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ORIGINAL ARTICLE

Population biology of the fiddler crab *Uca maracoani* (Crustacea, Ocypodidae) inhabiting an impacted mangrove area on the southern coast of São Paulo state, Brazil

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ABSTRACT

Fiddler crabs are important components of intertidal benthic macrofauna in estuarine habitats. However, these invertebrates often inhabit areas under anthropogenic-driven changes. In this study, we evaluated the habitat quality and the population biology of the fiddler crab *Uca maracoani* (Latreille, 1802) in a mangrove area under anthropogenic influence, on the southern coast of São Paulo state, Brazil. Sediment samples for ecotoxicological analyses and data on the population biology of *U. maracoani* were collected monthly between October 2008 and October 2009. Contamination was observed in sediment samples from all months, indicating that benthic organisms inhabiting the study area are continuously exposed to toxicity. The sex ratio did not deviate from 1:1 for the whole population of *U. maracoani*, within any given month (except in October 2008, when males outnumbered females). Adult males and females showed a similar size, while juvenile females were larger than juvenile males, probably reflecting that females attained sexual maturity at a larger size than males. For both juvenile and adult stages, the major cheliped propodus length and height in males and the abdomen width

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in females showed positive allometry. The size-frequency distribution of the studied population varied from unimodal to bimodal. Juveniles were recorded in all months, suggesting the studied population has continuous recruitment. In contrast, ovigerous females were not found in the study area for several months. Although *U. maracoani* is continuously exposed to contamination present in the sediment, it presents a well-established population and seems to persist in the study area.

Keywords

Allometry, crabs, ecotoxicology, pollution, population dynamics

Introduction

Invertebrates, such as crustaceans, mollusks, and annelids, represent most of the benthic macrofauna inhabiting estuarine systems. They have an important role as a trophic link in estuarine food webs, supporting higher trophic levels by consuming producers, primary consumers, and detritus (McLusky and Elliott, 2004). Some estuarine invertebrates constitute a significant fraction of fishery resources, having important economic and nutritional value for human populations (Severino-Rodrigues *et al.*, 2001; McLusky and Elliott, 2004; Duarte *et al.*, 2014). Among crustaceans inhabiting estuaries, crab species are highly abundant and may account for most of the biomass in these systems (Koch and Wolff, 2002; Hogarth, 2007).

Fiddler crabs inhabit the intertidal zone of tropical, subtropical, and warm temperate regions (Crane, 1975). These benthic crustaceans are often found in estuarine habitats, such as salt marshes and mangroves, and are deposit feeders, ingesting organic material on the sediment surface, such as detritus, bacteria, and microalgae (Teal, 1958; Dye and Lasiak, 1986; Wolfrath, 1992; Meziane and Tsuchiya, 2002; Hogarth, 2007). One of the most notable morphological features of these animals is the marked sexual dimorphism, in which males have one cheliped much larger than the other one, while females have chelipeds of similar size (Crane, 1975). Also, they are known as important ecosystem engineers because they can affect the soil composition and biogeochemistry through burrowing and feeding behaviors at the sediment surface (Kristensen, 2008). However, the role of fiddler crabs may be under threat in some estuaries since these organisms can be directly and indirectly affected by anthropogenic impacts on coastal areas (*e.g.*, Krebs and Burns, 1977; Capparelli *et al.*, 2019). For instance, the pollution of water and sediment can affect biochemical and physiological parameters of fiddler crabs, as well as cause changes in the behavior and morphology of these animals (Krebs and Burns, 1977; Weis *et al.*, 1987; Penha-Lopes *et al.*, 2009; Bartolini *et al.*, 2009; Capparelli *et al.*, 2016). Also, environmental pollution can indirectly influence the feeding activity and biomass of fiddler crabs by promoting changes in the availability of food sources ingested by these consumers (Meziane and Tsuchiya, 2002; Cannicci *et al.*, 2009; Penha-Lopes *et al.*, 2009). Either way, anthropogenic-driven contamination in estuarine areas can ultimately affect the population biology of fiddler crabs and their role as ecosystem engineers (Krebs and Burns, 1977; Krebs and Valiela, 1978; Bergey and Weis, 2008; Bartolini *et al.*, 2009).

Currently, ten fiddler crab species belonging to three genera (*Uca* Leach, 1814 [in Leach, 1813-1815], *Leptuca* Bott, 1973, and *Minuca* Bott, 1954) occur in Brazil (Melo, 1996; Thurman *et al.*, 2013; Shih *et al.*, 2016). Among these species, *Uca maracoani* (Latreille, 1802) is the only representative of the genus *Uca* and the largest species occurring in Brazil (Crane, 1975; Melo, 1996). This fiddler crab species is distributed from the Gulf of Paria (eastern Venezuela and Trinidad) to Guaratuba bay (Paraná, Brazil), occurring in open areas with a muddy substrate (Crane, 1975; Thurman *et al.*, 2013). Although it has a widespread distribution, information on aspects of *U. maracoani* population biology is still scarce, limited to a few Brazilian states (Paraná, Rio de Janeiro, Pernambuco, Rio Grande do Norte, and Pará) (Koch *et al.*, 2005; Hirose and Negreiros-Fransozo, 2008; Di Benedetto and Masunari, 2009; Silva *et al.*, 2016; Azevedo *et al.*, 2017). Also, the areas of occurrence of *U. maracoani* (*i.e.*, muddy flats) may be affected by anthropogenic-driven changes, such as the expansion of urban areas and construction of marinas (Hirose and Negreiros-Fransozo, 2008; Di Benedetto and Masunari, 2009; Checon and Costa, 2017). The contamination status of the sediment is unknown for areas where studies on the population biology of this fiddler crab have previously been carried out. In this sense, studying the population biology of this species and the quality of its habitat could provide insights to support its conservation, especially where no information is available yet, such as mangrove areas along the coast of the state of São Paulo (Southeastern Brazil).

The Santos Estuarine System (SES) is one of the main areas of occurrence of mangroves in the state of São Paulo (Schmiegelow *et al.*, 2008). However, many portions of the SES are considered degraded as a result of human activities, such as dredging, port activities, and disposal of industrial and domestic waste (Abessa *et al.*, 2001; 2008; Cesar *et al.*, 2006; Cordeiro and Costa, 2010; Pereira *et al.*, 2016). Specifically, sediments are of major concern because they have been considered contaminated in many SES areas, with high toxicity to benthic macrofauna (Abessa *et al.*, 2008; Sousa *et al.*, 2014). Herein, we evaluated the habitat quality and the population biology of *U. maracoani* in a mangrove area under anthropogenic influence within the SES.

MATERIAL AND METHODS

Study area

The study was carried out from October 2008 to October 2009 in a mangrove area known as "Portinho" (23°59'S 46°24'W), which is part of the municipality of Praia Grande, located on the southern coast of the state of São Paulo, Brazil. This mangrove is located within the São Vicente Channel, which is part of the Santos Estuarine System (SES), and is composed of the following mangrove species - *Rhizophora mangle* L., *Laguncularia racemosa* (L.) C.F.Gaertn., and *Avicennia schaueriana* Stapf & Leechm. ex Moldenke trees, with a dominance of the latter (Mano-Clara and Schmiegelow, 2015). The study area has several observable sources of anthropogenic impacts, which are mostly related to the existence of houses, a recreational marina, and paved roads separating mangrove patches (Mano-Clara and Schmiegelow, 2015). Previous studies reported low to moderate levels of contaminants and improper disposal of solid residues (mainly plastic and wood) in the São Vicente Channel (Abessa *et al.*, 2008; Cordeiro and Costa, 2010), which are all capable of negatively affecting the benthic communities (Abessa *et al.*, 2019). Despite the anthropogenic influence, at least seven fiddler crab species are found in the study area (Checon and Costa, 2017). An unvegetated muddy flat site (~ 100 m^2) within a recreational marina and surrounded by concrete and wood structures and small motorboats was selected as the sampling area. This area was chosen due to the high density of *U. maracoani* individuals and the observable signs of human-driven contamination, such as oil spots on the sediment surface and improper disposal of waste from the marina.

Sediment toxicity

Toxicity tests have been used in environmental evaluations, as they are cost-effective, simple, easy to do, and produce reliable information on the environmental quality (Chapman and Long, 1983; Lamberson *et al.*, 1992). When contamination is due to multiple sources and its chemical composition is unknown or complex, the use of toxicity tests to estimate the effects of contaminants may be more effective than chemical analyses (Rojíčková-Padrtová *et al.*, 1998; Abessa *et al.*, 2001) since they provide direct and integrated responses resulting from the mixture of pollutants (Burton and Scott, 1992). Therefore, in the present study, sediment toxicity was used as the main variable describing environmental quality. The sediment was evaluated for toxicity using benthic copepods of the genus *Nitocra* Boeck, 1865, according to Fleeger and Lotufo (1998) and Lotufo and Abessa (2002). Harpacticoid copepods, such as the genus *Nitocra*, have been used as test organisms in sediment quality assessments conducted worldwide (Dave and Nilsson, 1994; Perez-Landa and Simpson, 2011). In Brazil, *Nitocra* has been routinely used in ecotoxicological assays to evaluate estuarine pollution, including the Santos Estuarine System (Buruaem *et al.*, 2013; Sousa *et al.*, 2014; Cruz *et al.*, 2019).

Composite samples of superficial sediment were collected monthly between November 2008 and October 2009 during the low ebb tide periods, stored in a laboratory at temperatures between 2 and 4°C until the analysis. As toxicity is a relative measure (always taken in relation to a control or reference), an external control was used for these tests. In this case, sediment collected in Ilhabela Channel, northern coast of São Paulo, was used as a control. This site is considered clean and has been used as a reference area in other ecotoxicological studies (Abessa *et al.*, 2001; Cesar *et al.*, 2006; Sousa *et al.*, 2008).

In the laboratory, sediments were homogenized and distributed in test chambers. Each test chamber was filled with 2 g sediment, and 8 mL autoclaved seawater (salinity 17 ± 5 ppt) and kept at 25°C for 24 hours prior to the test. Three replicates were used for each sample. An additional replicate was prepared and used to evaluate the overlying water's pH and salinity in the test chambers before the beginning of the tests. The next day, five ovigerous female *Nitocra* specimens were added to each test chamber. Test chambers were kept without aeration for ten days at 25°C in the presence of light. The number of young copepods (nauplii and copepodites) was recorded to determine the fecundity of these organisms. The Student's t-test was used to compare the fecundity of copepods between controls and tested samples. The Cochran test was applied to assess the assumption of homogeneity of variances and, when necessary, a fourth root transformation was used. The sediment was classified as toxic when the fecundity of a sample was lower than that observed for the external control.

Population biology of Uca maracoani

Crabs were sampled monthly by excavation during low tide between October 2008 and September 2009. We used a catch-per-unit-effort (CPUE) methodology, with two people searching and collecting crabs for 1 hour. In each month, individuals were counted and sexed by checking the abdomen morphology or the number of pleopods to estimate the sex ratio. The occurrence of ovigerous females was recorded to evaluate the reproductive period. The following linear measurements were recorded to determine the size at onset of morphological sexual maturity: carapace width (CW), carapace length (CL), abdomen width (AW) at the basis of the 5th somite for both sexes, and major cheliped length (MCL) and major cheliped height (MCH) only for males. Measurements were made using calipers to the nearest 0.01 mm. The choice of these body structures was based on Hartnoll (1974). All animals were returned to their environment after data collection.

For allometry analyses, specimens with regenerating or missing chelipeds, or injury and/or malformation in other structures were excluded. Carapace width was considered an independent variable, and the remaining measurements, dependent. Changes in the proportion of body dimensions in relation to CW were tested using the allometric equation $y = ax^b$. This equation was linearized ($\ln y = \ln a + b \ln x$), where x represents the independent variable (CW), and y represents the dependent variables (all other body measurements) (Huxley, 1950). We used regression models with segmented relationships to test if the relationship between CW and each dependent variable changes throughout the range of measurements observed. Such analysis can estimate the breakpoint between two segments, which represents the point of change in the relationship between two variables, as well as providing the estimated slopes and intercepts for each segment (Muggeo, 2008). The Davies' test was used to compare the slopes between consecutive segments. All these analyses were performed using the software R version 4.0.0 (R Development Core Team, 2020) with the package 'segmented' (Muggeo, 2003; 2008). Also, we used Student's t-test to evaluate if the slope (b) of each estimated segment deviates from 1 and then classified the growth as isometric ($b = 0$), negative allometric ($b < 1$) or positive allometric ($b > 1$).

From the estimated onset of morphological sexual maturity, crabs were grouped into five demographic categories: juvenile males, adult males, juvenile females, adult non-ovigerous females, and ovigerous females. The population dynamics was evaluated from the monthly size-frequency distribution (using CW as a size measure) of each demographic category. In this case, because of the low occurrence of ovigerous females (see Results), the categories "adult non-ovigerous females" and "ovigerous females" were grouped as "adult females". Also, the occurrence of juveniles was used to estimate the recruitment period. Because of the low number of crabs in some months and/or size classes, we used the exact binomial test of goodness-of-fit to compare the proportion of males and females for the entire population, within each month and each size class. For both juveniles and adults, Student's t-test was used to compare the CW between males and non-ovigerous females. All tests were run using the software R.

RESULTS

Sediment toxicity

The pH of the water in the test chambers ranged from 7.08 to 7.93, while salinity ranged from 19 to 25 (Tab. 1). For all sediment samples collected at the study area, the fecundity of copepods (*i.e.,* the number of young individuals) was lower than controls, indicating the presence of toxicity in all months (Tab. 1).

Population biology of Uca maracoani

A total of 594 crabs were collected, of which 320 were males and 274 females. The highest and lowest abundance values of crabs were recorded in March 2009 (113 crabs) and December 2008 (21 crabs), respectively. The sex ratio did not deviate from 1:1 for the whole population (Exact binomial test of goodness-of-fit, $p = 0.065$), within each month ($p > 0.05$), except in October ($p = 0.029$), when males outnumbered females (Fig. 1A). Males dominated the 30-33 mm size class ($p = 0.0001$). Although only males were observed in the largest size class (33-36 mm CW), they occurred in low number (N=3) and, thus, the observed sex ratio in this size class was not statistically different from the expected one (1:1) (Fig. 1B; Exact binomial test of goodness-of-fit, $p = 0.25$).

For allometric analyses, a total of 557 crabs were used (292 males and 265 females). For males, the CW × AW, CW × MCL, and CW × MCH relationships were represented by two straight lines with different slopes (Davies' test, $p < 0.05$). For both juvenile and adult males, MCL and MCH showed positive allometry, indicating that cheliped propodus length and height grow at higher rates than CW. A similar result was observed for AW of juvenile males, but not for adults, which presented isometric growth (Tab. 2). No difference in slope was found between consecutive segments in the CW × CL relationship for both males and females. Also, for that body dimension, males and adult females showed negative allometry, while juvenile females showed isometric growth (Tab. 2).

Table 1. Abiotic variables (pH and salinity) and number (mean ± standard deviation) of young copepods of *Nitocra* sp. by treatment. Each control represents the sediment reference tested with a set of sediment samples collected monthly in the study area. For the comparison of young copepods between each month and its respective control, t-value and respective *p*-value are presented. * indicates when the fourth root transformation was necessary to meet the assumptions of the analysis. For all months, t-tests were made assuming equal variances between groups, except for 'March 2009', in which a t-test was made assuming unequal variances.

Treatment	pH	Salinity	Young copepods	t	*p*
Control 1	7.75	22	127.3±70.4	---	---
Nov/2008	7.62	24	9.0±4.6	4.33*	0.012
Dec/2008	7.93	24	2.3±1.5	5.86*	0.004
Jan/2009	7.77	25	5.0±4.0	4.70*	0.009
Feb/2009	7.91	24	1.0±1.0	5.12*	0.007
Control 2	7.56	20	70.0±13.7	---	---
Mar/2009	7.61	21	12.0±0.0	7.31	0.018
Apr/2009	7.28	19	29.0±15.4	3.44	0.026
May/2009	7.09	20	7.0±8.9	6.67	0.003
Jun/2009	7.26	20	2.0±1.0	14.04*	<0.001
Control 3	7.60	21	137.7±15.8	---	---
Jul/2009	7.32	20	4.7±6.4	13.49	<0.001
Aug/2009	7.25	20	21.0±15.9	9.02	<0.001
Sep/2009	7.24	20	30.0±13.0	9.11	<0.001
Oct/2009	7.08	20	10.0±5.3	13.25	<0.001

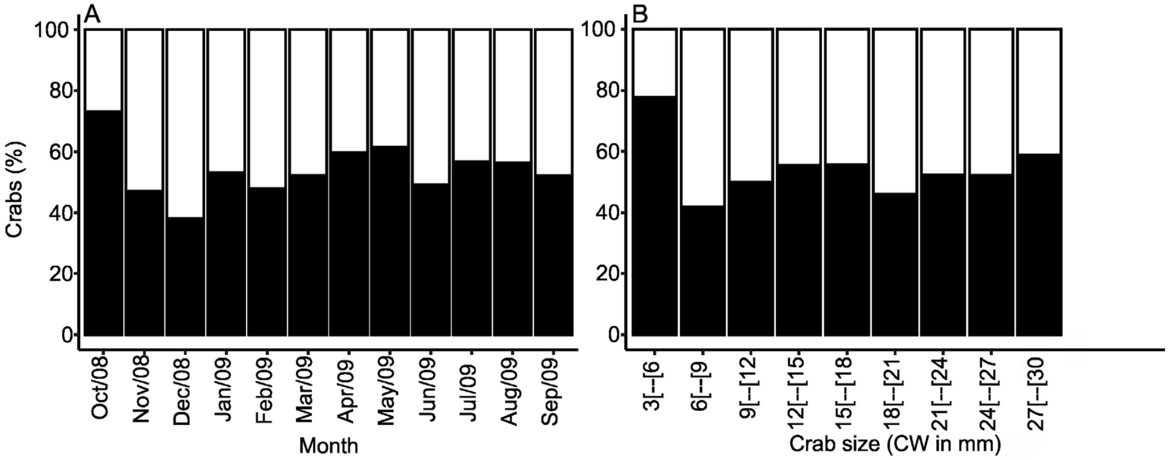

Figure 1. Proportion of females (white bars) and males (black bars) of *Uca maracoani* by (**A**) Month and (**B**) Crab size (CW in mm).

Table 2. Regression models with segmented relationship for males and females of *Uca maracoani*, Davies' test for difference between consecutive slopes and t-test for deviations of slope (*b*) from 1.

Sexes	Relationship	Estimated break point CW (mm)	N	Stage	Intercept (a)	Slope (*b*)	R^2	Davies' test (*p*-value)	Allometry	t-value	*p*-value
Males	CW vs. CL	21.50	155	J	-0.19	0.95	0.99	0.48	-	5.98	<0.001
			137	A	-0.07	0.91			-	3.31	0.001
	CW vs. AW	6.40	7	J	-3.37	2.08	0.94	< 0.001	+	4.08	0.007
			285	A	-1.37	1.00			0	0.02	0.982
	CW vs. MCL	17.36	88	J	-1.67	1.53	0.99	< 0.001	+	29.22	<0.001
			204	A	-3.08	2.02			+	42.25	<0.001
	CW vs. MCH	7.10	11	J	-4.03	2.37	0.95	0.002	+	5.42	<0.001
			281	A	-2.33	1.50			+	18.28	<0.001
Females	CW vs. CL	6.24	3	J	-2.46	2.19	0.98	0.70	0	0.90	0.46
			262	A	-0.24	0.98			-	2.29	0.023
	CW vs. AW	13.46 and 20.35	53	J	-1.90	1.32	0.99		+	7.69	<0.001
			84	T	-3.80	2.05		< 0.001 (J × T)	+	14.31	<0.001
			128	A	-1.23	1.20		< 0.001 (T × A)	+	3.34	0.001

CW: carapace width, CL: carapace length, AW: abdomen width at the basis of the 5th somite, MCL: major cheliped length, MCH: major cheliped height, A: adult, J: juvenile, T: transitional, N: number of individuals; R^2: determination coefficient; (0) = isometry; (+) = positive allometry; (-) = negative allometry.

For females, and using AW as a dependent variable, we found three distinct segments with different slopes (Davies' test, $p < 0.05$) and two estimated breakpoints: 1) a segment lower than 13.46 mm CW, probably represented only by juveniles (*i.e.*, immature females); 2) a segment between 13.46 mm CW and 20.35 mm CW, representing a transitional stage; 3) a segment larger than 20.35 mm CW, probably represented only by adults (*i.e.*, mature females) (Fig. 2, Tab. 2). For all those segments, females showed positive allometry.

For the population structure analysis, we used the breakpoints of CW × MCL (17.36 mm CW, 95 % CI: 16.47 mm CW - 18.30 mm CW) and CW × AW (20.35 mm CW, 95 % CI: 19.49 mm CW - 21.24 mm CW) relationships to estimate the size at onset of sexual maturity for males and females, respectively. For females, although we found two breakpoints for the CW × AW relationship, we used the upper one to estimate the size at onset of sexual maturity because it probably completely separates mature females from immature ones. Also, the selection of such a breakpoint is supported by the size of the smallest ovigerous female found in the present study (21.4 mm CW, Tab. 3).

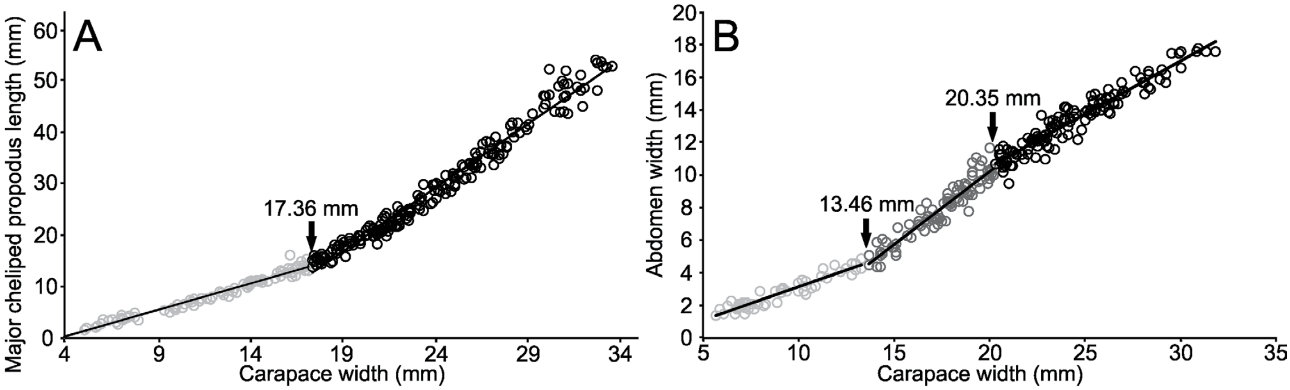

Figure 2. Regression between carapace width and major cheliped propodus of males (**A**), and carapace width and abdomen width for females of *Uca maracoani* (**B**). In (**A**), light gray circles represent juveniles and black circles represent adults. In (**B**), light gray circles represent juvenile females, gray circles represent transitional phase, and black circles represent adult females.

Table 3. Abundance and range (minimum and maximum) and mean carapace width (CW in mm) (± standard deviation) of *Uca maracoani* by demographic category. N = number of crabs.

Demographic category	**N**	**Min – Max**	**Mean±sd**
Adult Males	223	17.4 – 33.6	24.13±4.28
Juvenile Males	97	3.9 – 17.3	12.15±3.83
Adult non-ovigerous Females	121	20.50 – 31.8	24.56±2.94
Juvenile Females	140	5.7 – 20.3	14.38±4.59
Ovigerous Females	13	21.4 – 28.0	24.53±1.76

Adult males and non-ovigerous females presented similar sizes (CW in mm) (t-test for unequal variances, $t = 1.10$, $p = 0.272$). In contrast, juvenile females had a size larger than juvenile males (t-test for unequal variances, $t = 4.06$, $p < 0.001$) (Tab. 3). The size-frequency distribution of the studied population was highly dynamic throughout the year, varying from unimodal (*e.g.,* November 2008) to bimodal (*e.g.,* October 2008) distribution (Fig. 3). Across all months, juveniles were recorded with the highest contribution to the whole population in December 2008 (Figs. 3 and 4). Ovigerous females represented only a small proportion of the entire population (~ 2 %) and were not found in the study area in January, June, July, August, and September 2009.

DISCUSSION

The studied *Uca maracoani* population inhabits a contaminated area, as supported by the toxicity tests of sediment. Overall, this population presented individuals of varying sizes throughout the year and similar proportions of male and female crabs. Although ovigerous females represented only a small proportion of the entire population, adults (males and females) and juveniles were found in all months, suggesting a well-established population. In this sense, despite the toxicity of the sediment, *U. maracoani* seems to persist in the study area.

Previous studies have reported toxicity of sediment in the same estuarine region of the study area (Abessa *et al.*, 2001; 2008; 2019; Cesar *et al.*, 2006; Pereira *et al.*, 2016). Such toxicity has been related to several sources of contamination in the region, such as industrial and harbor activities and untreated domestic sewage discharges (Abessa *et al.*, 2001; Cesar *et al.*, 2006; Pereira *et al.*, 2016). Specifically, improper disposal of waste and oil spots on the sediment surface observed in the study area may represent important sources of contamination. Some studies have reported the contamination of sediments by metals and detergents in the São Vicente Channel, where the sampling site is located, which could also explain the toxicity observed in our study area (Cesar *et al.*, 2006; 2007; Abessa *et al.*, 2008; 2019).

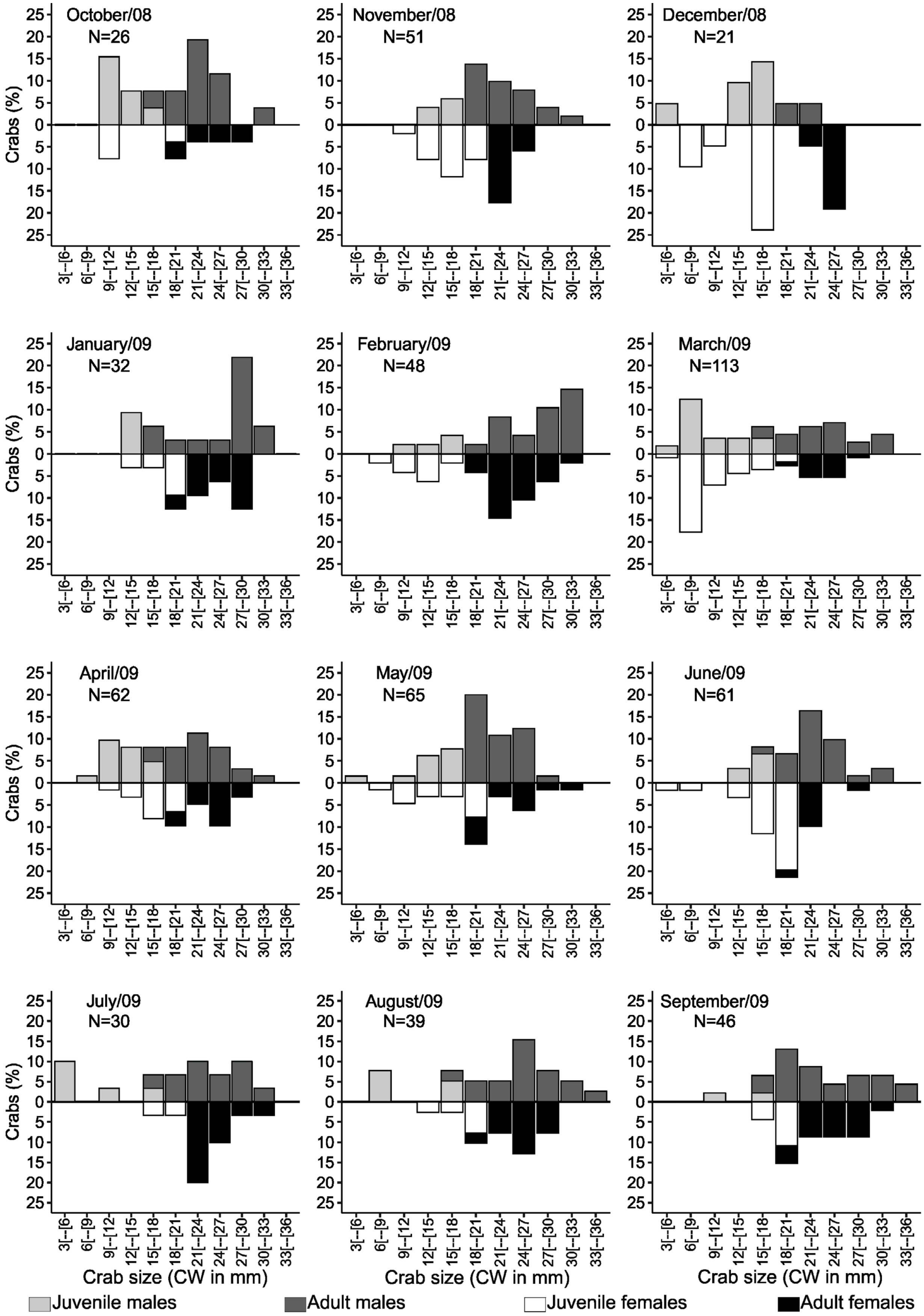

Figure 3. Frequency of juveniles, adult males, and adult females of *Uca maracoani* by crab size and month.

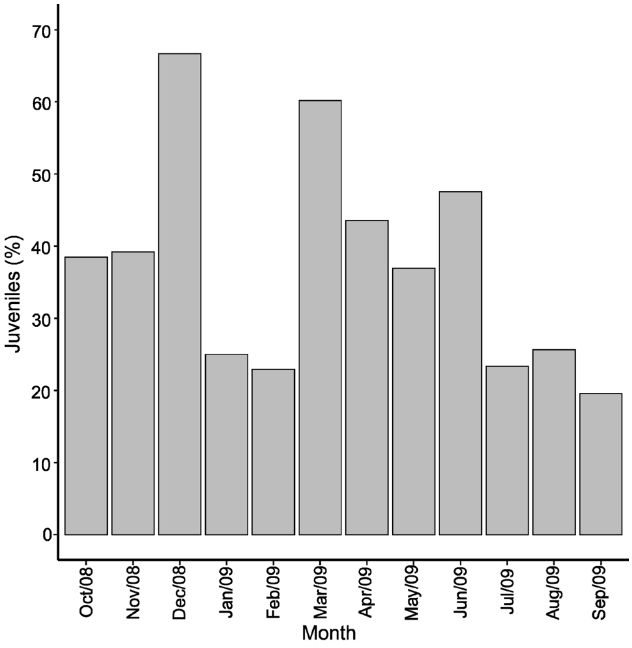

Figure 4. Frequency of juveniles (%) of *Uca maracoani* by month.

Furthermore, the presence of toxicity throughout the whole year may be a consequence of a continuous anthropogenic impact and may reflect the high susceptibility of estuarine ecosystems to long-term accumulation of contaminants (Kennish, 1997). Our results highlight the importance of constant monitoring of sediment quality in estuarine areas under continuous anthropogenic influence to understand and predict possible impacts on benthic organisms and marine ecosystems.

In the present study, the overall sex ratio of *U. maracoani* did not deviate from 1:1. Also, the same result was observed when the proportion of males and females was analyzed monthly; except in October, when males outnumbered females. Overall, such results are not in agreement with the general trend of male-biased sex ratios observed for fiddler crab populations (review in Johnson, 2003). Although the deviation in sex ratio can be explained by several ecological factors, such as differential mortality and habitat use between sexes (Johnson, 2003), it also depends on the sampling techniques employed. Costa and Negreiros-Fransozo (2003) found males of *Leptuca thayeri* (Rathbun, 1900) outnumbered females when they applied a transect technique, but both sexes were found in similar proportions when catch-per-unit-effort methodology (CPUE) was used, such as in the present study.

Usually, the investment of female crabs in reproduction is high, which can limit the available energy towards growth (Hartnoll, 2006). Also, because females cannot molt when incubating eggs, female body growth is constrained, contributing to smaller sizes of females than males (Hartnoll, 2006). In the present study, although the dominance of *U. maracoani* males in the largest size classes, adult males and females showed a similar size. Also, juvenile females were larger than juvenile males, probably reflecting that females attained sexual maturity at a larger size than males. The unusual pattern found in the present study (*i.e.,* females with size at onset of sexual maturity larger than males) could be related to the transitional stage observed for females in the CW × AW relationship. Hirose and Negreiros-Fransozo (2007) were able to identify three growth stages for males and females of a population of *U. maracoani* from Paraty (RJ): undifferentiated (smaller group), juvenile (intermediate group), and adult (larger group) stage. These authors suggested that the intermediate group represents the start of the gonad maturation for these crabs. A transitional stage for female growth was also reported for the fiddler crab *Leptuca thayeri* (Negreiros-Fransozo *et al.*, 2003). Negreiros-Fransozo *et al.* (2003) pointed out that such an intermediate stage likely consists of both immature and mature female crabs. In contrast, the first (< 13.46 mm CW) and third (> 20.35 mm CW) groups are probably represented by immature and mature females, respectively. In this case, it is possible that some *U. maracoani* females within the transitional stage reach sexual maturity at a size similar to, or smaller than, the estimated size at onset of sexual maturity for males.

Among the analyzed crab body traits, the major cheliped propodus length and height in males and the abdomen width in females showed positive allometry in *U. maracoani* juveniles and adults. Such results corroborate the important role of these body traits throughout the life history of male and female crabs (Hartnoll, 1974). The major cheliped of male fiddler crabs plays a fundamental role in the interaction of males with conspecifics in the population (*e.g.,* combat and attraction of females for mating) (Crane, 1975; Christy, 1988; Fogo *et al.*, 2019). On the other hand, the large abdomen of female crabs, due to positive allometric growth throughout ontogenesis, is crucial for successful reproduction since such a structure offers support and protection for developing eggs, functioning as an incubation chamber in ovigerous females (Hartnoll, 1974).

The crab size-frequency distribution varied throughout the year from unimodal to bimodal. Bimodality is often related to seasonal recruitment, variation in growth rates, and differential mortality rates (*e.g.*, size-dependent predation) (Tegner and Dayton, 1981; Spivak *et al.*, 1991; Vadas *et al.*, 2002), while unimodality is typical of a population with constant recruitment and mortality rates (Díaz and Conde, 1989; Litulo, 2005a). Although juveniles were recorded in all months in the present study, suggesting continuous recruitment, the contribution of such a demographic group to the whole population was highly variable throughout the year, which could partially explain the dynamic size-frequency distribution of *U. maracoani*. Also, such continuous recruitment may indicate constant reproduction of *U. maracoani* in the study area. The recruitment and breeding period of brachyurans is often related to several factors, such as latitude, temperature, salinity, and food supply (Pillay and Nair, 1971; Emmerson, 1994; Hirose and Negreiros-Fransozo, 2008). For instance, tropical and subtropical fiddler crab species usually present continuous reproduction (often with a peak at a specific period) or a longer reproductive period compared with their temperate counterparts (Colby and Fonseca, 1984; Spivak *et al.*, 1991; Costa and Negreiros-Fransozo, 2003; Litulo, 2005a; 2005b). Furthermore, larval development in brachyuran crabs, which is an important step for juvenile recruitment into the population, is greatly influenced by the combined effect of temperature and salinity (Ong and Costlow, 1970; Christiansen and Costlow, 1975; Vinuesa *et al.*, 1985). Development and survival of decapod larvae are enhanced by rising temperatures until upper limits are reached. After this point, these processes are impaired, resulting in declines caused by the warming of sea surface temperatures (Caputi *et al.*, 2013; Quinn, 2017).

Only a small number of ovigerous females (13 individuals) were sampled, and they were not found in the study area in all months. Such results may represent a methodological artifact or behavioral changes during egg incubation rather than an accurate representation of the population under investigation. Some fiddler crab females remain inside burrows while incubating their eggs, presenting reduced activity on the sediment surface (Christy and Salmon, 1984; Nakasone and Murai, 1998). Also, the muddy and unstable substrate where *U. maracoani* occurs could make it difficult to track and capture ovigerous females inside their deep burrows. Thus, this demographic group may have been underestimated in the present study. Furthermore, even if the studied population has few ovigerous females, the high larval dispersal potential of *U. maracoani* (Wieman *et al.*, 2014) could allow this population to be partially supported by larvae from other sites throughout the year.

Populations of *U. maracoani* from different sites vary regarding some population parameters, especially those related to size, reproductive period, and sex ratio (Koch *et al.*, 2005; Hirose and Negreiros-Fransozo, 2008; Di Benedetto and Masunari, 2009; Silva *et al.*, 2016; Azevedo *et al.*, 2017). Differences among fiddler crab populations have been reported and seem to be associated with several factors, such as latitude, food availability, and anthropogenic impact (Colpo and Negreiros-Fransozo, 2004; Castiglioni and Negreiros-Fransozo, 2005; Bergey and Weis, 2008; Hirose *et al.*, 2013). For example, Hirose *et al.* (2013) found a latitudinal difference in the body size of *Leptuca uruguayensis* (Nobili, 1901). For *U. maracoani*, the considerable variation in adult body size among populations (difference up to ~ 8 mm in average CW) is unlikely to be explained by the latitude. For example, higher and lower mean body sizes of adult males (32.0 mm CW and 24.1 mm CW) were reported for populations from similar latitudes (23°12'S 44°43'W in Rio de Janeiro and 23°59'S 46°24'W in São Paulo) (Hirose and Negreiros-Fransozo, 2008; present study), while intermediate mean sizes were registered at both lower (4°55'S 37°04'W in Rio Grande do Norte) and higher latitudes (25°52'S 48°36'W in Paraná) (Di Benedetto and Masunari 2009; Silva *et al.*, 2016). Also, the contamination found in the study area may affect the body size of *U. maracoani*, but further studies are required to confirm this hypothesis.

We found evidence that the *U. maracoani* population inhabits a chronically contaminated mangrove area. Bergey and Weis (2008) reported that size, density, and recruitment of the fiddler crab *Minuca pugnax*

(Smith, 1870) varied between populations under different anthropogenic influences. Because *U. maracoani* in the study area presents some population parameters comparable with populations from other mangrove areas (*e.g.*, continuous recruitment, sex ratio), contamination may have a minor effect on this fiddler crab. Alternatively, contamination could have sublethal effects on *U. maracoani*. Such effects are represented by biological variables not measured in the present study, such as biochemical, physiological, and behavioral parameters (Bartolini *et al.*, 2009; Penha-Lopes *et al.*, 2009; Capparelli *et al.*, 2016). Besides, the studied population possibly developed some degree of resistance to contaminants, as reported for other fiddler crab species exposed to sub-lethal levels of contaminants (Callahan and Weis, 1983; Weis, 1985). Further studies are required to elucidate if (and how) such observed contamination affects the population of *U. maracoani*.

Fiddler crabs are common components of estuarine benthic communities, playing an important role as trophic links in food webs and ecosystem engineers (Hogarth, 2007; Kristensen, 2008). However, anthropogenic-driven impacts can affect the biological aspects of these animals (Bergey and Weis, 2008; Bartolini *et al.*, 2009; Capparelli *et al.*, 2016). *Uca maracoani* can be found in areas under anthropogenic influence (Di Benedetto and Masunari, 2009; present study) and, thus, constant monitoring of environmental quality and population parameters can contribute to the conservation of this fiddler crab. Despite the toxicity of sediment, *U. maracoani* presents a well-established population and seems to persist in the study area.

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