SCI. MAR., 68 (1): 139-146 SCIENTIA MARINA 2004

Comparison of the population structure of the fiddler crab *Uca vocator* (Herbst, 1804) from three subtropical mangrove forests*

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SUMMARY: The population structure of *U. vocator* was investigated during a one-year period in three mangrove forests in southeast Brazil. The study specifically addressed comparisons on individual size , juvenile recruitment and sex-ratio. The structure of the mangrove forests, i.e. density, basal area, and diameter, and the physical properties of sediments, i.e. texture and organic matter contents, were also examined. A catch-per-unit-effort (CPUE) technique was used to sample the crab populations using 15-min sampling periods by two people. Males always outnumbered females, probably due to ecological and behavioural attributes of these crabs. The median size of fiddler crabs differed among the sampled populations. The mangroves at Indaiá and Itamambuca showed higher productivity than those at Itapanhaú, where oil spills impacting the shore were reported. Marked differences were found regarding individual size , either their size at the onset of sexual maturity or their asymptotic size, suggesting that food availability may be favouring growth in the studied populations.

Key words: population structure, mangrove crab, Ocypodidae, *Uca vocator*.

RESUMEN: COMPARACIÓN DE LA ESTRUTURA POBLACIONAL DE *UCA VOCATOR* (HERBST, 1804) EN TRES MANGLARES SUBTROPICALES. – La estructura poblacional de *U. vocator* fue investigada por 1 año in tres manglares del sudeste brasileño. El estudio estuvo dirigido a la comparación de la talla de los individuos, reclutamiento de los juveniles y la razón sexual. La estructura del bosque de los manglares, i.e., densidad, área basal y diámetro, y las propiedades físicas del sedimento, i.e., textura y contenido orgánico, también fueran evaluadas. Dos personas durante 15 minutos (técnica de captura por una unidad de tiempo) hicieran un muestreo de las poblaciones de cangrejos. Los machos siempre estuvieran en más numero que las hembras, probablemente por sus distintos comportamientos. La talla mediana de estos cangrejos difirió entre las poblaciones estudiadas. Los manglares de Indaiá y Itamambuca presentaran una productividad más grande que Itapanhaú, donde ocurrió un impacto ambiental debido a un derramamiento de petróleo. Las diferencias significativas encontradas tanto en la talla de la maturidad como en la talla asintótica de los cangrejos, sugieren que la disponibilidad de alimento puede estar favoreciendo el crecimiento en las poblaciones estudiadas.

Palabras clave: estructura de población, cangrejo de mangle, Ocypodidae, *Uca vocator*.

INTRODUCTION

Crabs are abundant in mangrove forests, but it is very difficult to quantify their population density accurately (Macintosh, 1988). The Grapsidae and Ocypodidae constitute most of the mangrove crab fauna (Jones, 1984). Robertson and Daniel (1989), studying Australian mangrove forests, observed that a crab community can process about 70% of the litter. In contrast, in Florida mangroves, most of the litter is exported by tide action, and its processing begins in subtidal regions, where leaves are frag-

*Received September 19, 2001. Accepted July 8, 2003.

mented by grazing action of crabs and amphipods, and decomposed by microbes (Twilley *et al*., 1995). Thus, crabs are important because they control the remineralisation rate of detritus (Robertson, 1991). Burrowing and foraging activities of fiddler crabs promote bioturbation of estuarine intertidal flats. They remove large amounts of sediment and change the substrate characteristics, increasing water and organic matter contents, as well as their penetration in the sediment layers (Botto and Iribarne, 2000; Meziane *et al*., 2002), and changing the nutrient dynamics which affects microbiotic growth and stimulates vegetal production (Genoni, 1985).

Mangroves show high primary production, and many authors have addressed the influence of crab activities on these ecosystems (Robertson, 1986; Macintosh, 1988; Robertson and Daniel, 1989; Robertson, 1991; Lee, 1999; Botto and Iribarne, 2000; Meziane *et al.*, 2002). However, the effects of mangrove forest productivity on crab populations are still poorly known (Conde *et al.*, 2000). The studies by Conde *et al.* (1989), Conde and Díaz (1992a, b) and Conde *et al.* (2000) have focused on body size and the plasticity of reproductive variables in the tree-climbing crab *Aratus pisonii* (H. Milne Edwards, 1837). These authors have suggested a possible effect of mangrove productivity on the measured variables, since significant differences were found among populations from nearby estuarine forests with a different tree composition and structure. In this study, among-population contrasts are examined in *Uca vocator* in order to verify whether intra-specific variability may also take place in other mangrove crabs. Besides size, which may be an indicator of habitat productivity, juvenile recruitment and sex-ratio are also examined in order to compare key processes ruling population dynamics.

MATERIALS NAD METHODS

Study areas

Three mangrove areas were investigated throughout one year (from August 1999 to July 2000). The sampled areas are shown in Figure 1. The vegetation at these sites was characterised in Colpo (2001), and the main features are described below. At Itapanhaú

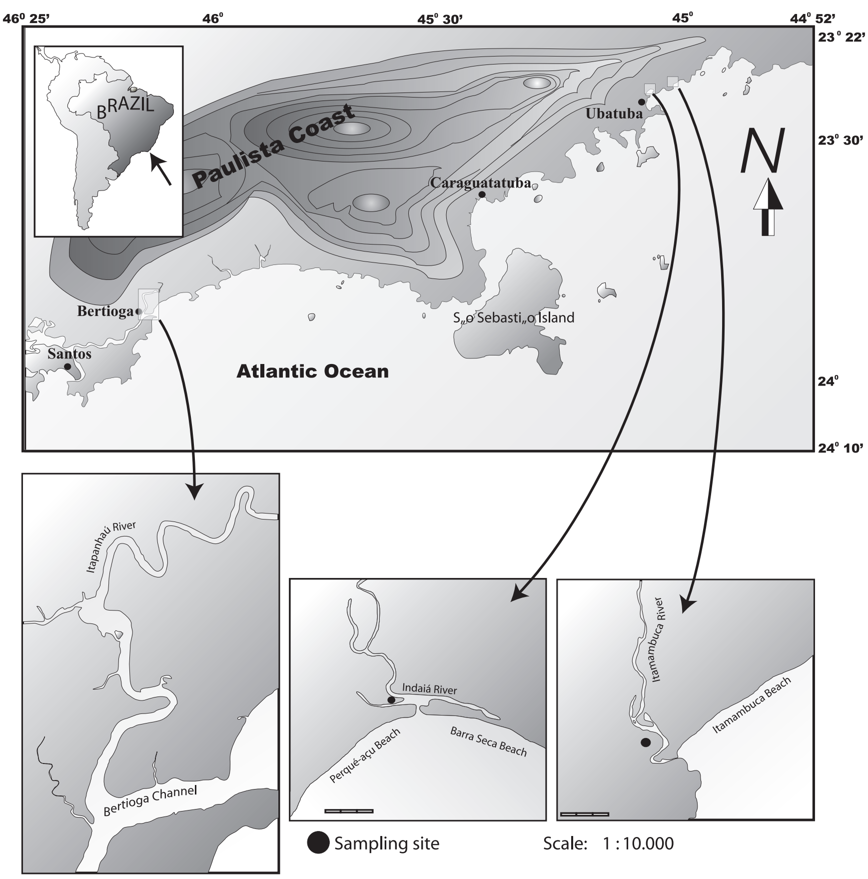

FIG. 1. – Map indicating the sampling areas.

(23°49'14"S; 46°09'14"W) the mangrove area extends over a larger tide flat. This is a mature mangrove, with an average density of 3,750 tree.ha^{-1}, a basal tree area of 8.2 m^2.ha^{-1} and a mean diameter breast height (dbh) of 34.2 cm. Three species were recorded at this mangrove site: *Laguncularia racemosa* L. (28.3%), *Rhizophora mangle* Gaertn and Leach (64.4%) and *Avicenia shaueriana* Stapf and Leechman (7.3%). The area has been heavily impacted by oil spills totalling 3.5 millions litres. Ponte *et al.* (1987 and 1990) recorded a reduced leaf production and a large amount of dead trees in the area. At Indaiá (23°24'51"S 45°03'14"W) the mangrove forest is younger. At this site, a mean density of 9,375 tree.ha^{-1}, a basal area of 13.3 m^2.ha^{-1}, and a mean dbh of 5.2 cm were recorded. *Laguncularia racamosa* was the most abundant tree species in this mangrove forest (97.2%), and *A. shaueriana* accounted for 2.8% of all recorded trees. Indaiá is located closer to the river mouth, and therefore more directly subjected to tidal action. At Itamambuca (23°24'43"S; 45°00'73"W), the mean tree density was estimated as 1,250 tree.ha^{-1}, and their basal area and mean dbh as 3.7m^2.ha^{-1} and 6.0 cm respectively. Only *L. racemosa* was recorded. This is a more upstream site, where ebbing tides do not seem to flush away all locally-produced propagules and litter. During the sampling period, a pronounced development of the mangrove vegetation was observed in this area.

Sampling, laboratory analyses and statistical procedures

Each month, three sediment samples (about 10 cm deep and 300 g) were randomly obtained over each sampling area (approximately 100 m^2). The texture of sediments was measured according to Suguio (1973) and the organic matter content was quantified by ash-free dry weighing (AFDW). To compare the sediment characteristics among mangroves, samples were pooled by seasons (Jul-Sep: Winter; Oct-Dec: Spring; Jan-Mar: Summer; Apr-Jun: Autumn), and comparisons were carried out by running one-way analyses of variance, followed by the *a posteriori* Tukey procedure (Zar, 1996).

Uca vocator inhabits partly shaded patches over mud flats (Crane, 1975). This crab feeds directly on the sediments, sorting detritus, microalgae and microorganisms. The three populations studied here were found in similar habitats. These fiddler crabs burrow in the substrate under trees, where falling leaves are readily decomposed by both micro- and macrofauna, if they are not removed by tide action. Temperature, photoperiod and flooding time were similar for all three sites (Colpo, 2001).

TABLE 1. – Size at first maturation in *Uca vocator* in each mangrove area. Values obtained using the allometric technique (after Colpo, 2001). CW = carapace width.

Site	Male size maturation (CW in mm)	Size at 50% females are mature (CW in mm)
Itapanhaú	12.7	11.4
Indaiá	10.0	12.1
Itamambuca	13.3	15.2

Fiddler crabs were always sampled at low tide. A CPUE method was used for sampling. For that, two people scanned the sampling area for 15 minutes for crab detection and removal. In the laboratory, the individuals were sorted and their sex was determined by checking the presence of gonopods and enlarged chelipeds in males, and the four pleopod pairs and symmetric chelipeds in females. For the smallest crabs, pleopod morphology was examined under a stereomicroscope. Maximum carapace width (CW) was recorded with a digital caliper to a precision of 0.01 mm. Size at the onset of sexual maturity was estimated using the allometric technique, and the overall results are shown in Table 1 (Colpo, 2001). Size-frequency distributions for the whole sample at each site departed significantly from normality and homoscedasticity (Shapiro-Wilk and Levene tests, respectively; Underwood, 1997). Therefore, male and female adult median sizes were compared among the three populations using the non-parametric Kruskal-Wallis test (Zar, 1996). Seasonal juvenile recruitment to each population was assessed by comparing monthly estimates of the juvenile proportion (Goodman test, Goodman, 1965). Departures from the 1:1 sex-ratio were tested using a χ^2 test (Sokal and Rohlf, 1995). The ovigerous proportion, as their relative frequency within mature females, was calculated each month. Paired Z-tests were used to compare overall juvenile, male, and ovigerous proportions between sampling sites (Sokal and Rohlf, 1995). The statistic significance level of 5% was used in all analyses.

RESULTS

The granulometric composition of sediments from Itapanhaú and Itamambuca showed a great proportion of silt/clay, while very fine sand pre-

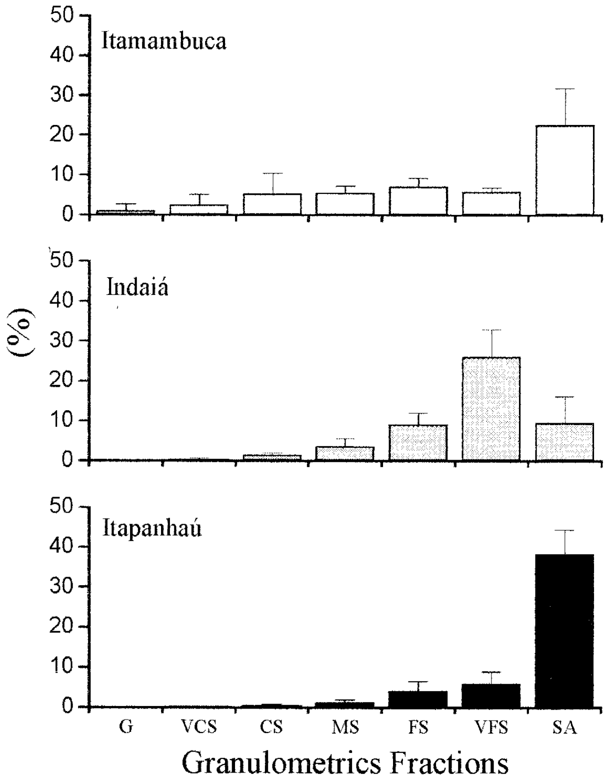

FIG. 2. – Comparison of the granulometric composition of sediments at each studied site. Bars indicate standard deviation. (G= gravel; VCS= very coarse sand; CS= coarse sand; MS= medium sand; FS= fine sand; VFS= very fine sand and S+C= silt+clay).

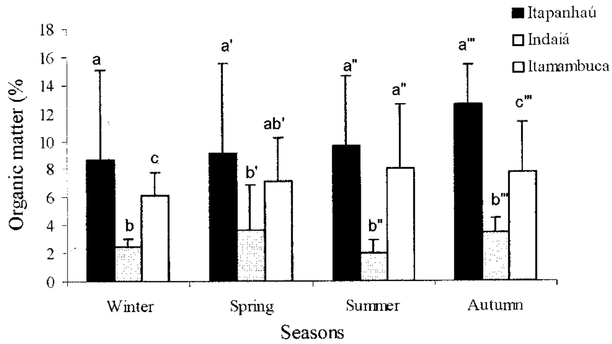

FIG. 3. – Organic matter contents recorded during each season at each studied site.

vailed at Indaiá (Fig. 2). The AFDW of sediments was greater at Itapanhaú, followed by Itamambuca and Indaiá in all seasons (Fig. 3).

A total of 1,061 fiddler crabs were sampled throughout the year from Itapanhaú, 1,024 from Indaiá, and 543 from Itamambuca. Size characteristics of crabs measured at each sampling site are shown in Table 2. Maximum crab size was lower at Itapanhaú (CW=21.2 mm) than at Indaiá and Itamambuca. At Indaiá, individuals larger than the maximum size at Itapanhaú composed 4.7% of the whole sample, while such crabs represented 70.2% of all individuals collected at Itamambuca (Table 3). The median size of adult males differed among mangroves (Kruskal-Wallis $p<0.05$). It was smaller at

TABLE 2. – Descriptive statistics of crab size (CW in mm) according to sex and development phase in *U. vocator*; CW = carapace width; N = number of crabs; SD = standard deviation.

Site	Demographic categories	N	CW mean (mm)	SD	CW minimum (mm)	CW maximum (mm)
Itapanhaú	Juvenile male	172	7.5	1.7	1.2	9.9
	Adult male	418	14.9	2.7	10.0	21.2
	Juvenile female	181	8.2	2.0	3.2	11.3
	Adult female	290	15.4	2.2	11.4	21.1
Indaiá	Juvenile male	239	10.2	2.4	1.3	13.2
	Adult male	402	16.8	2.5	13.3	23.7
	Juvenile female	146	9.5	2.0	4.7	12.1
	Adult female	237	15.7	2.6	12.0	23.7
Itamambuca	Juvenile male	97	12.4	3.2	5.9	12.6
	Adult male	208	21.0	2.0	12.7	27.0
	Juvenile female	44	11.4	3.0	4.2	15.1
	Adult female	194	19.7	2.1	15.2	24.8

TABLE 3. – Maximum values of carapace width (mm) of *U. vocator* at each site, and proportion of adult crabs equal to or larger than 21.2 mm (largest crab found at Itapanhaú).

Sites	Adult males (N)	Adult females (N)	Largest crab (mm)	Number (%) of crabs ≥21.2
Itapanhaú	229	165	21.2	1 (0.25)
Indaiá	515	288	23.7	38 (4.7)
Itamambuca	208	164	27.0	146 (70.2)

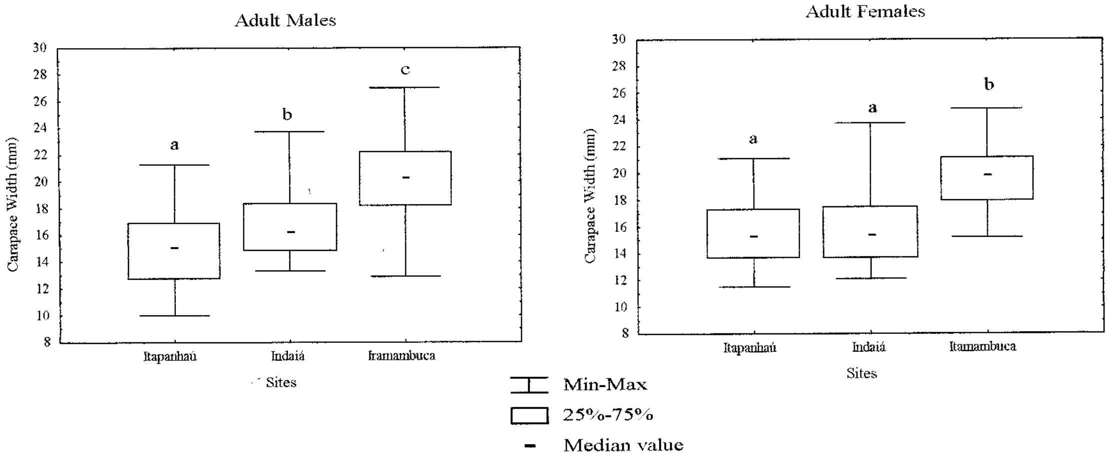

FIG. 4. – Comparison of the median size of adult males and females of *U. vocator* in the three mangrove forests. Median values are not statistically different among sites sharing the same letter (p>0.05).

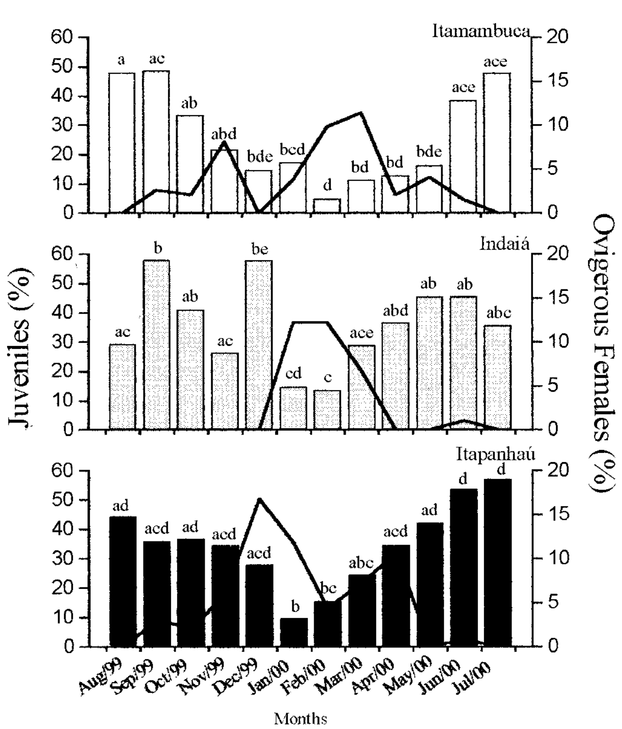

FIG. 5. – Recruitment of juvenile individuals and ovigerous-ratio in *U. vocator* at each studied site. Columns and discontinuous lines depict seasonal variation of juvenile recruitment and ovigerous ratio respectively.

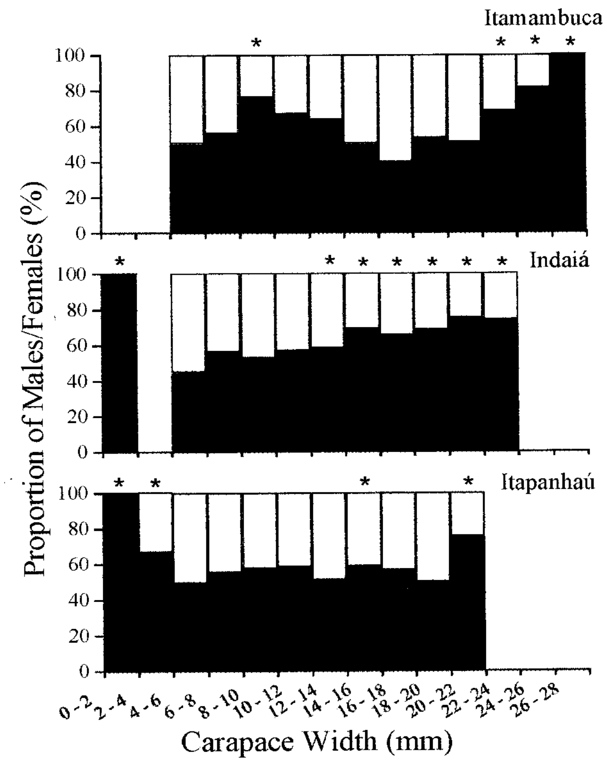

FIG. 6. – Sex-ratio in each size class and sampled mangrove for *U. vocator*. Dark and white columns represent the male and female proportions respectively. Asterisks indicate significant departures ≠from the 1:1 ratio.

Itapanhaú (13.1 mm of CW), intermediate at Indaiá (14.6 mm of CW), and largest at Itamambuca (19.5 mm of CW) (Fig. 4). The median size of adult females was greatest at Itamambuca (18.9 mm of CW), with no significant differences recorded between Itapanhaú (13.3 mm of CW) and Indaiá (13.1 mm of CW) (Fig. 4). Juvenile recruitment was continuous at all sites, with lower proportions of recruits recorded during summer (from November to March), when reproductive activity was highest (Fig. 5). The overall juvenile percentage at Itamambuca (16.9%) was significantly lower than at Itapanhaú (33.3%) and Indaiá (37.8%). Differences between the two latter sites are not significant (Z test, p>0.05). In all populations, the sex ratio was male-biased (χ^2 test, p<0.05): Itapanhaú (1:0.52), Indaiá (1:0.56), and Itamambuca (1:0.78). The male proportion at Indaiá (62.6%) was significantly higher than at Itapanhaú (55.6%) and Itamambuca (56.2%) (Z test, p<0.05) (Fig. 6).

DISCUSSION

Ecosystem productivity is often estimated by assessing the rate of net carbon fixation, taking into account photosynthesis and respiration (Kjerfve and Lacerda, 1993). Based on this premise, mangroves show a relatively high productivity ratio among aquatic ecosystems (Por, 1984; Macintoch, 1988; Kjerfve and Lacerda, 1993). Mangrove stands exhibit wide regional and local variation in structural characteristics due to specific differences at each site, even among nearby areas (Cíntron and Schaeffer-Novelli, 1984; Lacerda *et al.*, 1993). These authors suggest that tree diameter, which can be converted into basal area (the area occupied by tree stems), and tree density are examples of structural parameters, which may be used to evaluate mangrove stand development. Litter is also used by several authors as an indicator of mangrove productivity (Robertson, 1986; Rodriguez, 1987; Twilley *et al.*, 1995). Robertson and Daniel (1989) compared three mangrove forests and verified that litter fall ratios were lower in a sparser canopy forest, as indicated by a lower tree density. Among the sites studied herein, the Itapanhaú forest showed the lowest tree density, so litter fall ratio and productivity are presumably lowest there. Lacerda *et al.* (1993) reported several studies about oil spills in American mangroves. In most cases, such a disturbance produced animal and plant mortality during the first few years. After that, the forests seemed to recover, but the oil remained in the sediment for a longer period, and the interstitial fauna was severely affected, thus causing a decrease in the rate of litter decomposition and therefore nutritional support for several species. The energy flow of the mangrove, and consequently its productivity, decreases after disturbance. The oil spill that took place in 1983 and the regular fuel release from boats may be affecting the productivity of the Itapanhaú mangrove. In contrast, the structural features of the Indaiá mangrove are indicative of high productivity. Negreiros-Fransozo *et al.* (2000) studied six mangrove areas in the southeastern coast of Brazil, and their results suggest that Indaiá is indeed a very productive mangrove area. Itamambuca is a recent mangrove area, where energy flow and nutrient turnover seem to be greatest, which may also enhance productivity.

The consumption of locally produced organic matter in a given mangrove is directly influenced by sediment texture and local hydrology. Muddy substrates (silt/clay predominant) retain more chemical elements than larger grains (Schaeffer-Novelli, 1990; Reitermajer *et al.*, 1998). The sedimentology at Itapanhaú and Itamambuca promote a better organic accumulation than at Indaiá. The highest organic matter content (AFDW) registered at Itapanhaú may indicate the presence of fuel-derived hydrocarbons and/or organic material still to be decomposed, since the interstitial community is known to have been affected (Ponte *et al.*, 1987, 1990; Lee and Page, 1997). At Indaiá, AFDW was lowest in spite of its high productivity. This is probably due to the fact that large grain fractions prevail at that site and that direct tide action may easily flush litter and other organic material seawards. At Itamambuca, muddy sediments are predominant and direct tide action is minimum, thus favouring the retention of organic matter. Identifying the source of organic material is often difficult, since this is not a direct result of mangrove productivity but depends also on the production of the interstitial community, geomorphology, tide action, and litter exportation that influence organic content retention (Por, 1984; Reice *et al.*, 1984; Twilley *et al.*, 1995; Moura *et al.*, 1998; Reitermajer, 1998).

Fiddler crabs sort food items (detritus resulting from litter fall decomposition, algae and infauna) from sediment grains (Miller, 1961; Icely and Jones, 1978). Robertson (1986) suggested that mangrove crabs would not rely solely on mangrove leaves for feeding, since their chemical composition would not supply the metabolic requirements of these consumers. In fact, their diet is complemented by bacteria and other microbes they remove from the mud surface layer. At Itapanhaú, the impacted infauna may not represent an adequate food source for the fiddler crab population. The interstitial community from Indaiá and Itamambuca may be more abundant than at Itapanhaú, so the source seems to be greater in those areas. Specific environmental conditions are likely to affect important biological processes in macroinvertebrates, such as growth and reproduction, as described for *U. vocator* by Colpo and Negreiros-Fransozo (2003). Such environmental constraints are thus reflected in population structure. The species *U. vocator* reach a markedly smaller size at Itapanhaú compared to Indaiá, which, in turn, is smaller than the size recorded at Itamambuca. Conde *et al.* (1989), Conde and Díaz (1992a,b) and Conde *et al.* (2000) associate the suppression and retardation of growth of the semiterrestrial crab *Aratus pisonii* with habitat productivity. Indicative data on productivity, contamination, and food availability seem to explain size differences among the populations compared. Furthermore, exposure to tide action seems to be important, since it may prevent retention of litter, as suggested at Indaiá. Otherwise, hydrological features, sedimentology and infauna composition at Itamambuca may favour growth and reproduction in *Uca vocator*. Proper testing on the effect of environmental constraints on key biological processes of mangrove macrofauna would, however, require intensive field sampling on several discrete mangrove areas, in order to allow site replication from impoverished to enriched environments.

Similar patterns of recruitment of the three populations suggest that larval release and development take place under similar conditions. Tidal water supply and the location of each sampling site within their respective estuary may explain, to some extent, the contrasting proportion of juveniles found in the studied mangroves (Conde *et al.*, 2000). Itapanhaú River is much larger and the sampled population at Indaiá is closer to the sea. These characteristics would favour megalopal settlement. In contrast, Itamambuca is a small river and the sampling area is more distant from the sea mouth, which would prevent the ingress of settlers on occasions other than spring high tides. It is put forward that mangrove exposure to tidal waters may be more important than habitat productivity with regard to settlement and juvenile recruitment. In the case of Itamambuca, the mangrove area is likely to provide more suitable conditions for the establishment of fiddler crab populations, but juvenile recruitment was found to be lowest at that site.

The sexual proportion of *U. vocator* favourable to males for all sampled populations was also observed in other fiddler crab populations, suggesting that sex ratio depends on both ecological and behavioural features, but perhaps not much on environmental conditions (Valliela *et al.*, 1974; Powers, 1975; Wolf *et al.*, 1975; Ahmed, 1976; Christy, 1982; Christy and Salmon, 1984; Spivak *et al.*, 1991).

Growth and the ontogenetic timing of sexual maturity seem to be highly variable in *Uca vocator*. Such variation seems to be largely dependent on habitat productivity and/or food availability. These characteristics are thought to be uncoupled to other processes shaping population structure, such as sex ratio and juvenile recruitment.

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Scient. ed.: J.M. Gili