may reflect a continuous recruitment, with no disruption of classes and constant mortality rates, indicating a stable population (Diaz & Conde, 1989), probably due to the more stable climate in tropical areas. The size-frequency distribution in the *U.* (*U.*) *maracoani* population studied by Hirose & Negreiros-Fransozo (2008) in a subtropical mangrove of southeastern Brazil showed variations, being that in some months these variations were bimodal for both sexes or bimodal for males and unimodal for females. However, ovigerous females and juveniles were found all year round, with higher frequencies in autumn, winter and spring, revealing a continuous reproduction period. The sub-tropical population analyzed by Benedetto & Masunari (2009) also shifted between unimodal in autumn, spring and winter and bimodal in summer. Ovigerous females were found throughout the year and the juvenile recruitment was also continuous, with two periods of intensity.

The presence of ovigerous females in the population can be used to define the reproductive period. However, in the present contribution, it was not possible to determine the peak of reproductive events due to the lower number of ovigerous females collected. This problem is common in studies on populations of *Uca* spp. Aciole *et al*. (2000) found only one ovigerous females among 351 collected females and Bezerra & Matthews-Cascon (2006) collected four ovigerous females among 520 females sampled, both of *U.* (*U.*) *leptodactyla* Rathbun, 1898 in one-year period. Bezerra & Matthews-Cascon (2007) found 14 ovigerous females of *U.* (*U.*) *thayeri* Rathbun, 1900 among 219

Table 2. *Uca* (*Uca*) *maracoani* morphometric data regression analyses, based on the growth differentiation between sexes. CW: carapace width; MPL: major propodus length; AW: abdomen width.

Sex	Morphometric relationships	Inflection point	Stage	n	Linearized equation log y = log a + b log x	r^2	a	b	Allometric growth
Males	CW x MPL	22.3	Juveniles	51	log MPL = 1.2016 + 1.8215 log CW	0.8578	15.908	1.8215	+
			Adults	243	log MPL = 1.4099 + 2.2458 log CW	0.9104	25.703	2.2458	+
Females	CW x AW	19.3	Juveniles	16	log AW = 1.0622 + 0.7170 log CW	0.4130	11.542	0.7170	-
			Adults	73	log AW = 0.2698 + 1.7526 log CW	0.9388	1.8615	1.7526	+

females collected all year round. Regarding *U.* (*U.*) *maracoani*, Benedetto & Masunari (2009) found 86 ovigerous females among 2165 females captured.

The lower number of ovigerous females collected in this study may be associated to the fact that ovigerous females of fiddler crabs remain inside the deep burrows to incubate their eggs. Litulo (2005a) found ovigerous females of *U.* (*Paraleptuca*) *annulipes* (H. Milne-Edwards, 1837) at depths of about 30 cm and ovigerous females of *U.* (*Cranuca*) *inversa* (Hoffman 1874) in burrows of about 50 cm (Litulo, 2005b).

Most population of *Uca* spp. from temperate and subtropical areas show a bimodal size distribution, with a well-pronounced reproduction activity, especially in warm months (Negreiros-Fransozo *et al.*, 2003; Colpo & Negreiros-Fransozo, 2004; Costa *et al.*, 2006). In general, some *Uca* spp. population from tropical areas show prolonged breeding seasons, or can have their reproductive period linked to the rainy season, as found by Bezerra & Matthews-Cascon (2007) for *U.* (*Minuca*) *thayeri* in a tropical mangrove of northeastern Brazil. In a tropical estuary in the State of Pará, *Uca* (*U.*) *maracoani* ovigerous females were mostly found in the drier season, but high levels of recruitment also occurred during the wet season (Koch *et al.*, 2005). The precipitation values observed during the study period (130-10.5 mm) were less than the expected amount for the region (600-1000 mm) (EMPARN). Northeastern Brazil was passing through a drought period, which is considered the driest season in the last 50 years (WMO, 2014). Consequently, comparisons between dry and wet periods were not reliable (Fig. 6). The proportion among males and females also reflects the population balance (Fisher, 1930). According to Geisel (1972), physiologic and behaviorally homeostatic populations living in a constant environment, present a 1:1 proportion, or a slightly male-biased ratio, while populations that inhabit inconstant environments will present deviations toward the females to maximize the evolutionary potential due to unequal selection between male and female.

Fiddler crab populations do not usually present significant deviations of the 1:1 sexual proportion (Costa & Negreiros-Fransozo, 2003; Koch *et al.*, 2005; Bezerra & Matthews-Cascon, 2006, 2007; Castiglioni *et al.*, 2010). However, it is possible to find populations of crustaceans with significant deviations from the expected proportion of 1:1, which can be caused by differences in birth rates or mortality rates between the sexes (Johnsson, 2003) and/or the sampling rates (Montague, 1980). Historically, some *Uca* populations have been recorded with significant deviations from the fisheries proportion (Wolf *et al.*, 1975; Frith & Brunenmeister, 1980; Colby & Fonseca, 1984; Spivak *et al.*, 1991; Emmerson, 1994; Litulo, 2005a; Bedê *et al.* 2008). In the present study, the sex ratio was skewed towards males, in a proportion of 3.5:1 (Table 3). This is a very high deviation, even when there are differences in sex ratio, as reported by Bedê *et al.*, (2008) for *U.* (*M.*) *rapax* (Smith, 1870) (1:0.55 skewed towards males), and for *U.* (*M.*) *thayeri* (1:1.68 skewed towards females). In respect to *U.* (*U.*) *maracoani*, previous studies have not recorded significant deviations of sex ratio (Koch *et al.*, 2005; Hirose & Negreiros-Fransozo, 2008).

The sampling method could be responsible for differences in sex ratio. Costa & Negreiros-Fransozo (2003) found males to be more numerous in the transect technique, while in the catch-per-unit-effort there were no differences between sexes. However, the male-biased proportion found in this study was obtained using the CPUE technique. Crabs collected by Costa & Negreiros-Fransozo (2003) using the CPUE technique were always larger than crabs collected using the transect technique. Larger crabs would be more readily located and caught when searching the study area using the CPUE technique. Moreover, males spend more time on the surface than females, performing defensive and mate-attracting waving, as well as feeding for longs periods to compensate for having only one small chela (Montague, 1980).

Another explanation of departures from the 1:1 proportion could be the differences in locomotor performance between males and females of fiddler crabs. Gerald & Thiesen (2014) show that the major claw of male fiddler crabs hinders their locomotor per-

Table 3. Main population aspects of *Uca* (*U.*) *maracoani* from different localities in Brazil. *Significantly statistical difference between mean size of males and females. [n]Statistical difference between mean size of males and females not calculated.

Locality	Capture method	Sampling regime	Amount of crabs collected	Sexual ratio (M:F)	Mean size adults males (CW, mm)	Mean size adults females (CW, mm)	Reproductive period	Size at sexual maturity (CW, mm)	Reference
Caeté River, Bragança, PA (01º03'46"S, 46º46'22"W)	Transect	Samples in intervals of 6 weeks over a period of 12 months	1917	1:1	35[n]	31[n]	Summer/spring (June-November, dry season in the region)	18 ± 0.3 average of the 5 smallest ovigerous females	Koch *et al.* (2005)
Jabaquara River, Paraty, RJ (23º12'10"S, 44º43'14"W)	CPUE (two persons/60 min)	Monthly over a one year period	1540	1:0.8 skewed towards males	32 ± 5.7*	28.6 ± 4.7	Continuously (peak in autumn/ winter)	-	Hirose & Negreiros-Fransozo (2008)
Jabaquara River, Paraty, RJ (23º12'10"S, 44º43'14"W)	CPUE (two person/60 min)	Monthly over a one year period	1540	-	-	-	-	21.2 males 19.4 females (Relative growth)	Hirose & Negreiros-Fransozo (2007)
Baixio Mirim, Guaratuba Bay, PR (25º50'S, 48º3'W)	CPUE (four persons/60 min)	Monthly over a one year period	7120	-	21,53[n]	19,13[n]	-	17.85 males 11.75 females (Relative growth).	Masunari *et al.* (2005)
Baixa Grande, RN (4°55'90"S, 37°04'51"W)	CPUE (one person/60 min)	Monthly over a one year period	404	3.5:1 skewed towards males	27.1 ± 5.47*	23.4 ± 4.2	Continuously	22.3 males 19.3 females (Relative growth)	Present study

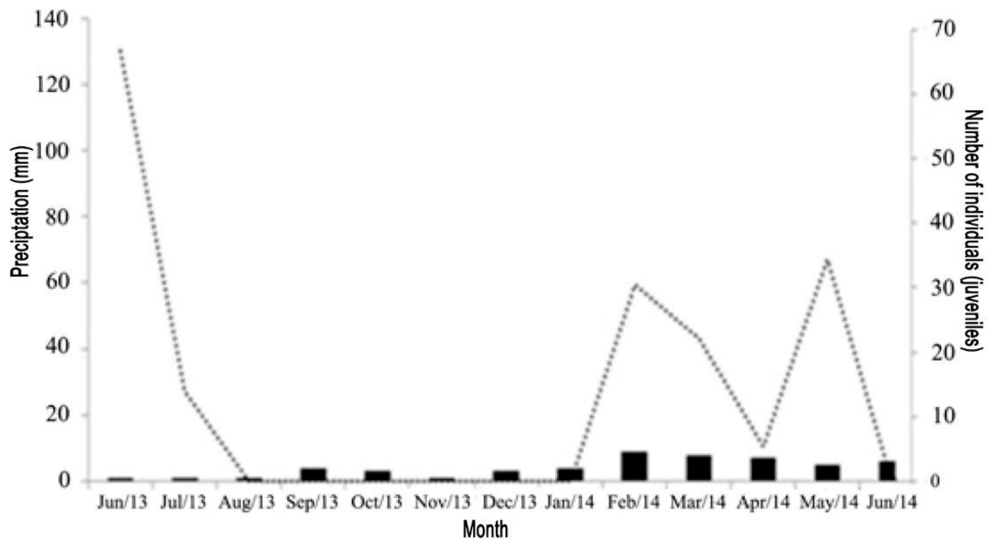

Figure 6. Monthly average rainfall (pointed line) of the Baixa Grande estuary and number of juveniles crabs collected (bars) at Baixa Grande Estuary from June 2013 to June 2014.

formance while moving on slopes, reducing both speed and endurance, but not during movement on level substrate. Moreover, the mass of the enlarged claw could be 36% of total body mass, increasing the energetic costs of locomotion (Full & Herreid, 1984; Gerald & Thiesen, 2014).

In this way, we suggests that males do not hide deep inside burrows when escaping from predators (or researchers), and are therefore easier to capture by the researcher using the CPUE technique than the transect technique, where squares are sampled and all burrows inside the squares are excavated. Although, Costa & Negreiros-Fransozo (2003) found more males using the transect technique, these authors did not use equally spaced squares to sample the area, which was the preferred method of Bezerra & Matthews-Cascon (2007) where all the burrows found inside the squares were excavated.

The study of handedness in fiddler crabs populations are very important, considering that handedness might be useful as a potential phylogenetic character (Jones & George, 1982; Rosenberg, 2001). Crane (1975) stated that the larger claw on *Uca* males is generally found on the right as well as the left side, and recent population studies have not found differences in relation to the side of the larger claw (Masunari *et al.*, 2005; Bezerra & Matthews-Cascon, 2006, 2007). However, predominantly right-handed specimens have been recorded for some Indo-West Pacific *Uca* species (Williams & Heng, 1981; George & Jones, 1982) and a left-handed population of *U.* (*M.*) *burgersi* Holthuis 1967 was reported in the West Indies (Gibbs, 1974).

In *U.* (*U.*) *maracoani*, Masunari *et al*. (2005) found a proportion of 1:1 between right-handed and left-handed males as found in the present study, showing that in *U.* (*U.*) *maracoani* both chelipeds have an equal potential of growing into a giant cheliped. The growth patterns observed in juveniles and adults males and females of *U.* (*U.*) *maracoani* in Baixa Grande Estuary are in agreement with previously studies for the *Uca* species in Brazil (Table 2).

In the ontogenesis of males, the analysis ascertained that 50% males are mature with 22.3 mm CW. This value is similar to that found by Hirose & Negreiros-Fransozo (2007) of 21.2 mm CW. The present contribution reports a positive allometry of cheliped for both juvenile and adult individuals in pre-puberty molt, reaching the highest level in the adult phase. Masunari *et al.*, (2005) and Hirose & Negreiros-Fransozo (2007) also reported a positive allometry in chelipeds of *U.* (*U.*) *maracoani* for juveniles and adults. The increase in allometry just after they reach sexual maturity can be because the behavior of cohorts is predominantly visual (Hirose & Negreiros-Fransozo, 2007), being that females are attracted by larger claws (Crane, 1975). Among *U.* (*U.*) *maracoani* females studied, 50% were morphological matures with about 19.3 mm CW, which was also similar to the values found by Hirose & Negreiros-Fransozo (2007) (19.4 mm CW). Masunari *et al*. (2005) founded a different value, which was of 11.75 mm CW. These differences could be the result of ecological factors such as substratum, availability and quality of food, salinity, and exposure to tides (Genoni, 1985).

Masunari *et al.*, (2005) reported isometric growth in juveniles and positive allometry in adults, and Hirose &

Negreiros-Fransozo (2007) found positive growth in both juveniles and adults. However, in the present contribution, allometric positive growth was found in juveniles and adults males and females. This pattern was also found in *U.* (*Leptuca*) *leptodactyla* studied by Masunari & Swiech-Ayoub (2003). According to Finney & Abele (1981), the abdomen growth rate decreases slightly as a result of sexual maturity, in which a high positive allometric growth occurs in juveniles, and a practically isometric growth occurs in adult females. This growth pattern may reflect the higher energetic investment of females in reproduction during the adult phase (Hirose & Negreiros-Fransozo 2007), where the ripening of gonads and formation of associated reproductive products represent the major energetic needs (Hartnoll, 2006).

In conclusion, the population of *U.* (*U.*) *maracoani* in Baixa Grande Estuary showed males significantly larger than females (ovigerous and non-ovigerous), with a unimodal distribution, reflecting a continuous recruitment. The handedness did not differ from the expected ratio of 1:1. Males attain sexual maturity with about 22.3 mm of CW, while females are mature about 19.3 mm of CW. The sexual ratio was skewed toward males in a proportion of 3.5:1. This deviation could be related to the CPUE technique used, once the larger males are more visible and due to male's locomotor performance, since the enlarged claw increases the energetic costs of locomotion. In this way, we suggest that the use of transect with equally spaced squares to sample the area could avoid this kind of bias in *Uca* population studies.

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