



Population biology of *Uca maracoani* Latreille 1802-1803 (Crustacea, Brachyura, Ocypodidae) on the south-eastern coast of Brazil

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Abstract. The population biology of *Uca maracoani* was investigated in an estuarine mudflat in the Jabaquara River, Paraty, Brazil. The following aspects of this population were analyzed: spatial distribution, body size, size-frequency distribution, sex ratio, recruitment of juveniles, and reproductive period. The population structure presented as a very dynamic population. The median carapace width of males (32.0 mm) was significantly larger than that of females (28.6 mm) ($p < 0.05$). Males predominated during most of the year, except in July and August when the proportion of females was higher. The major pulse of recruitment occurred during winter and spring, probably as a consequence of high reproductive activity in the autumn and winter. Such information is important for conservation of this species, because it is becoming uncommon along the northern coast of the state of São Paulo, near the studied site, in south-eastern Brazil.

Key words: Reproductive period, spatial distribution, recruitment, sex-ratio, population structure.

Resumen. Población biológica de *Uca maracoani* Latreille 1802-1803 (Crustacea, Brachyura, Ocypodidae) en la costa sudeste del Brasil. La población biológica de *Uca maracoani* fue analizada en un manglar estuarina del Río Jabaquara, Paraty, Brasil. Los siguientes aspectos de la población fueron analizados: distribución espacial, tamaño del cuerpo, distribución de frecuencia, razón sexual, captura de los jóvenes y período reproductivo. La estructura de la población se presentó muy dinámica. El tamaño mediano del cuerpo de los machos (32.0 mm) fue mayor que el de las hembras (28.6 mm) ($p < 0.05$). Los machos predominaron durante la mayor parte del año, excepto en Julio y Agosto, cuando la proporción de hembras fue superior. El pulso más grande de captura de los jóvenes se produjo durante el invierno y la primavera, posiblemente como consecuencia de la elevada actividad reproductiva en el otoño y invierno. Tales informaciones son importantes para la conservación de esta especie, ya que su presencia en la costa norte del Estado de São Paulo, muy cerca del sitio de este estudio al sudeste de Brasil, no es común.

Palabras clave: período reproductivo, distribución espacial, captura de jóvenes, razón-sexual, estructura de la población.

Introduction

Crabs of the genus *Uca* Leach, 1804 are one of the most characteristic inhabitants of estuarine intertidal zones in tropical and subtropical regions (Jones 1984). These crabs are found occupying muddy beaches, mangroves, protected bays, sandy banks, and mudflats that are covered by the sea at high tide and uncovered at low tide. The crabs build complex burrows in the substratum, and display particular behaviour associated with burrow utilization. Both activities follow a tidal rhythm (Crane 1975, Macintosh 1988, Costa & Negreiros-

Fransozo 2003). During flood tide periods, the individuals remain in their burrows and during ebb tides they usually feed, fight or copulate (Crane 1975, Backwell *et al.* 1999).

The genus *Uca* includes approximately 100 species (Rosenberg 2001), of which 10 occur on the Brazilian coast (Melo 1996). Species of fiddler crabs can be divided roughly into two groups by the width of the space between the eyestalks (narrow and broad front) (Crane 1975). Among the Brazilian species just *Uca maracoani* Latreille (1802 - 1803)

present a narrow front, this characteristic is most common in the Indo-West Pacific species while in the New World broad fronts are the majority. According to Melo (1996), *Uca maracoani* is distributed through the Western Atlantic, in the Antilles, Venezuela, and the Guyanas, and along nearly the entire coast of Brazil from Maranhão to Paraná. However, nowadays this species is not found on the northern shore of the state of São Paulo (Negreiros-Franozo, personal communication).

There are several reports on population studies of species of *Uca*, among them: Frith and Brunenmeister (1980) with *U. forcipata* (Adams & White 1848), *U. urvillei* (H. Milne-Edwards 1852), *U. vocans* (Linnaeus 1758) and *U. lactea* (De Haan 1835), Colby & Fonseca (1984) with *U. pugilator*, Spivak *et al.* (1991) with *U. uruguayensis*, Mouton & Felder (1996) with *U. spinicarpa* and *U. longisignalis*, Costa & Negreiros-Franozo (2003) with *U. thayeri* Rathbun 1900, Colpo *et al.* (2004) with *Uca vocator* (Herbst 1804), Litulo (2005) with *U. annulipes* and Castiglioni *et al.* (2005) with *Uca rapax* (Smith 1870).

Studies directly concerned with *U. maracoani* are few, and related to behavioural, systematic, phylogenetic or growth aspects (Crane 1958, Crane 1975, Rosenberg 2001, Masunari *et al.* 2005, Hirose & Negreiros-Franozo 2007). The present study analyses certain biological aspects of *U. maracoani*: spatial distribution, body size, size-frequency distribution, sex-ratio, recruitment, and reproductive period (based on ovigerous-ratio) of a population living on the Jabaquara mudflat near the town of Paraty, state of Rio de Janeiro, Brazil.

Material and Methods

Samplings were carried out monthly, from May 2003 through April 2004, on a muddy beach named Jabaquara, in the town of Paraty on the southern coast of Rio de Janeiro (23°12'10"S and 44°43'14.1"W) (Fig. 1). The intertidal zone of the beach is wide, gently sloped bare of vegetation, and is near a stand of mangroves. The shallowest area of the beach is composed of coarse sand, which is abruptly replaced by mud lower in the intertidal zone, this area is flooded during high tide.

Two collectors spent 20 minutes monthly (CPUE – capture per unit effort), manually sampling fiddler crabs at each collecting site (S1, S2, and S3), at low tide, removing them from their burrows. The burrows of *Uca maracoani* are about 1 m deep, dug in a muddy substrate with no roots or any other hard structure. This facilitates the capture of crabs, because the collector is able to insert his or her entire arm into a burrow.

The collecting sites were classified according to the intertidal area, as follows: site S1 was established nearest the supralittoral zone, i.e., 1 m distant from the shoreline, S2 was 15 m from the shoreline, and S3 was farthest from the shoreline (approximately 30 m). Each point of collection represents an area of approximately 20 m long (parallel to the supralittoral zone) by 5 m wide, totalling 100 m² of area. The distance between one site and the next was about 10 m.

Sediment and water were obtained monthly at each site to determine the sediment texture and organic-matter content, and the water salinity. The surface temperature of the sediment at each site was also taken (Mercury column thermometer). In order to determine the size of the first juvenile stage, some additional collections during the month of June (2003) were made at Site 1 (a period when the presence of megalopae was observed). The megalopae were collected using a small teaspoon. The other collection sites were not sampled, because the muddy sediment made sampling impracticable.

The crabs were stored in plastic bags, labelled, and kept on crushed ice in an insulated container until they were measured in the laboratory. The megalopae collected were isolated in plastic boxes and transported to the laboratory. Transportation from the collecting site to the laboratory took approximately one hour.

In the laboratory, the specimens of *U. maracoani* were sorted and their sex assessed by observing the chelipeds, abdominal external morphology, and the number of pleopods. The presence of eggs was recorded. The carapace width (CW) was measured with a digital caliper (0.01 mm) and recorded on charts according to the collecting site. The megalopae were kept isolated in acrylic containers with approximately 20 ml of seawater (salinity 26) and fed daily with nauplii of *Artemia* sp. until they reached the juvenile stage at which the species could be determined. Crabs smaller than 4 mm CW from megalopae and the megalopae were measured under a stereoscopic microscope provided with an imaging and measurement tool.

The morphological sexual maturity of the fiddler crabs was estimated by means of the allometric technique, according to Hirose & Negreiros-Franozo (2007). Males and females attained the size at onset of morphological maturity at 21.2 and 19.4 mm of CW, respectively. Smaller specimens were considered juveniles.

The fiddler crabs were distributed monthly in 11 size classes each of 4 mm, beginning with 4 mm CW and after that classified according to the

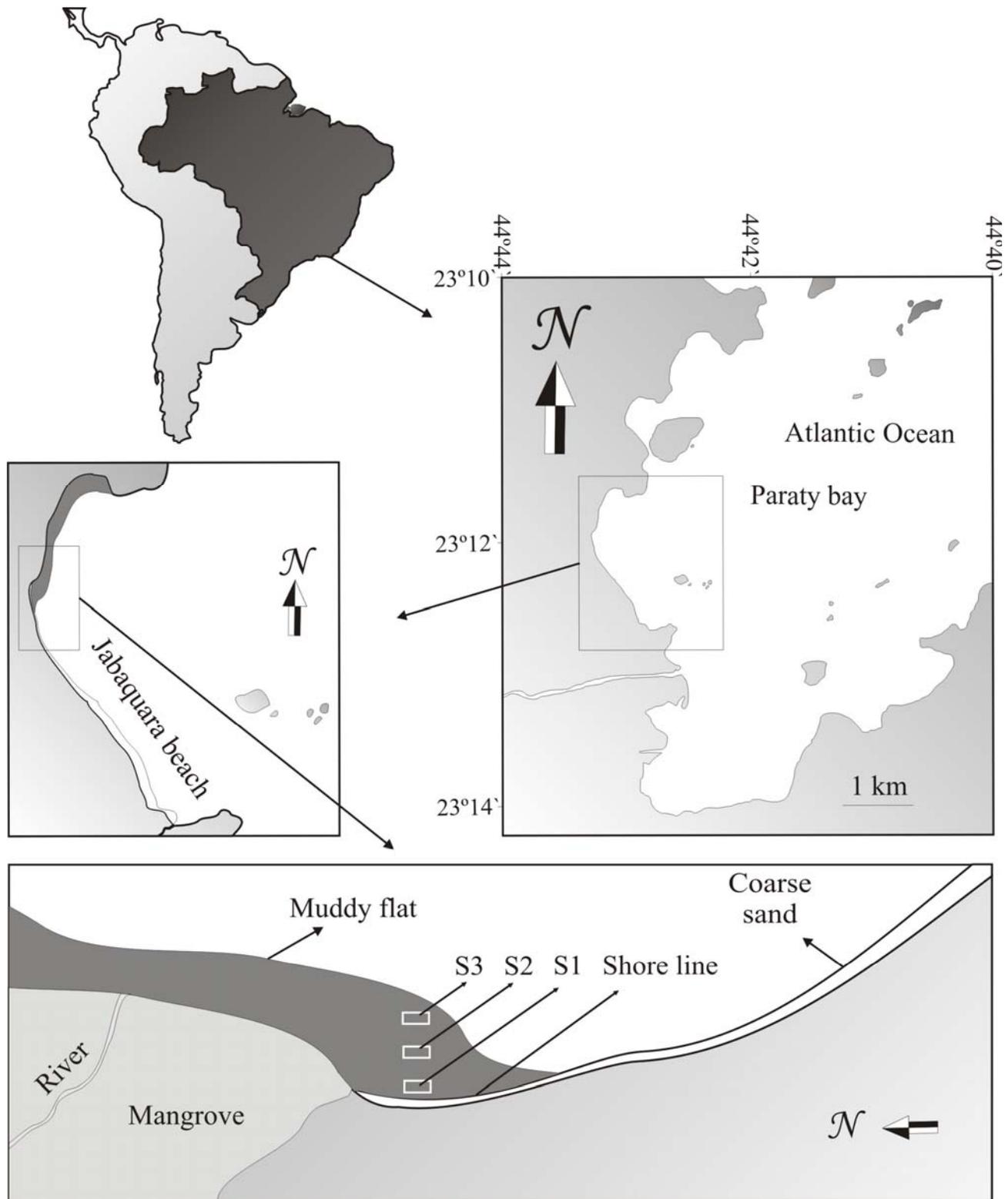


Figure 1. Map of Paraty Bay, State of Rio de Janeiro, Brazil, showing the location of the sampling site (S1, S2, and S3 are the collecting sites).

following demographic categories: juvenile males (<21.2 mm CW), adult males (≥ 21.2 mm CW), juvenile females (< 19.4 mm CW), adult females (≥ 19.4 mm CW), and ovigerous females (≥ 19.4 mm CW, with eggs attached to the pleopods).

The number of classes was obtained by Sturge's formula (Conde *et al.* 1986).

$$K = 1 + 3.22 \log N$$

Where K= class number and N = number of crabs

Monthly substrate samples were analyzed for particle size assessment based on Wentworth

(1922), adopting the American scale. The organic-carbon content was estimated by combustion of part of each sample in an oven at 500 °C and measuring the residual weight. Salinity was estimated by an optical refractometer.

Statistical Analyses

Tests of normality (Kolmogorov-Smirnov) and homoscedasticity (Levene) were carried out prior to the analyses, as pre-requisites for the statistical tests used.

The mean sizes for males and females among collecting sites were compared by means of an Analyses of variance (ANOVA, $\alpha=0.05$). To determine the significant differences among groups, a posteriori Tukey test was applied. To compare the size between males and females, the data of all sites were grouped and a non parametric test (Mann-Whitney) was utilized ($\alpha=0.05$) (Zar 1996).

The proportions of juveniles and ovigerous females in each season were compared by the Goodman's test utilizing the statistical software MANAP (Curi & Moraes 1981), which analyzes the contrasts between and within multinomial proportions ($\alpha=0.05$).

A Chi-square test for goodness of fit ($\alpha=0.05$) was performed to verify whether the sex ratio in the population, in each month, in each size class and for the entire year departed significantly from 1:1 (Sokal & Rohlf 1995).

An analysis of variance was used to compare the mean values of organic matter, granulometric composition, salinity and temperature (for collecting sites and seasons). Subsequently, a

posteriori Tukey's test was performed to determine significant differences among groups ($\alpha=0.05$) (Sokal & Rohlf 1995).

A possible correlation between the frequency of juveniles and environmental factors (the monthly temperature of the surface sediment and salinity) was evaluated by means of a cross-correlation analysis.

Results

A total of 1540 crabs (816 males and 724 females) and 17 megalopae were collected. Of these, 557 were collected at site S1 (341 males, 216 females, and 17 megalopae), 503 at site S2 (248 males and 255 females), and 480 at site S3 (227 males and 253 females).

The mean size of the crabs was smallest at site S1 for males and females ($p<0.05$) (Fig. 2 and Tab. I). Descriptive statistics for each demographic category and the first juvenile stage are shown in Table II. Differences in the median size (for all crabs grouped) between males (32.0 mm) and females (28.6 mm) were statistically significant ($p=0.00$) (Tab. II).

Table I. Results of the Analyses of Variance (ANOVA) and posteriori Tukey test for males and females for the sampling sites.

SEX	ANOVA (p-value)	Tukey (p-value)		
		Sites	S2	S3
Males	0.011*	S1	0.290	0.008*
		S2	-	0.328
Females	0.005*	S1	0.007*	0.017*
		S2	-	0.944

* Significantly statistical differences

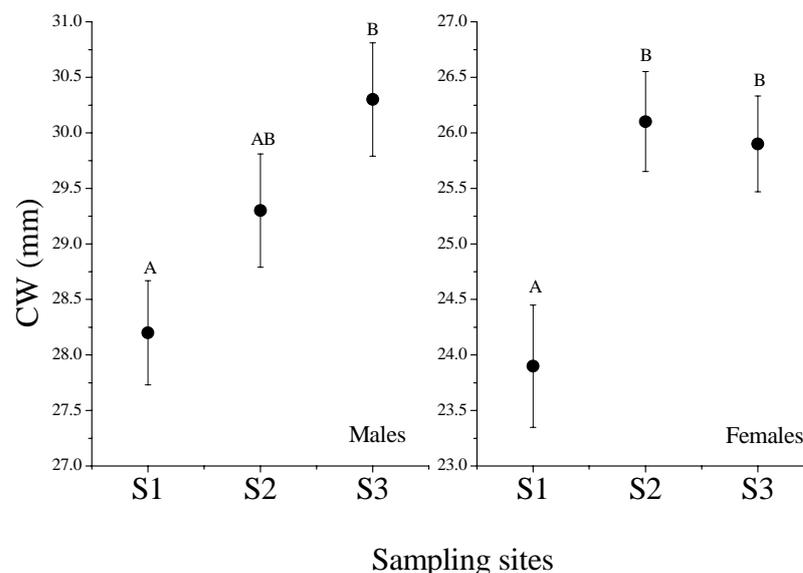


Figure 2. *Uca maracoani*. Mean values and standard deviation of the carapace width for males and females at each sampling site (S1, S2, and S3). Sites sharing at least one letter in common did not differ statistically (ANOVA, $\alpha=0.05$).

Table II. *Uca maracoani*, descriptive statistics for each demographic category and the first juvenile stage.

Demographic category	N	Min-max (CW mm)	median	Mean ± sd
J1	17	1.16 – 1.48	1.44	1.30 ± 0.07
JM	144	4.9 – 21.1	16.0	15.5 ± 4.1
AM	672	21.3 – 45.0	32.0*	32.0 ± 5.7
JF	138	5.1 – 19.4	15.6	14.7 ± 3.9
AF	503	19.4 – 40.2	28.6*	28.7 ± 4.7
OF	83	22.5 – 37.3	29.8	29.8 ± 3.1

N = number of crabs, CW = carapace width, sd = standard deviation, J1= first juvenile stage, JM = Juvenile Males, AM = Adult Males, JF = Juvenile Females, AF = Adult Females, OF = Ovigerous Females. * Statistically significant (Mann-Whitney, p = 0.00).

The size-frequency distributions showed variations, i.e., some months were bimodal (June, July, and August), or bimodal for males and unimodal for females (May, November). We also found a shifting of the modes (June to July, September to October, November to December). The largest males disappeared in May, June, December, and January, revealing a very dynamic population (Fig. 3).

Juveniles and ovigerous females occurred year-round, with the highest frequency during

autumn, winter and spring and the lowest in summer (P<0.05) (Fig. 4A and B). Juveniles were more frequent principally during the period of June to November of 2003 (Fig. 3).

Analyzing the total number of fiddler crabs during the entire year, the sex ratio was skewed toward males (53%, χ^2 , P<0.05), with a ratio of 1:0.8 (males: females). When the sex-ratio was analyzed monthly, males were significantly more numerous than females in May and December 2003 and March and April 2004. Females were more

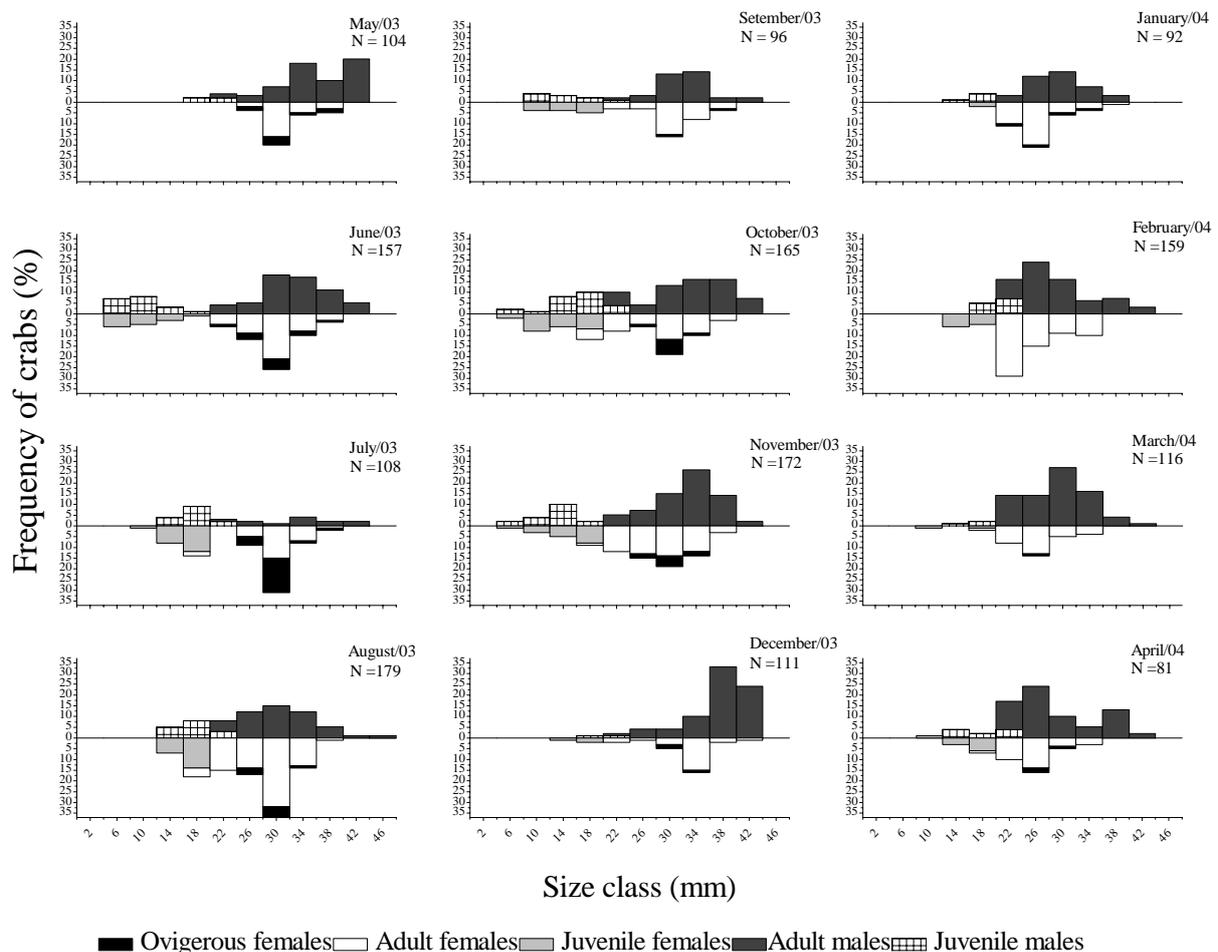


Figure 3. *Uca maracoani*. Size-frequency distribution of each demographic category during the course of one year.

abundant than males only during July and August 2003 (Fig. 5A). The sex-ratio in size classes remained in the proportion 1:1, with a deviation toward males only in the largest size classes (Fig. 5B).

Concerning the environmental factors analyzed in the study area, the sediment was composed mainly of silt + clay with a high percentage of organic matter (Table III). A small percentage of fine sand was found in the area, the

percentage at site 1 differed significantly from the other sites (Tab. IV).

The temperature of sediment and salinity does not present statistical differences when analysed in relation of sites ($p= 0.89$ and $p= 0.7$ respectively), but in relation of the sample period (seasons), the temperature and salinity present significantly fluctuations ($p= 0.00$ and $p= 0.00$ respectively) (Tab. V and VI).

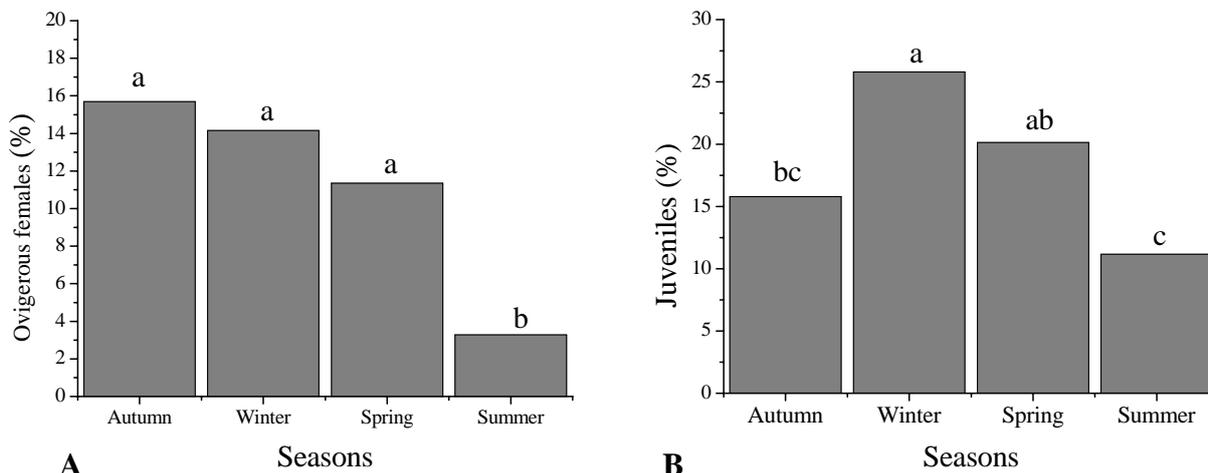


Figure 4. *Uca maracoani*. A = Ratio of ovigerous females and B = Ratio of juveniles in each season. Bars with at least one letter in common did not differ statistically (Goodman's test $\alpha=0.05$).

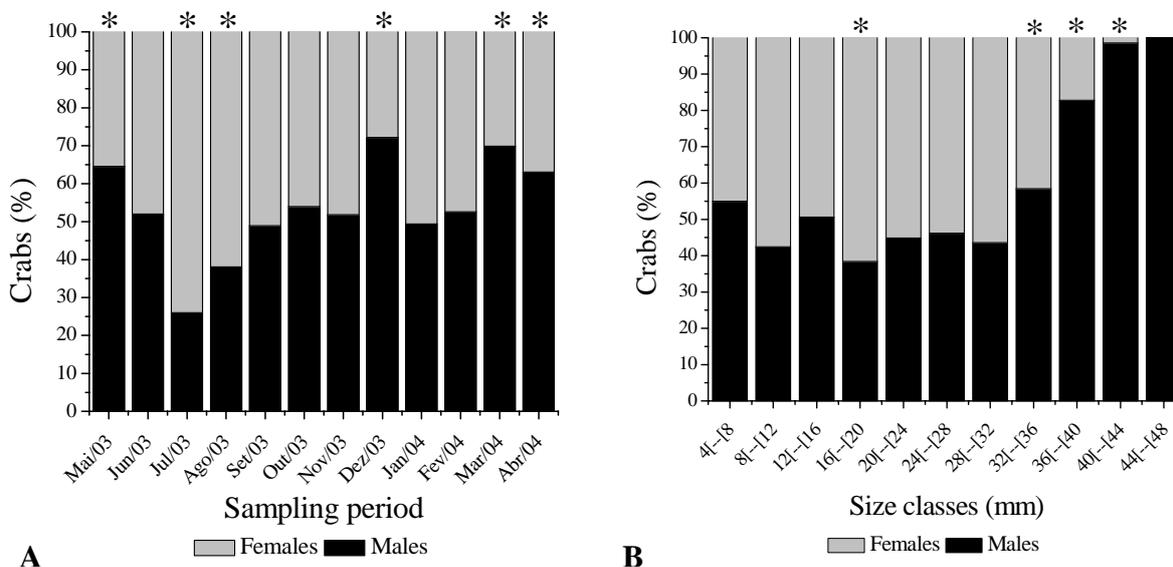


Figure 5. *Uca maracoani*. A = Percentage of males and females in each month and B = Percentage of males and females in each size class (CW, mm). * indicates statistical significance (χ^2 , $p<0.05$).

Table III. *Uca maracoani*, Descriptive statistics for each environmental factor at the collecting sites of the Jabaquara mudflat.

SITES	S/C (%)	FS (%)	OM (%)	Water	Temperature °C
	mean± sd	mean± sd	of the sediment mean± sd	salinity mean± sd	mean± sd
S1	92.0±7.8	8.0±7.8	10.9±2.3	27±7.0	28.93±4.0
S2	99.4±0.3	0.64±0.3	11.7±1.7	25±8.1	28.33±2.9
S3	99.4±0.2	0.63±0.19	12.5±1.7	25±9.6	28.47±4.4

S/C = Silt/clay, FS = Fine sand and OM = organic matter

The crosscorrelation analysis indicated a time lag of one month between the number of juveniles and the monthly superficial sediment temperature with a negative correlation ($p = 0.00$

and $R = - 0.64$) (Fig. 6). To the juveniles and monthly salinity the analysis indicate a time lag of two month with a positive correlation ($p = 0.00$ and $R = 0.66$) (Fig.7).

Table IV. Results of the Analyses of Variance (ANOVA) and posteriori Tukey test for the fine sand among sites ($\alpha=0.05$).

Factor	ANOVA (p-value)	Tukey (p-value)		
		Sites	S2	S3
Fine sand	< 0.001*	S1	0.00*	0.00*
		S2	-	1.00

* Significantly statistical differences

Table V. *Uca maracoani*, Descriptive statistic of superficial temperature of sediment and salinity in each season throughout the sample period in mudflat of Jabaquara mangrove.

Seasons	Temperature °C			Salinity		
	Mean ± sd	Max. value	Min. value	Mean ± sd	Max. value	Min. value
Autumn	28 ± 5.32	34	21	27.7 ± 9.2	36	10
Winter	25.8 ± 1.39	27	23.5	32.7 ± 0.5	33	32
Spring	29.1 ± 2.92	35	26	24.4 ± 6.6	35	14
Summer	32.2 ± 2.99	36	30	17.9 ± 5.7	26	8

Table VI. Results of the Analyses of Variance (ANOVA) and posteriori Tukey test for the environmental factors with significantly statistical differences ($\alpha=0.05$).

Factor	ANOVA (p-value)	Tukey (p-value)			
		Seasons	Autumn	Winter	Spring
Temperature	<0.001*	Summer	0.053	0.001*	0.217
		Autumn	-	0.242	0.884
		Winter	0.242	-	0.061
		Spring	0.025*	0.001*	0.196
Salinity	<0.001*	Autumn	-	0.414	0.744
		Winter	0.414	-	0.072
		Spring	0.072	0.414	-

* Significantly statistical differences

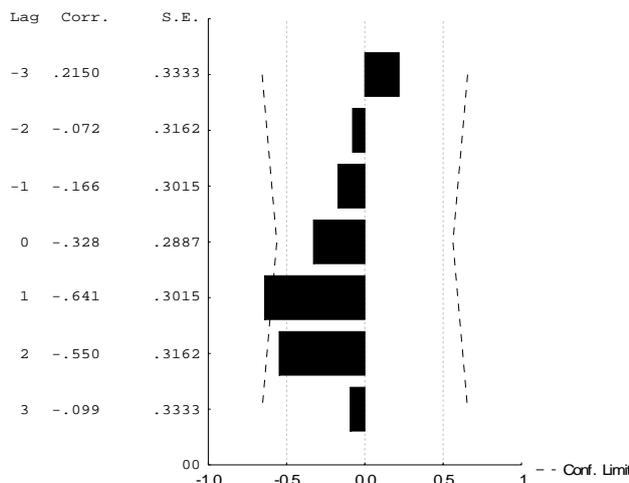


Figure 6. Crosscorrelation analysis between juvenile frequency and monthly superficial sediment temperature of the collecting site of Jabaquara mudflat during the sample period ($\alpha=0.05$).

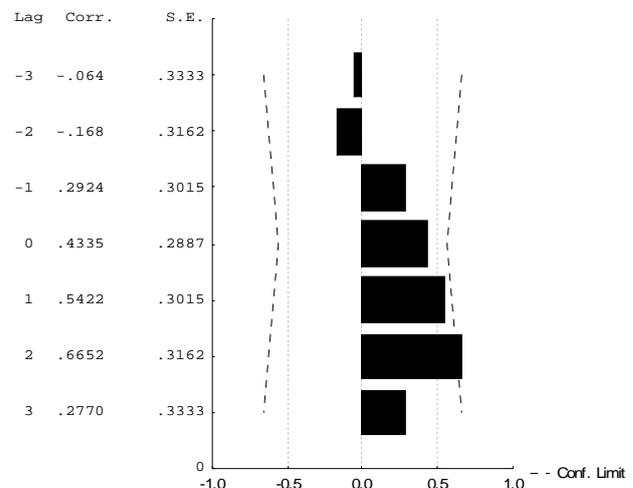


Figure 7. Crosscorrelation analysis between juvenile frequency and monthly salinity of the collecting site of Jabaquara mudflat during the sample period ($\alpha = 0.05$).

Discussion

The mean sizes of both sexes of *U. maracoani* collected at site S1 (near the coarse sand of the beach) were smaller than at the other sites. This may be related to a higher recent juvenile recruitment rate at that site, the presence of megalopae indicate, that the site really can be a settling area utilized by this species. This higher juvenile recruitment may be influenced by the swift currents during rising tides, which affect larval settlement (Dittel *et al.* 1991, Olmi III 1994, Lochmann *et al.* 1995), facilitating the transport of megalopae to the upper limit of the intertidal zone. Another possibility is that the rough texture from the sand fraction at site 1 may favour larval establishment or settlement.

Settlement location for some kinds of larvae appears to be random or primarily influenced by physical factors such as currents, salinity, and light. However, other kinds of larvae respond to positive or negative environmental cues, leading to preferential settlement in, or avoidance of, specific habitats or areas (Banks & Dinnel 2000).

Other possibility for the differential size distribution of the crabs may be behavioural, migration and/or differential mortality among the sites. Contests in fiddler crabs is a common event among the species (Crane 1975, Hyatt & Salmon 1978) and consist of a series of behavioural elements (Pratt *et al.* 2003) were normally smaller crabs avoid combat with the larger, dominant individuals, leaving the interaction area. Thus, the difference of crab sizes among the sites can represent a preferential area for *Uca maracoani* where the sites more distant of supralittoral zone were preferred for the larger (dominant) individuals.

Predation pressure may be higher at site 1, because this site is nearest the supralittoral zone, and in consequence is more exposed to terrestrial predators. Johnson (2003), studying *Uca pugilator* (Bosc 1802), calculated the size of predated crabs from chelipeds found in nature, and reported in such population that larger crabs were preferred by predators.

The analysis of size-class distribution revealed a very dynamic population, which in some months showed bimodality and in others, unimodality. This may indicate the existence of two different age groups, or that variations found for *U. maracoani* are related to migration, differential mortality, and growth rates (Diaz & Conde 1989, Yamaguchi 2001).

In this population, the males reach larger sizes than females. In other brachyurans (Warner 1967, Benetti & Negreiros-Franzo 2003, Johnson

2003, Luppi *et al.* 2004, Litulo 2005), a similar pattern was recognized in which males show a protracted period of somatic growth and/or a higher molt increment. The energy allocated to reproduction should be proportionally greater in females, because more energy is needed for the production of oocytes than spermatocytes, and thus females can interrupt or reduce their somatic growth during the period when they are incubating eggs (Alunno-Bruscia & Sainte-Marie 1998, Haltvoll 2006).

Slower growth can also reflect reduce energy intake because of restriction on feeding. In females, a more general phenomenon is a restriction on feeding during incubation. A further limitation on growth in reproducing females is they cannot molt while incubating eggs (Hartnoll 2006).

Reflecting this differential growth, the proportion of males and females differed from 1:1 only in the classes of larger crabs, and maintained Fisher's proportion in the others. According to Wenner (1972), such a sex-ratio pattern is described as "standard".

Montague (1980) suggested that male biases in fiddler-crab populations are sampling artefacts resulting from a focus on surface sampling and failure to incorporate differential habitat use. In *Uca vocans* (Linnaeus) studied by Murai *et al.* (1983), and *Uca tangeri* Eydoux 1835 studied by Crane (1975), the behaviour of foraging (known as droving) in nearby areas is predominantly displayed by males. Ovigerous females may spend prolonged periods underground and, when on the surface, often forage closer to water sources, creating spatial separation from foraging males (Montague 1980, Macia *et al.* 2001, Skov & Hartnoll 2001).

In a recent review of biased sex-ratios in fiddler crabs, Johnson (2003) documented that in at least 14 species, males exceeded females, suggesting that this bias has an ecological significance, rather than being a sampling artefact.

During July and August 2003, females outnumbered males, which coincided with the highest frequency of ovigerous females. One can infer from this that during incubation of the eggs, females may be more susceptible to capture, which is reflected in the estimated sex-ratio.

Although the proportion of ovigerous females did not exceed 16%, they were present in all seasons, which indicate a continuous reproductive period. However, during summer the ovigerous-ratio was lower (<5%), suggesting that the other seasons were more favourable for gonadal and embryonic development.

Among the factors that seem to affect crab reproduction and larval development timing are environmental conditions (temperature, salinity, luminosity, tide range, marine currents) and biological factors (food availability, competition) (O'Connor 1993, Rodrigues & Jones 1993). The mudflat of Jabaquara beach is characterized by absence of vegetation, and consequently also is disproved of shadowed areas. Thus, the Jabaquara mudflat receives a direct and intense solar radiation during all time. This strong incidence of solar radiation is responsible by an increase in the superficial temperature of sediment during the low tides periods, which in the summer can reach extreme values. The summer also presented the lowest values of salinity, probably related to higher rates rainfall for this season.

This may be responsible for the low reproductive intensity in the summer. The high temperature and the low salinity may be a limitation for embryonic development and/or a critical feature in the settlement of larvae and/or establishment of early recruits. Sulkin *et al.* (1996), in a study of the effects of elevated temperature on the development of megalopae and early juveniles of *Cancer magister*, concluded that the high temperatures in the shallow-water benthic habitat during the period when peak settlement and early juvenile growth are occurring could result in a high mortality of subsequent juvenile stages. In this context, Nurdiani & Zeng (2007), in a study of the effects of temperature and salinity on the survival and development of *Scylla serrata* (a mud crab), observed that the interaction between these two factors (temperature and salinity) significantly affected the larval survival. Lower salinity (15gL^{-1}) results in no larval survival to the first crab stage for all temperatures tested, but, in contrast, the combination of low temperature and high salinity ($25^{\circ}\text{C}/35\text{gL}^{-1}$) resulted in one of the highest rates of survival to the megalopa stage (Nurdiani & Zeng 2007).

The hypothesis that the interaction of high temperature and low salinity in the summer affects the reproduction and recruitment of *U. maracoani* on the mudflat of Jabaquara Beach is supported by the negative correlation of juveniles and temperature

and a positive correlation of juveniles and salinity, which are released with a one-month lag and a two-month lag, respectively.

A juvenile recruitment pulse during winter and spring suggests a higher reproductive activity during the autumn and winter, when the ocypodid crabs required 20 ± 8 days to incubate their eggs and the larvae required 29 ± 16 days to complete their metamorphosis until the first juvenile stage (Hines 1986), when they reach 1.33 ± 0.10 mm CW. We note that crabs less than 5 mm CW, i.e., recent established recruits, were not obtained. This suggests a deficiency in sampling and probably the lag existent in the correlation of juveniles, temperature and salinity can be a result of this deficit.

Although the results of this study tend to indicate constant recruitment, further studies should focus on larval establishment and/or juvenile recruitment, in order to gain a better comprehension of the replacement of individuals in the population.

According to Emmerson (1994), the majority of tropical species has a continuous reproductive period throughout the year, or have longer reproductive seasons than do species living at higher latitudes. Thus, continuous reproductive activity is common for fiddler crabs, which are typically adapted to living in warm regions (Crane 1975).

The variations in the population structure found for *U. maracoani* are apparently related to the behaviour of the species or responses to natural process. However, human activities, such as construction of piers or residential developments for touristic purposes near the mudflat estuary and neighbouring shores, may change the environment drastically. Thus, the information reported here may help in the conservation of this species, which is becoming uncommon on the northern coast of São Paulo state.

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