Comparative population biology of *Uca rapax* (Smith, 1870) (Brachyura, Ocypodidae) from two subtropical mangrove habitats on the Brazilian coast

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Abstract

The structure of two populations of the fiddler crab *Uca rapax* in two subtropical mangrove habitats near Ubatuba, State of São Paulo, Brazil were compared. The size–frequency distribution, sex ratio, and recruitment were evaluated. Sampling was performed monthly from April 2001 to March 2002 in the Itamambuca and Ubatumirim habitats. Crabs were caught manually for 15 min by two collectors during low tide. The carapace width of each crab was measured with a digital caliper, and the sex and ovigerous state were recorded. The median size of the carapace width of males was greater than that of females at both sites \((P<0.05)\). The median size of the crabs from Itamambuca was larger than at Ubatumirim \((P<0.05)\). Only 28 ovigerous females were obtained from both mangroves, which suggested that females might remain in their burrows during the incubation period. The highest recruitment pulse occurred in winter for both populations, probably as a consequence of high reproductive activity during summer. The sex ratio in the size classes showed an anomalous pattern, with a higher frequency of females in the intermediate size classes. This may be related to a greater energy requirement for reproduction in females, thus delaying growth. The variable environmental conditions to which *Uca rapax* populations are subject appear to act directly or indirectly on the population, causing variations in growth and reproductive processes in the different populations investigated here.

Keywords: Decapoda, Brachyura, Uca rapax, population biology

Introduction

Many species of the fiddler crab genus *Uca* Leach, 1814 in the tropics or subtropics occur along sand–mud beaches of protected bays, mangals, sheltered banks near river mouths, or mud banks formed during high tides (Crane 1975). Fiddler crabs can adjust to wide variations of temperature, humidity, and salinity. The tidal cycle is the most important factor influencing ocypodid ecology (Smith and Miller 1973; Crane 1975). The activities of fiddler crabs are closely related to the tidal cycle, as the individuals remain in their burrows
during flood tide periods, and usually feed, fight or copulate during ebb tides (Crane 1975; Caravello and Cameron 1987; Backwell et al. 1999).

According to Christy (1978), food availability may regulate growth, reproductive output, and ultimately the settlement rate and survivorship of both juvenile and adult crabs. The main food resource is organic matter in the muddy substrates (Crane 1975).

The population structure of several crab species from estuarine habitats has been analysed, mainly with reference to the distribution of individuals in size classes, seasonal abundance, population density, recruitment, sex ratio, dispersion, and growth, birth and mortality rates (Simons and Jones 1981; Colby and Fonseca 1984; Díaz and Conde 1989; Snowden et al. 1991; Spivak et al. 1991; Mantelatto et al. 1995; Santos et al. 1995; Trott 1996; Flores and Negreiros-Fransozo 1999; Negreiros-Fransozo et al. 1999).

The deposit-feeding ocypodid crabs of the genus *Uca* are typical representatives of the mangrove habitat invertebrate fauna along the Brazilian coast (Colpo and Negreiros-Fransozo 2003). *Uca rapax* (Smith, 1870) is one of the most abundant species, living in burrows excavated in coarse wet sediment in mangrove habitats along the northern coast of São Paulo State, Brazil. It occurs from Florida south through the Gulf of Mexico, Antilles, and Venezuela to Brazil (from Pará to Santa Catarina) (Melo 1996).

Most of the papers dealing with *U. rapax* treat its behaviour or physiology (Salmon 1971; Greenspan 1980; McNamara and Moreira 1983; Genomi 1985, 1991; Salmon and Kettler 1987; Zanders and Rojas 1996a, 1996b, 1996c). Because of the ecological importance of this species in recycling organic matter, this study aimed to provide basic information on the population ecology of two populations living in the Itamambuca and Ubatumirim mangals, both located in Ubatuba municipality on the northern coast of São Paulo. Structural aspects were evaluated as follows: frequency distribution, minimum, maximum, mean and median sizes, sex ratio, and recruitment. The environmental factors of temperature, salinity, substratum, and organic matter content of the sediment were analysed to better comprehend the ecological aspects.

**Material and methods**

Fiddler crabs were obtained monthly from April 2001 to March 2002 at Itamambuca mangrove, Cavalo River (23°24'43"S, 45°00'73"W), and at Ubatumirim River mangrove (23°20'17.8"S, 44°53'2.2"W). For sampling we used the procedure of capture per unit effort (cpue), for 15 min by two collectors at low tide. In the laboratory, the carapace width (CW) of crabs was measured with a digital caliper accurate to 0.01 mm, and the sex of each specimen was also recorded.

The Itamambuca mangrove vegetation consists entirely of *Laguncularia racemosa* (Linnaeus). According to Colpo and Negreiros-Fransozo (2003), the tree density in Itamambuca reaches 1250 trees per hectare, with a mean height of 4.8 m and mean diameter at breast height of 6 cm. In contrast (M. L. Negreiros-Fransozo, personal observation), at Ubatumirim there is also *Avicennia shaueriana* Stapf. and Leech, but in low frequency; this site has 6250 trees per hectare, with a mean height of 10.6 m and mean diameter at breast height of 4.7 cm.

Fiddler crabs were grouped into demographic categories (juvenile and adult males, juvenile and adult females, and ovigerous females). These categories were established according to the size at sexual maturity for each sex and site (Castiglioni 2003). In Itamambuca, males with CW smaller than 15.2 mm and females with CW smaller than 12.1 mm were considered as juveniles. In Ubatumirim these sizes were 13.6 and 11.4 mm,
respectively, for males and females. These sizes were obtained by means of the allometric technique.

The size of the carapace width for each sex and mangrove was compared by the Mann–Whitney test ($\alpha=5\%$; Zar 1996).

Crabs were grouped into 10 CW size classes (2.5 mm amplitude) for characterisation of the population structure. The frequency distribution of size classes for males and females was analysed monthly during a 1-year period, in order to follow temporary variations in population frequency distribution, and to analyse seasonal recruitment. The normality of the frequency distributions was compared by the Shapiro–Wilk test ($\alpha=5\%$; Zar 1996).

The sex ratio was analysed for each month and size class. A chi-square test for goodness of fit ($\chi^2$; $\alpha=5\%$) was used to evaluate the sex ratio, and to compare the percentages of males and females per month.

To estimate recruitment, crabs with carapace width less than the values determined for the sexual maturity of males and females at the two localities, mentioned above, were considered juveniles (Castiglioni, 2003). The proportion of juveniles was compared among seasons using the multinomial proportions test (MANAP; $\alpha=5\%$; Curi and de Moraes 1981).

The air and burrow temperatures, and river and burrow–water salinity were monitored monthly with three replicates. Then, a comparison was performed between sites and among seasons by analysis of variance (ANOVA; $\alpha=5\%$; Zar 1996).

The granulometric composition and the organic matter content of the sediment at each site were determined from three samples taken at each site in each season. Each sediment sample was oven-dried at 60°C for 48 h. For each sample of dried sediment, three subsamples of 10 g were placed in an oven at 500°C for 3 h and then weighed. The organic matter content of samples in terms of percentage was estimated from the ash-free dry weight.

The sediment was sieved, each fraction was weighed in a precision scale (0.001 g), and the percentage of granulometric fractions obtained for each sample. Samples were then classified according to the American scale (Wentworth 1922).

**Results**

A total of 1294 crabs was obtained at Itamambuca: 667 males (319 juveniles and 348 adults) and 627 females (267 juveniles and 360 adults). Only eight ovigerous females were obtained during the study period in this habitat. At the Ubatumirim River, 2107 specimens were collected: 1117 males (432 juveniles and 685 adults) and 990 females (330 juveniles and 660 adults). In this habitat, 18 ovigerous females were obtained.

The organic matter content of the sediment at Itamambuca was higher than at Ubatumirim in all seasons ($P<0.05$; Figure 1).

The environmental temperature was similar among seasons for the two sites, except for autumn when the mean temperature was significantly lower ($P<0.05$; Table I). There was no difference in burrow temperature between the sites in each season ($P>0.05$; Table I).

There was no significant difference between environment and burrow temperature for all seasons ($P<0.05$), although the environmental temperature was higher than the burrow temperature (Table I). The mean environmental temperature was significantly lower in autumn at both sites ($P<0.05$), and burrow temperature was higher in summer ($P<0.05$).

The mean salinity of the river water differed significantly between the two habitats in winter, spring, and summer ($P<0.05$), and was similar in autumn ($P>0.05$). However, the
burrow-water salinity of *U. rapax* was significantly different between habitats for all seasons \((P<0.05)\). The mean salinity of the burrow water was significantly higher than the mean river salinity at both sites \((P<0.05; \text{Table I})\).

Table II shows the results of the analysis of central tendency and degree of sorting for the granulometric classification of the sediment for each mangrove. At Itamambuca medium sand predominated, whereas at Ubatumirim very fine sand predominated.

The carapace width of males ranged from 4.0 to 26.6 mm, and of females from 3.9 to 25.5 mm in Itamambuca, whereas at Ubatumirim the capapace width of males ranged from 3.5 to 24.9 mm, and that of females from 3.6 to 22.5 mm. The Mann–Whitney test showed that median size of the males was larger than females \((P<0.05)\) (Figure 2A). There was a significant difference in median size \((P<0.05)\) between crabs from each site. Crabs from Itamambuca reached larger sizes than those from Ubatumirim (Figure 2B).

Normality was rejected for the overall frequency distributions obtained for both sites \((P<0.05)\), considering all pooled data. The graphs show two modal groups for Itamambuca

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**Table I.** Means of the air and burrow temperatures, and of river- and burrow-water salinity.

|                 | Air temperature \(\degree C\) | Burrow-water temperature \(\degree C\) | River-water salinity | Burrow-water salinity |
|-----------------|--------------------------------|----------------------------------------|----------------------|-----------------------|
|                 | Ita                            | Uba                                   | Ita                  | Uba                   | Ita                  | Uba                   |
| Autumn          | 24.6 b A                        | 25.0 b A                              | 25.0 bc A            | 24.7 b A              | 2.0 a A              | 3.5 c A              | 8.9 a A              | 22.4 a B              |
| Winter          | 30.1 a A                        | 28.2 ab A                             | 22.8 c A            | 26.7 b A              | 5.7 a B              | 10.5 b A            | 12.8 a A              | 25.9 a B              |
| Spring          | 31.1 a A                        | 27.8 ab A                             | 27.5 bc A            | 25.1 b A              | 4 a B                | 11.0 b A            | 10.8 a A              | 22.8 a B              |
| Summer          | 32.9 a A                        | 32.4 a A                              | 31.6 ab A            | 31.6 a A              | 3.8 a B              | 15.6 a A            | 11.7 a A              | 31.2 b B              |

Ita, Itamambuca; Uba, Ubatumirim. Lowercase letters correspond to comparisons within the same environmental factor among seasons of the year; uppercase letters correspond to comparisons within the same environmental factor and season but between sites. Values with at least one letter in common did not differ statistically (ANOVA; \(z=0.05\)).

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**Figure 1.** *Uca rapax*. Median values \((\pm SD)\) of the organic matter content of the sediment at Itamambuca and Ubatumirim. The statistical comparisons were performed for each season between sites (Kruskal–Wallis, \(z=0.05\)). White bars with at least one letter in common did not differ statistically.
and only one for Ubatumirim. Nevertheless, the monthly size–frequency distributions of *U. rapax* represented in Figure 3 (Itamambuca) and Figure 4 (Ubatumirim) evidenced bimodality for populations from both sites. At Itamambuca there were clearly two age groups in the size–frequency distributions during almost all the months, while at Ubatumirim two age groups could be perceived from March to September.

The sex ratio obtained in most months at Itamambuca was close to 1:1 ($\chi^2=1.23; P>0.05$). There was a significant difference ($P<0.05$) in the frequency of crabs only in July 2001, when the proportion of males was higher (65.0%) than that of females (35.0%), and in September females (67.0%) were more frequent than males (33.0%). The sex ratio of the total population from Itamambuca followed the proportion 1:1 (0.94 male: 1 female) ($\chi^2=1.23; P>0.05$). The proportion favoured males, 1 male: 0.88 female ($\chi^2=7.65; P<0.05$; Figure 5A) at Ubatumirim.

Sex ratios were calculated for each CW size class. In most size classes, for both sites, there was no significant difference between sex ratios ($P>0.05$; Figure 6). However, at Itamambuca females prevailed in the second ($\chi^2=3.88; P<0.05$) and third classes ($\chi^2=5.34; P<0.05$), and at Ubatumirim, in the fourth class ($\chi^2=7.34; P<0.05$). Males were more abundant in the eighth, ninth, and tenth classes at Itamambuca, and the seventh, eighth, and ninth classes at Ubatumirim ($P<0.05$; Figure 5B).

The populations contained the highest percentage of juveniles in autumn (37.9%) at Itamambuca; and in autumn and winter at Ubatumirim (32.0% and 26.4%, respectively) (Figure 6).

**Discussion**

According to Schaeffer-Novelli and Citrón (1994), organic matter content and nutrients in the mangal substratum are related to tidal energy, because at sites where tidal action is low, litter exportation is also low, and there is, consequently, an increase in the decomposition rate. The sediment texture is influenced not only by tidal action but also by wave energy and the pluvial regime; muddy substrata allow greater retention and accumulation of organic matter than substratum, consisting predominantly of coarse fractions.

The decomposition of the litter produced by mangroves is an important stage in nutrient recycling, and important for organic matter availability for estuarine trophic chains (Panitz 1987). The Itamambuca substratum contained more organic matter than Ubatumirim in all seasons, a result of the high primary productivity at Itamambuca. According to Colpo (2001), this mangrove is an ecosystem with increasing productivity, and with hydrological and sediment retentive characteristics, constituting a rich and suitable environment for development of fiddler crab populations.

The substratum of the Ubatumirim habitat is moderately sorted, with very fine sand strongly predominating, which allows higher retention of organic matter among the

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**Table II. Values of phi ($\phi$) which express the central tendency and degree of sorting ($\sigma$) of the granulometric composition at each site.**

| Mangrove     | Central tendency ($\phi$) | Category | Degree of sorting ($\sigma$) | Category |
|--------------|---------------------------|----------|-------------------------------|----------|
| Itamambuca   | 1.95                      | Medium sand | 1.93                          | Poorly sorted |
| Ubatumirim   | 3.57                      | Very fine sand | 0.63                          | Moderately sorted |

*aClassification according to Suguio (1973).
particles than at Itamambuca. The high organic content input of the Itamambuca sediment may result from the youth and increasing productivity of this habitat.

Temperature and salinity variations are two great problems faced by crabs that live in intertidal estuarine areas. The habitat surface can attain 44°C, which is 1–3°C above the lethal limit for fiddler crabs (Edney 1961; Macintosh 1982). Species of *Uca* and other

Figure 2. *Uca rapax*. Comparison of the median sizes of males and females at each site (A) and comparison of the median size of each sex and site (B). Boxes with at least one letter in common showed no statistically significant difference ($P > 0.05$).
Figure 3. *Uca rapax*. Monthly size–frequency distributions for the Itamambuca population.
Figure 4. *Uca rapax*. Monthly size–frequency distributions for the Ubatumirim population.
ocypodids visit their burrows more often to compensate for the high temperatures, because the burrow water cools their body temperature by evaporation (Smith and Miller 1973). In this study, the environmental and burrow temperatures did not differ at either site, perhaps because the crabs were sampled in exposed areas with sparse vegetation cover which reduced the incidence of solar rays directly on the substratum.

The salinity of the burrow water at Ubatumirim was higher than at Itamambuca, probably because of the lack of vegetation covering the burrows and, consequently, a higher evaporation rate, increasing salt concentrations inside the burrows. Burrow-water salinity was higher than river-water salinity, because of the higher evaporation rate of interstitial water during low tides, increasing the salinity in the substratum as well as inside the burrows.

Males reached larger sizes (measured as carapace width) than did females ($P<0.05$). According to Warner (1967) and Díaz and Conde (1989), the size differences between males and females in brachyuran species are due to males showing a higher growth rate, or a longer growth period, while females spend a significant amount of energy on the reproductive process. Different mortality rates between sexes (Wolf et al. 1975), migration (Montague 1980), higher tolerance of one sex to environmental adversity, differential spatial and temporal utilisation of resources, and distinct behaviour patterns between sexes (Giesel 1972) may be some of the factors which influence size differences between males and females.

According to Hyman (1922) and Crane (1975), male and female crabs cannot be equally sensitive to food supply, because of differences in the efficiency of feeding, assimilation or
use of food, or because of the dominance of males or large crabs, which may limit the availability of food resources for other crabs. Consequently, one sex can grow larger than the other.

The larger sizes of both males and females of *U. rapax* at Itamambuca may be related to the high productivity and organic matter content in the substratum. Similarly, Colpo (2001) observed that *U. vocator* (Herbst, 1804) grew larger at Itamambuca because of favourable conditions and better food supply than at Indaí (Ubatuba) and Itapanhau (Bertioga).

Henmi (2000) considered that food supply was the most important factor in the life cycle of the ocypodid *Macrophthalmus japonicus* (de Haan) in Fukuoka, Japan: population density was higher at sites where sediment particles were finer and the nitrogen content was higher. However, the crabs were more abundant at sites with coarser sediments and low nitrogen input, because of the high survival rate at these sites. Low survival in ecosystems with high food availability may be due to competition at high population densities.

The population size–frequency distribution is a dynamic feature that can vary through the year, as a result of reproduction and rapid larval recruitment (Thurman 1985). According to Díaz and Conde (1989), unimodality in size–frequency distributions is
usually characteristic of a stable population, which shows continuous recruitment and a constant mortality rate through different life phases. However, bimodality or polymodality may result from slow growth at the immature or mature phase, recruitment pulses, migration, mortality, or differential behaviour.

The bimodality in size–frequency distribution of the U. rapax population at Itamambuca is probably a result of the species having two reproductive peaks. This was also observed by Thurman (1985) in a population of U. subcylindrica (Stimpson, 1859), in which the bimodality in the frequency distributions was correlated with fast larval development and seasonal recruitment. Spivak et al. (1991), studying the population biology of U. uruguayensis Nobili, 1901 in Mar Chiquita, Argentina, and Costa and Negreiros-Franoso (2003) with U. thayeri Rathbun, 1900 in Ubatuba, Brazil, also observed bimodal size–frequency distributions. However, the unimodality shown by U. rapax at Ubatumirim is probably a result of the occurrence of one, more intense peak at the reproductive period, although a study of gonadal development would be necessary to prove the existence of such a pattern. Unimodal size–frequency distributions have been most often recorded in fiddler crabs of temperate areas, suggesting that reproduction occurs with more intensity in a determined period of the year (Thurman 1985).

The sex ratio is usually 1:1 in animals with sexual reproduction. According to Wilson and Pianka (1963), this pattern is favoured by natural selection, but differences usually appear after the parental care period, because the animals remain more susceptible to factors that can act on the sex-ratio deviation. These deviations can internally regulate population size, because they affect reproductive potential (Giesel 1972). This could apply to species with differential growth rates and/or different life expectancies for each sex, producing larger and older individuals in one sex.

Males constituted 51.4% of the individuals in the Ubatumirim habitat. Powers (1975) and Ahmed (1976), studying the same species, observed that males represented 52% and 59% of the population, respectively. Males dominate in several other species of Uca, as observed by Spivak et al. (1991) in U. uruguayensis; Wolf et al. (1975) in U. pugnax (Smith, 1870), and Emmerson (1994) in U. lactea annulipes H. Milne Edwards, 1837, U. chlorophthalmus chlorophthalmus (H. Milne Edwards, 1852), U. urvillei (H. Milne Edwards, 1852), and U. vocans hesperiae Crane, 1975. Deviations from the normal proportion of sexes appear to be related to the reproductive system. Males spend more time moving their great cheliped, holding and disputing territory to attract females, and feeding over long periods to compensate for the presence of a single cheliped which is used in food capture, and consequently are easily captured (Valiela et al. 1974; Christy and Salmon 1984; Emmerson 1994). Wolf et al. (1975) suggested that deviations in sexual proportion of U. pugnax result from differential mortality caused by the high susceptibility of female crabs to predators, while males can defend themselves with their major cheliped.

Colby and Fonseca (1984) first described the dominance of females in a Uca population, showing that females of U. pugilator (Bosc, 1802) were more abundant than males, because of the higher rate of predation. In a population of Macrophthalmus grandidieri A. Milne Edwards studied by Emmerson (1994) in South Africa, there were more females than males, and this deviation was directly related to the sampling procedure, or the study area selected and the consequences for the analyses. Moreover, growth rates, life cycles, environmental pressures, fragmented habitats, suitable food, different reproductive behaviour and strategies can affect sexes to a different extent, thus causing deviations to one sex throughout development. This suggests that the sexes occupy distinct
microhabitats, leading to imbalances in the sex ratios (Wilson and Pianka 1963; Wenner 1972; Trott 1996).

The sex ratio investigated in the size classes of *U. rapax* showed an anomalous pattern, similar to that described by Wenner (1972), in which the proportions differed in intermediate classes, favouring one sex (females), and in larger classes favouring the opposite sex (males). This may be related to the large energy investment in reproduction, because while females are incubating eggs, somatic growth, which is antagonistic to reproductive events, ceases, consequently delaying their growth (Adiyodi and Adiyodi 1970). Another cause of low growth rates in females is that fiddler crabs with a broad front are known not to feed when they are incubating eggs in their burrows, consequently limiting growth. Similar anomalous patterns have been observed in other decapods such as *Aratus pisonii* (H. Milne Edwards, 1837), studied by Diaz and Conde (1989); *Cyrtograpsus angulatus* Dana, 1851, studied by Castiglioni and Santos (2001); *Callinectes ornatus* Ordway, 1863, studied by Negreiros-Fransozo et al. (1999), and *Eurytium limosum* (Say, 1818), studied by Guimarães (2002).

Spivak et al. (1991), analysing the life history and population structure of *U. uruguayensis*, showed that the crabs recruited with greater frequency in the autumn, and ovigerous females were most frequent in summer. The occurrence of most intense recruitment of *U. rapax* in autumn for populations from both habitats, implies that the reproductive period is more intense in the hot months (spring and summer), considering the time elapsed from hatching to the first juvenile stages.

The different environmental conditions to which *U. rapax* populations are subject, mainly organic matter content in the sediment, river and burrow-water salinity, and granulometric composition of the substratum, appear to act directly or indirectly on the aspects of the population, and also on growth, causing variations in this process for the different populations investigated. This phenotypic plasticity has been observed in other species of mangrove crabs such as *Aratus pisonii*, studied by Conde and Diaz (1989) and Negreiros-Fransozo (2002), and *Uca vocator*, analysed by Colpo (2001).

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