Population and reproductive biology of the crab *Uca burgersi* (Crustacea: Ocypodidae) in three subtropical mangrove forests

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Abstract: Population and reproductive biology were studied in three populations of the crab *Uca burgersi* Holthuis, 1967, in the Indaiá, Cavalo and Ubatumirim mangrove forests (Ubatuba, São Paulo State, Brazil). Crabs were collected during low tide (August 2001 through July 2002), by digging the sediment, with a standard capture effort (two persons for 30 min.). Carapace width was measured, and gonad developmental stage was recorded from all specimens. *U. burgersi* was most abundant in the Cavalo mangrove, where the largest male was found. Juvenile crabs were found year-round at all three sites. However, the ratio of ovigerous females was very low, even null in the Cavalo mangrove. The gonad development rate indicated that *U. burgersi* was reproducing continuously, but more intensively during spring and summer, with recruitment occurring in winter. The synchrony between the populational and reproductive biology in the three areas showed that local features were not the limiting factors. It is suggested that this species is a habitat generalist. Rev. Biol. Trop. 55 (Suppl. 1): 55-70. Epub 2007 June, 29.

Key words: fiddler crab, reproductive cycle, population structure, Brazilian mangroves

Ocypodid crabs of the genus *Uca* Leach, 1814 are the most characteristic group of invertebrates associated with estuaries of tropical and subtropical coasts, mainly mangroves. These crabs live in muddy areas and feed on organic matter deposited on the sediment surface (Jones and Simons 1983, Costa and Negreiros-Fransozo 2003). They have the habit of burrowing in the sediment, building complex galleries. These refuges protect the crabs from extreme temperatures, salinity variations and predators (Macintosh 1988), and they are also used for reproduction and molting (Crane 1975, Hyatt and Salmon 1978).

Crab populations have several features or properties, such as density, biotic potential, recruitment and growth, which are not attributes of an isolated organism, but when grouped they coordinate the dynamics of a natural population (Hutchinson 1981, Jones and Simons 1983). The individuals which are part of these populations interact, competing for food, refuge and reproductive pairing, among other resources, and the intra- and interspecific relationships maintain the equilibrium of the community (Fontelles-Filho 1989).

The population biology of ocypodid crabs has been analyzed mainly based on the distribution of individuals in size classes, seasonal abundance, population density, sex ratio, juvenile recruitment and reproductive intensity (Spivak *et al.* 1991, Trott 1996, Negreiros-Fransozo *et al.* 1999, Costa and Negreiros-Fransozo 2003, Litulo 2005). Information about a population provides knowledge of the ecological stability of the species in a certain habitat, as well as extending understanding of the biology of a species (Pillay and Nair 1971, Hutchinson 1981, Jones and Simons 1983, Santos *et al.* 1995).

These populations usually pass through long reproductive periods, when the females spawn several egg masses. Accordingly, the modal class varies as a result of reproduction and juvenile recruitment (Thurman II 1985, Macintosh 1988, Castiglioni and Negreiros-Fransozo 2005).

The study of the recruitment biology of crabs comprises two distinct aspects: events related to the cohort, and processes which precede and affect the mating behavior and the reproductive cycle of a species, i.e., maturity, egg development, and the relationship between molt and reproduction. Evaluation of these characteristics requires periodic sampling of the natural population (González-Gurriarán 1985).

The reproductive period for most brachyurans can be estimated by means of gonad development, and also by the ratio of ovigerous females throughout the year (Pilay and Nair 1971, Murai *et al.* 1987, Henmi 1992, Mouton and Felder 1995, Rodríguez *et al.* 1997, Chacur and Negreiros-Fransozo 2001, Flores *et al.* 2002, Negreiros-Fransozo *et al.* 2002, Colpo and Negreiros-Fransozo 2003). The size at onset of sexual maturity, based on external morphological features, can sometimes be mis-estimated when the curves for immature and mature specimens overlap (Somerton 1980a, b). Several researchers (Conan and Comeau 1986, Choy 1988, Fontelles-Filho 1989) mentioned that in some species, morphological sexual maturity does not coincide with physiological sexual maturity. The latter is related to the presence of gonads that are mature, i.e., producing gametes. Thus, when one intends to estimate the size at first maturation of a brachyuran, the degree of gonad development beyond the external morphological features should be considered (Watson 1970, Brown and Powell 1972).

Among the few published reports concerning the biology of *Uca burgersi* Holthuis, 1967 are those of Gibbs and Bryan (1972) who studied the account of strontium, magnesium and calcium in the environment and exoskeleton of decapods. Gibbs (1974) performed ecological studies in Barbuda, and von Hagen (1982, 1984) investigated behavioral aspects. In Brazilian mangroves, Rieger (1998) worked on the larval development, Benetti and Negreiros-Fransozo (2003) studied the morphological sexual maturity, and Benetti and Negreiros-Fransozo (2004 a, b) studied the relative growth at two different sites and the symmetry of the chelipeds, respectively.

In this investigation we analyzed the population structure (size-frequency distribution, sex ratio) and the reproductive cycle of *U. burgersi* based on gonad development and molt stage.

MATERIALS AND METHODS

Three mangrove areas in Ubatuba, State of São Paulo, Brazil, were chosen for this study: the Indaiá River (23°24'58" S, 45°43'13" W), the Cavalo River (23°23'48" S, 44°00'36" W) and the Ubatumirim River (23°20'18"S, 44°53'02"W).

The canopy of the Indaiá and Ubatumirim rivers is composed of *Laguncularia racemosa* (L.) and *Avicennia schaueriana* Stapf and Leecheman (Colpo 2001). The Cavalo River has only *L. racemosa*; because of its location about 300 m from the river, the canopy is not directly influenced by the mechanical changes of the tides.

Three samples of substrate (10 g) from each of the three study sites were collected for analyses of organic matter content in each season of the year. The samples were dried at 60 °C to constant weight, then incinerated for three hours at 500 °C and reweighed. The organic matter content was determined from the ash-free dry weight, and the means were compared by variance analysis (ANOVA; α=0.05) complemented by *a posteriori* Tukey's test among the mangroves and by year season; the significance level adopted was 5 %.

Crabs were sampled monthly (August 2001 through July 2002) during low tide by digging the burrows and removing the crabs during a period of 30 min. in a fenced area of approximately 0.01 ha, summing 12 samples.

Crabs were identified according to the key provided by Melo (1996). Cheliped size, abdominal morphology, and the number of pleopods assessed the sex of each crab. The ovigerous condition was also noted.

The carapace width (CW) of all crabs was measured to the nearest 0.1 mm using a caliper. For the population study, the values of carapace width were grouped into size classes, which were analyzed monthly for the three populations studied. The median size of each category, based on the carapace width, was compared among localities by Kruskall–Wallis, complemented by Dunn´s test (α=0.05).

The proportion of males was analyzed by means of a chi–square test for goodness of fit (α=0.05; Sokal and Rohlf 1987).

All individuals captured were classified as juvenile or adult, based on carapace width values obtained for sexual maturity, which have been assessed previously for the same populations by Benetti and Negreiros–Fransozo (2004a). These cutoff values were 7.8, 8.8 and 7.5 mm for males and 6.2, 6.2 and 6.8 mm for females from Indaiá, Cavalo and Ubatumirim mangroves, respectively. Thus, crabs with smaller carapace width than the above–mentioned values for each site were considered as juveniles, and larger ones as adults. Recruitment in each population was estimated monthly from the ratio of juveniles to the total number of crabs collected. The proportion of juveniles was compared among the seasons of the year for each population, using the multinomial proportions analysis (Curi and Moraes 1981).

To assess the degree of gonad development, all crabs were dissected and the gonads observed with the aid of an optical stereomicroscope. The stages of gonad development were determined according to the patterns described for other brachyurans (Haefner 1976, Abelló 1989 a, b, Wenner 1989), as listed in Table 1.

Crabs were grouped as “reproductively inactive” (IM and RU; see Table 1) and “reproductively active” (ED, DE and AV; see Table 1). Subsequently, the relative frequency of these groups was determined for each sex and season. The proportions of the reproductively active group were compared by the multinomial proportions test (Curi and Moraes 1981).

Evaluation of the molt stage for each crab was based on the exoskeleton hardness and was confirmed by dissecting the crab. The molt–stage features adopted were those proposed by Drach and Tchernigovtzeff (1967), Warner (1977) and Abelló (1989 a, b). Crabs were grouped into two categories according to molt stages: molt activity (stages A, B, D and E) and intermolt (stage C). The proportions of crabs in molt activity were compared by multinomial proportions analysis (Curi and Moraes 1981).

RESULTS

The organic–matter content (%) in the sediment (mean ± SD) was higher (5.11±0.5 %) in the Cavalo mangrove than in the Ubatumirim (1.71±0.25 %) and Indaiá (2.12±0.06 %) mangroves. Among the year seasons (Table 2), the content of organic matter did not differ statistically (ANOVA; α=0.05).

The numbers of crabs obtained from the three study sites as well as the descriptive measures of each demographic category of the populations are presented in Table 3.

In November 2001 in the Indaiá mangrove, a crab was found that possessed male abdominal morphology with gonopods, but it also had a pair of small chelipeds. Benetti and Negreiros–Fransozo (2003) described this intersex specimen.

U. burgersi was more abundant in the Cavalo mangrove (n=1 952 specimens) than in Ubatumirim and Indaiá with 925 and 933 specimens, respectively. Ovigerous females were very scarce during the study period, comprising only 0.42 % of the population at

TABLE 1
Uca burgersi. *Description of each gonadal stage for males and females and reproductive condition.*

Stages (abbreviation)	Males	Females	Reproductive condition
Immature (IM)	Non-differentiated gonads, associated with juvenile morphology	Non-differentiated gonads, associated with juvenile morphology (see Material and Methods for explanation)	Inactive
Rudimentary (RU)	Deferent vessels filamentous and colorless	Filamentous and translucent ovary	Inactive
In development (ED)	Deferent vessels beginning the reeling, occupying few reduced in the body cavity; translucent/white coloration	Ovary small, in "H" shape; pink coloration	Active
Developed (DE)	Gonads very voluminous, occupying ¼ of the thoracic cavity; milky-white coloration	Very voluminous ovary, occupying great part of thoracic cavity; dark-red coloration	Active
Advanced (AV)	–	Very voluminous ovary, occupying the major part of thoracic cavity; wine-colored	Active

TABLE 2
Organic matter content (%; mean ± SD) in the sediment from studied sites.

Season	Indaiá	Cavalo	Ubatumirim
Autumn	2.77±0.06	4.60±0.10	1.40±0.00
Winter	1.50±0.00	4.87±0.25	2.00±0.70
Spring	2.00±0.10	5.20±0.10	1.73±0.06
Summer	2.20±0.10	5.77±0.40	1.71±0.44
Total	2.12±0.06	5.11±0.50	1.71±0.25

TABLE 3
Uca burgersi. *Descriptive measure for each demographic category, in the localities studied.*

Mangrove	Sex	N	Carapace width Mean ± sd	Range	
Indaiá	JM	128	6.6±0.93	3.3	7.7
	AM	433	10.8±2.00	7.8	18.1
	JF	36	5.1±0.63	3.6	6.0
	AF	334	9.7±1.96	6.2	15.4
	OF	1	(CW=12.6mm)		
	Intersex	1	(CW=8.0mm)		
Cavalo	JM	145	7.3±1.00	4.1	8.7
	AM	929	12.6±1.81	8.8	18.5
	JF	39	5.6±0.67	4.1	6.4
	AF	839	11.1±2.07	6.5	16.6
Ubatumirim	JM	42	6.1±1.05	3.8	7.4
	AM	440	11.7±2.75	7.5	18.2
	JF	19	5.1±0.84	3.4	6.1
	AF	418	11.5±2.49	6.2	17.2
	OF	6	11.8±2.80	9.6	14.3

JM = juvenile male, AM = adult male, JF = juvenile female, AF = adult female, OF = ovigerous female, CW = carapace width.

Indaiá during spring, and 2.76 % and 1.38 % at Ubatumirim during spring and summer, respectively (Table 3).

The median size (CW) between the sexes differed from site to site. Adult males from the Cavalo mangrove were significantly larger than those from the other sites; adult females were largest at Ubatumirim (Kruskall–Wallis, complemented by Dunn´s test; α=0.05) (Fig. 1).

The histograms of frequency distribution of crabs captured at each site are presented in Fig. 2, 3 and 4. Juvenile crabs were not found in July (winter) in the Indaiá and Cavalo mangroves, or during March (summer) and April (autumn) in the Ubatumirim mangrove (Fig. 4). Ovigerous females were obtained only during November (Indaiá mangrove, Fig. 2) and November and January (Ubatumirim mangrove, Fig. 4). No ovigerous females were found in the Cavalo mangrove (Fig. 3).

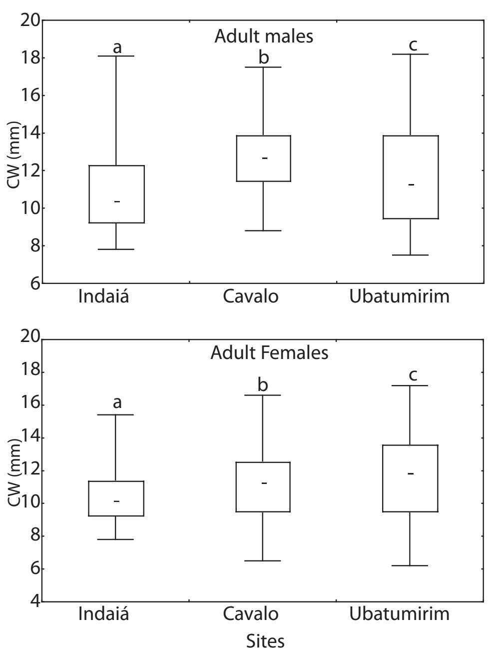

Fig. 1. *Uca burgersi*. Comparison of the median size for adult males and adult females at the three study sites. CW = carapace width (mm). Box plots with at least one common letter above did not differ significantly (– = median; box = standard error; whiskers = minimum and maximum sizes).

The total sex ratio (male:female) observed was 1:0.65 for crabs in the Indaiá mangrove (χ^2 = 39.2; d.f.=1; α=0.05) , 1:0.87 in the Cavalo mangrove (χ^2 = 9.0; d.f.=1; α=0.05) and 1:0.90 at Ubatumirim (χ^2 = 2.2; d.f.=1; α=0.05). The proportion of males was higher in the largest size classes (Fig. 5).

The recruitment rate differed significantly among seasons in Ubatumirim (being higher during the winter) and was continuous throughout the year (multinomial proportions analysis; α=0.05) (Fig. 6).

The number of reproductively active crabs increased in early summer (multinomial proportions test; α = 0.05) (Fig. 7–8). For males, the higher proportions of active crabs were found in spring, and the inactive ones were recorded in autumn, presenting significant differences. The females showed a similar pattern, with exception of the Cavalo River population, where the proportions of active and inactive female did not differ statistically between autumn and summer.

The proportion of molting crabs was always lower than that of intermolting crabs. In the Indaiá mangrove, molting crabs were more frequent during the summer months. However, for molting crabs from the Cavalo mangrove during spring and summer and among those from the Ubatumirim mangrove, there were no significant differences (multinomial proportions test; α = 0.05) (Fig. 9).

DISCUSSION

The rate of production and export of organic matter characterize the mangroves as the most productive ecosystems on Earth. Because of this, mangroves play an important role in the maintenance of ecological equilibrium in estuaries where they are present (Odum and Heald 1972, Koch and Wolff 2002). Maintenance and retention of organic matter and nutrients in the mangroves are also influenced by the local hydrology and the sediment texture. At sites with less tidal action, the production of organic matter is increased

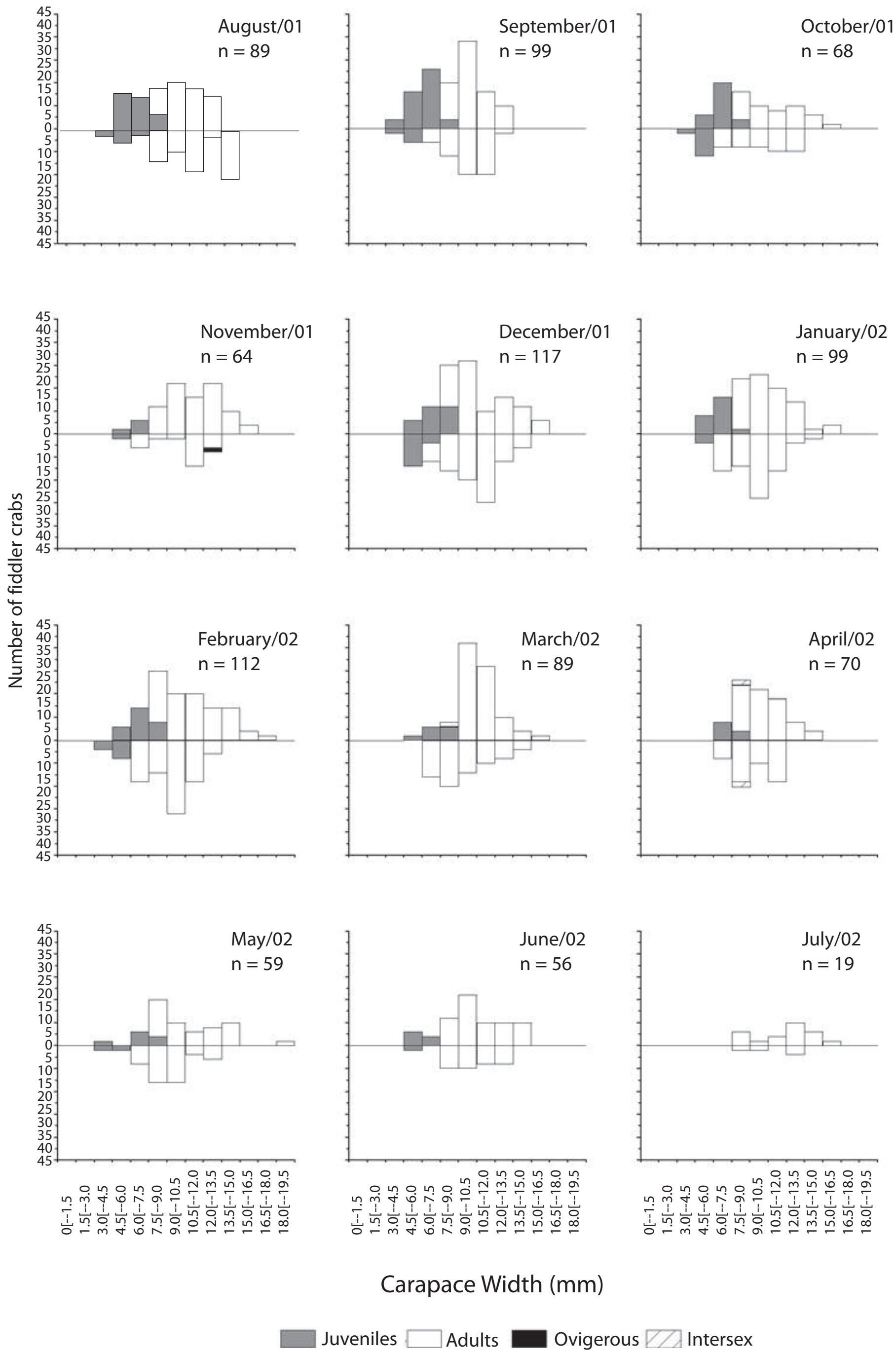

Fig. 2. ***Uca burgersi*****. Monthly distribution of crabs for each demographic category in the Indaiá population. Upper bars indicate males; lower bars indicate females.**

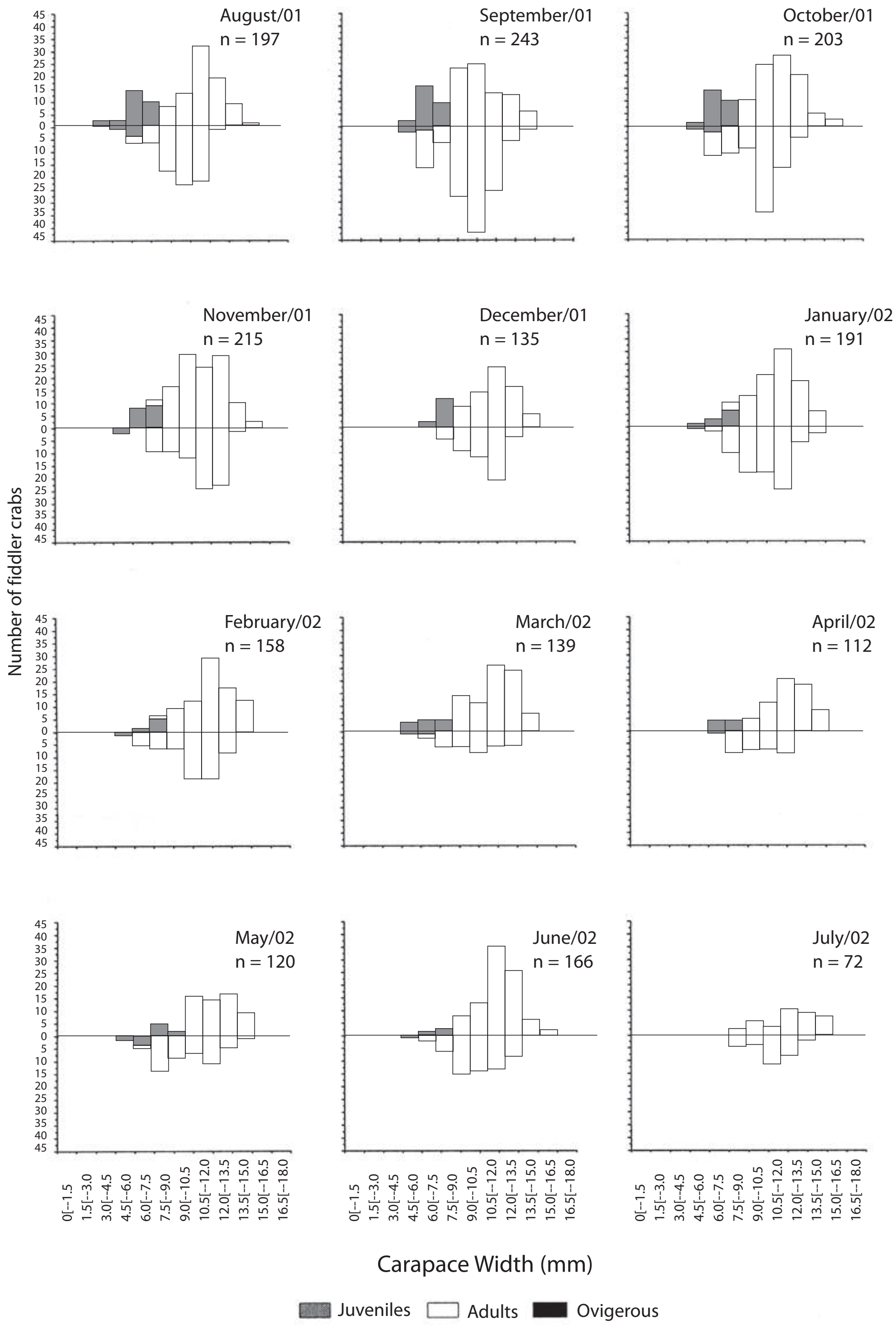

Fig. 3. *Uca burgersi*. **Monthly distribution of crabs for each demographic category in the Cavalo population. Upper bars mean males and lower bars, females.**

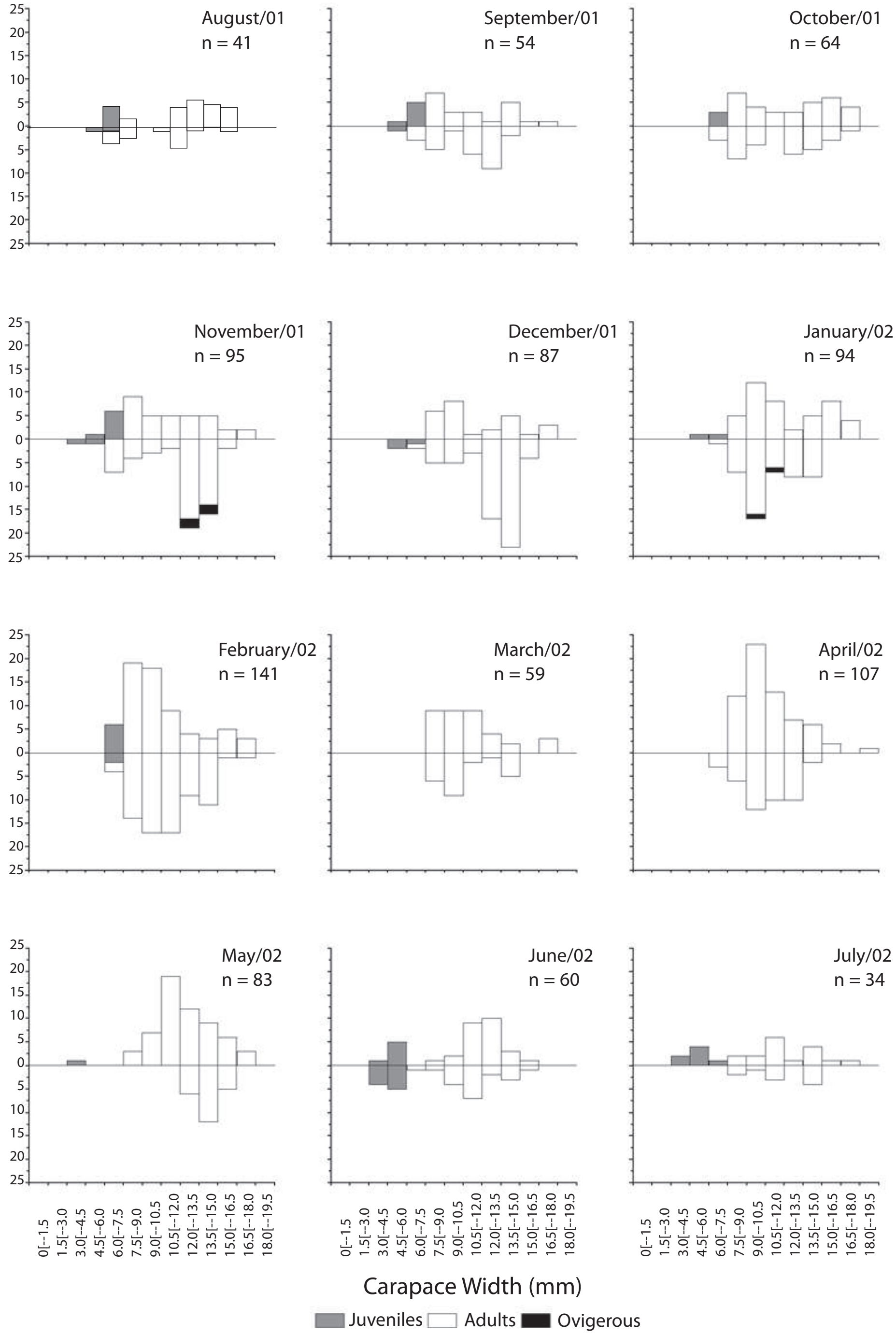

Fig. 4. ***Uca burgersi*****. Monthly distribution of crabs for each demographic category in the Ubatumirim population. Upper bars mean males and lower bars, females.**

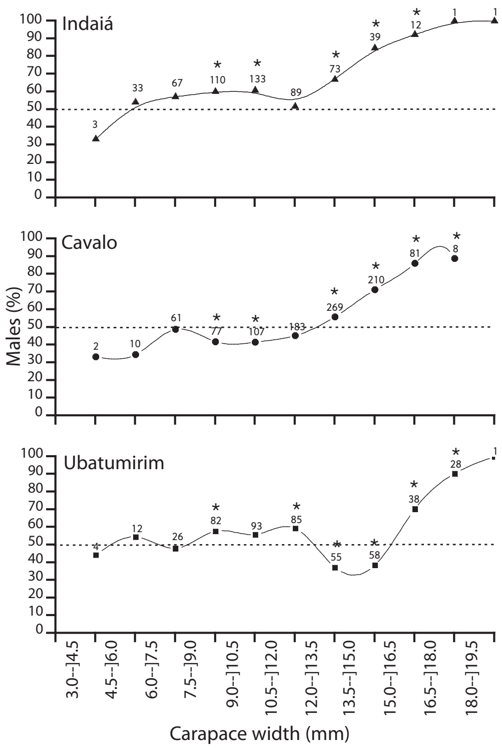

Fig. 5. *Uca burgersi*. Proportion of males in each size class. Values above the line represent number of males. * indicates statistically significant difference (chi-square; α=0.05).

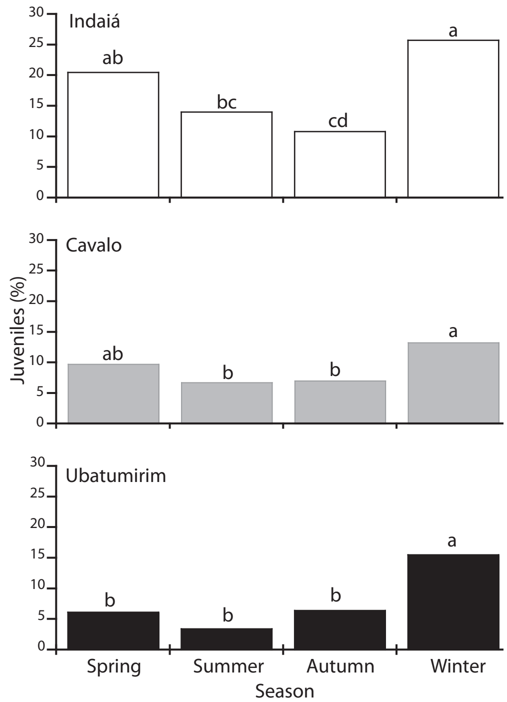

Fig. 6. *Uca burgersi*. Comparison of proportions of juveniles among seasons. Bars with at least one letter in common did not differ significantly (multinomial proportions analysis; α=0.05).

while export of litter is diminished and the decomposition rate is higher (Twilley 1985).

Fiddler crabs present a behavioral pattern associated with the sediment features (both grain size and organic matter content). Such behavior can be exemplified by both the burrows and the feeding activities. Several species of the genus *Uca* present a spatial distribution according to the grain size (Thurman II 1987, Macintosh 1988, Mounton and Felder 1996) and some morphologic features adapted to the organic matter extraction of the sediment during feeding (Costa and Negreiros-Fransozo 2001)

Because *U. burgersi* showed no preference for a particular kind of substratum or organic matter content, we suggest that it is a generalist species with respect to its habitat. According to Costa and Negreiros-Fransozo (2001), this species is capable of extracting organic matter from several fractions of sediment, aided by several types of setae on the mouth appendages, which allow them to filter the ingested sediment.

Many environmental factors seem to act on the population growth of *U. burgersi* in the sites studied. Scarcity or low quantities of food, latitudinal variations, and adverse environmental factors (salinity, temperature, air exposure and pollution) have been pointed out as the main factors influencing the growth of decapods (Conde and Díaz 1989, 1992, Hines 1989, O'Connor 1990, Costa and Negreiros-Fransozo 1998).

Considering that fiddler crabs feed on particulate organic matter, the organic content of the sediment can promote better nutritional conditions for them. In this sense, we expected to found larger crabs in sites with

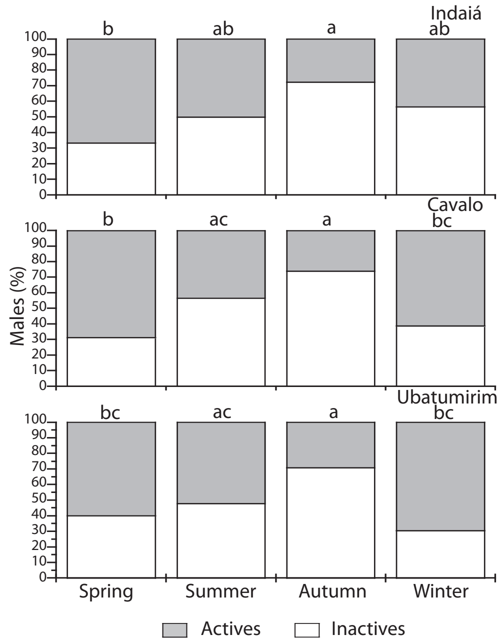

Fig. 7. *Uca burgersi*. Proportions of actively reproducing and inactive males. Comparisons were made among seasons, for each site. Bars with at least one letter in common did not differ significantly (multinomial proportions analysis; α=0.05).

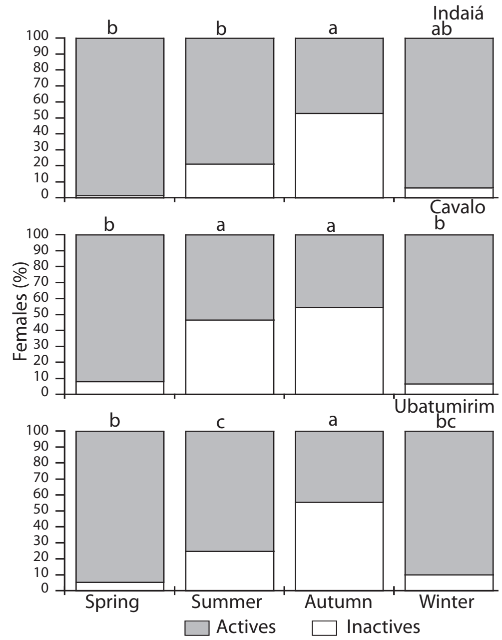

Fig. 8. *Uca burgersi*. Proportions of actively reproducing and inactive females. Comparisons were made among seasons, for each site. Bars with at least one letter in common did not differ significantly (multinomial proportions analysis; α=0.05).

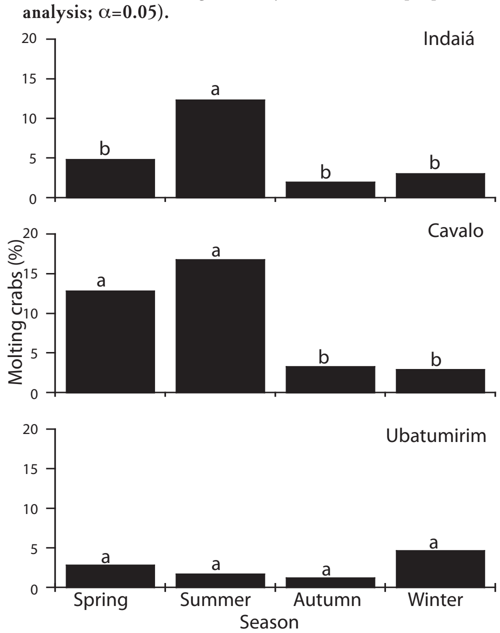

Fig. 9. *Uca burgersi*. Proportions of molting individuals. Comparisons were made among seasons, for each site. Bars with at least one letter in common did not differ significantly (multinomial proportions analysis; α=0.05).

higher organic matter content. Thus, the larger males of *U. burgersi* were found in the Cavalo River mangrove, as it was expected because this is the most productive of the sites studied. Nevertheless, females grew larger in the Ubatumirim River mangrove than at the Cavalo River; but this case suggest a sampling artifact, as the area in which crabs were found is very small compared to other sites. If one considers the predation risk, males being more conspicuous to predators than females because of their major chelipeds, they therefore might suffer higher mortality rates and do not reach larger sizes. Nevertheless, another hypothesis may explain the observed size differences: females grow slower than males because they invest more energy in the production of gametes (with yolk) than in somatic tissue.

The sex ratio of fiddler crabs is usually biased toward one sex or the other (Genoni 1985). In the present study, *U. burgersi* showed a higher proportion of males in the intermediate size class in the Indaiá and Ubatumirim mangroves. This difference is common among marine crustaceans, and can be attributed to several factors, as droving for males, which can favor one sex over the other. The tendency toward biased sex ratios is notable in species of *Uca* as mentioned by Wenner (1972) and Johnson (2003).

Some studies (Frith and Brunenmeister 1983, Emmerson 1994, Croll and McClintock 2000), using sampling techniques with sediment excavation and wide temporal and spatial variability, have shown a tendency in fiddler crabs toward male-biased sex ratios. Johnson (2003) mentioned that 14 species of fiddler crabs tend toward male-biased sex ratios, suggesting that this tendency has an ecologic meaning and does not represent a sampling artifact.

Rieger (1998), studying the larval development of *U. burgersi*, collected ovigerous females during November and February, i.e., spring and summer. The same pattern occurred in the present investigation, with seven ovigerous females recorded in spring and summer.

All the egg masses found were in the final embryonic developmental stage. This indicates that these females may be ready to disperse the larvae in the estuary. According to Salmon (1987), females of broad-fronted fiddler crabs as *U. burgersi*, can incubate their eggs underground to protect them from extreme environmental conditions and to provide a uniform environment, thus promoting synchrony in embryonic development and larval hatching. Christy and Salmon (1984), Murai *et al.* (1987) and Henmi (2003) also observed such behavior in *Uca pugilator* (Bosc, 1802), *Uca lactea* (DeHaan, 1875) and *Uca perplexa* (H. Milne Edwards, 1837) respectively. Moreover, ovigerous females with large broods remained in their burrows during the entire incubation period and did not feed during this phase. It can be inferred that ovigerous females of *U. burgersi* have the same kind of behavior in the mangroves studied by us.

Usually female fiddler crabs move to the entrance of their burrow during the highest high-tide (spring-tide) to disperse their offspring, and larvae will be transported to the sea. Thus leaving their burrow would not improve larval dispersal, but would increase predation risk.

The similarity of juvenile recruitment among the three populations shows that larval development must be occurring under the same near-shore conditions. Recruitment was observed year-round, which may indicate that reproduction is continuous, as in other intertidal brachyurans (Leme 2002).

The definition of the reproductive period as the time interval when ovigerous females are present in the population (Sastry 1983) cannot be adopted for this fiddler crab species, considering that they incubate their eggs inside the burrows (Salmon 1987). Other reports have emphasized that *U. pugilator* (see Christy and Salmon 1984) and *U. lactea* (see Koga *et al.* 2000) incubate their eggs underground and do not feed during this period.

The many factors influencing the reproductive cycle, such as sexual maturity, can be endogenous or exogenous, or a result of the interaction between them. Most ocypodid crabs from temperate regions show seasonal reproduction, e.g., *U. lactea, U. pugilator, U. pugnax, Macrophthalmus japonicus, Scopimera globosa* and *Ilyoplax stevensi* (see Greenspan 1982, Christy and Salmon 1984, Henmi 1989, Snowden *et al.* 1991, Koga *et al.* 2000). Even some subtropical crab species can show seasonal reproduction: *Pachygrapsus transversus* Gibbes, 1850 (see Flores and Negreiros-Fransozo 1998) and *Uca rapax* (Smith, 1870) (see Castiglioni *et al.* 2007). The reproduction of *U. burgersi* was continuous in the area studied, with pronounced peaks during spring and summer. Cardoso (2003), studying *U. leptodactyla,* and Costa and Negreiros-Fransozo (2003), studying *U. thayeri*, both in the same region as the present investigation, found that reproduction occurs throughout the year. This reinforces the supposition that favorable conditions for intertidal fiddler crabs exists continuously in the area.

The ratio of molting individuals of *U. burgersi* was very low (<20 %) throughout the year in all three mangroves, which is expected for terrestrial or semi terrestrial crabs. Because the molt is a critical period, crabs remain inside the burrows to prevent attacks by predators (Hyatt and Salmon 1978, Christy and Salmon 1984, Salmon 1987, Atkinson and Taylor 1988, Koga *et al.* 2000).

Terrestrial and semi terrestrial crabs (males and females) are known to copulate even in intermolt periods, as long as the female's genital opening is not calcified. In contrast, most aquatic crabs copulate just after the female has molted (Bliss 1968, Greenspan 1982). *U. burgersi* showed a high proportion of females in the intermolt stage with developed ovaries. This may indicate that mating occurred during the intermolt.

The antagonism between the processes of reproduction and growth is widely known among crabs, because of the competition for energy resources for each process. Thus, there is a wide diversity of growth and reproduction patterns, which allow each species to maximize its reproductive potential within the limits of its plasticity (Hartnoll 1985). Certainly this argument can be admitted for *U. burgersi* as a result of the interaction between reproduction and growth. The findings presented here clearly indicate a growth period prior to the spawning season in spring and summer, and a peak in the establishment of juveniles in the subsequent autumn and winter. Molting preceding the reproductive period has also been reported in other semi terrestrial crabs (Pillay and Ono 1978, Fukui 1990, Flores and Negreiros-Fransozo 1999).

According to the present data, *U. burgersi* presents similar patterns of both population structure and reproductive cycle among the three studied sites, despite of the different environmental features encountered in each site. Benetti (2003) studied the Cavalo River mangrove and found its sediment is mainly compounded by coarse sand, and organic matter content is higher than in the other two mangroves. She also found monotypic vegetation: only *L. racemosa* inhabits this area. In the other study areas (Indaiá and Ubatumirim rivers), which are exposed to mechanic effects of wave action, very fine sand were predominant (Benetti 2003), and the vegetation was composed by *L. racemosa* and *A. schaueriana*.

The synchrony between the population and reproductive biology of *U. burgersi* in the three studied areas shows that the specific features of each site were not the limiting factors in its biology and, probably other factors (biotics and or abiotics), or also the interaction among them, are the cause of the stability and synchrony of its life cycle. Moreover, it is suggested that *U. burgersi* is a generalist with respect to the habitat.

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RESUMEN

Estudiamos la biología poblacional y reproductiva de tres poblaciones de *Uca burgersi* Holthuis, 1967, en los manglares de Indaiá, Cavalo y Ubatumirim (Ubatuba, São Paulo, Brasil). Los cangrejos fueron recolectados por excavación de sedimentos, con un esfuerzo de captura estándar (dos personas por 30 min), durante la marea baja, entre agosto 2001 y julio 2002. En todos los especimenes se midió la anchura del caparazón y se registró la etapa de desarrollo gonadal. Esta especie fue más abundante en Cavalo, donde se halló el macho de mayor tamaño. Encontramos juveniles en los tres sitios, durante todo el período de estudio. Sin embargo, la proporción de hembras ovígeras fue muy baja (nula en Cavalo). Según el desarrollo gonadal, el periodo reproductivo fue continuo allí, pero más intenso durante la primavera y el verano, con reclutamiento en el invierno. La sincronía entre la biología poblacional y reproductiva de las tres poblaciones, demuestra que las características locales no fueron los factores

limitantes. Se sugiere que esta especie es generalista con respecto al hábitat.

Palabras clave: cangrejo violinista, ciclo reproductivo, estructura poblacional, manglares, Brasil.

REFERENCES

Abelló, P. 1989a. Reproductive biology of *Macropipus tuberculatus* (Roux, 1830) in the northwestern Mediterranean. Ophelia 30: 47-53.

Abelló, P. 1989b. Reproduction and molting in *Liocarcinus depurator* (Linnaeus, 1758) (Brachyura: Portunidae) in the northwestern Mediterranean Sea. Sci. Mar. 53: 127-134.

Atkinson, R.J.A. & A.C. Taylor. 1988. Physiological ecology of burrowing decapods. Symp. Zool. Soc. Lond. 59: 201-226.

Benetti, A.S. 2003. Aspectos biológicos de *Uca burgersi* Holthuis, 1967 (Crustacea, Brachyura, Ocypodidae) no litoral norte paulista. Master of Science Dissertation, Instituto de Biociências, Universidade Estadual Paulista - Botucatu, São Paulo, Brazil. 141 p.

Benetti, A.S. & M.L. Negreiros-Fransozo. 2003. Madurez sexual morfológica del cangrejo *Uca burgersi* Holthuis, 1967 (Brachyura, Ocypodidae) de una área de manglar subtropical de Brasil. Rev. Univ. Cien. Mexico 19: 1-16.

Benetti, A.S. & M.L. Negreiros-Fransozo. 2004 a. Relative growth of fiddler crab *Uca burgersi* Holthuis, 1967 (Crustacea, Ocypodidae) from two mangroves in the southeastern Brazilian coast. Iheringia, Porto Alegre 94: 67-72.

Benetti, A.S. & M.L. Negreiros-Fransozo. 2004 b. Symmetric chelipeds in males of the fiddler crab *Uca burgersi* Holthuis, 1967 (Decapoda, Brachyura, Ocypodidae). Nauplius 11: 141-144.

Bliss, D. 1968. Transition from water to land in decapod crustaceans. Am. Zool. 8: 355-392.

Brown, R.B. & G.C. Powell. 1972. Size at maturity in the male Alaskan Tanner Crab, *Chionoecetes bairdi*, as determined by chela allometry, reproductive tract weights, and size of procopulatory males. J. Fish. Res. Bd. Can. 29: 423-427.

Cardoso, R.C.F. 2003. Biologia populacional comparativa de *Uca leptodactyla* Rathbun, 1898 (Crustacea, Brachyura, Ocypodidae) nos manguezais dos rios Indaiá e Ubatumirim, Ubatuba, SP. Master of Science Dissertation, Instituto de Biociências, Universidade Estadual Paulista, Botucatu, São Paulo, Brazil. 119 p.

Castiglioni, D.S. & M.L. Negreiros-Fransozo. 2005. Comparative population biology of *Uca rapax* (Smith, 1870) (Brachyura, Ocypodidae) from two subtropical mangrove habitats on the Brazilian coast. J. Nat. Hist. 39: 1627-1640.

Castiglioni, D.S., M.L. Negreiros-Fransozo & R.C.F. Cardoso. 2007. Breeding season and molt cycle of the fiddler crab *Uca rapax* (Brachyura, Ocypodidae) in a subtropical estuary, Brazil, South America. Gulf Carib. Res. 19:11-20

Chacur, M.M. & M.L. Negreiros-Fransozo. 2001. Spatial and seasonal distribution of *Callinectes danae* (Decapoda, Portunidae) in Ubatuba Bay, São Paulo, Brazil. J. Crust. Biol. 21: 414-425.

Choy, S.C. 1988. Reproductive biology of *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae) from the Gower Peninsula, South Wales. Mar. Biol. 9: 227-241.

Christy, J.H. & M. Salmon. 1984. Ecology and evolution of mating systems of fiddler crabs (Genus *Uca*). Biol. Rev. 59: 483-509.

Colpo, K.D. 2001. Biologia populacional comparativa de *Uca vocator* (Herbst, 1804) em três localidades do litoral norte paulista. Master of Science Dissertation, Instituto de Biociências, Universidade Estadual Paulista. Botucatu, São Paulo, Brazil. 104 p.

Colpo, K.D. & M.L. Negreiros-Fransozo. 2003. Reproductive output of *Uca vocator* (Herbst, 1804) from three subtropical mangroves in Brazil. Crustaceana 76: 1-11.

Conan, G.Y. & M. Comeau. 1986. Functional maturity and terminal molt of male snow crab *Chionoecetes opilio*. Can. J. Fish. Aquat. Sci. 43: 1710-1719.

Conde, J.E. & H. Díaz. 1989. The mangrove tree crab *Aratus pisonii* in a tropical estuarine coastal lagoon. Estuar. Coast. Shelf Sci. 28: 639-650.

Conde, J.E. & H. Díaz. 1992. Variation in the intraspecific relative size at the onset of maturity (RSOM) in *Aratus pisonii* (H. Milne Edwards, 1837) (Decapoda, Brachyura, Grapsidae). Crustaceana 62: 214-216.

Costa, T.M.C. & M.L. Negreiros-Fransozo. 1998. The reproductive cycle of *Callinectes danae* Smith, 1869

(Decapoda, Portunidae) in the Ubatuba region, Brazil. Crustaceana 71: 615-627.

Costa, T.M. & M.L. Negreiros-Fransozo. 2001. Morphological adaptation of the second maxilliped in semiterrestrial crabs of the genus *Uca* Leach, 1814 (Decapoda, Ocypodidae) from a subtropical Brazilian mangrove. Nauplius 9: 123-131.

Costa, T.M. & M.L. Negreiros-Fransozo. 2003. Population biology of *Uca thayeri* Rathbun, 1900 (Brachyura, Ocypodidae) in a subtropical South American mangrove area: results from transect and catch-per-unit-effort techniques. Crustaceana 75:1201-1218.

Crane, J. 1975. Fiddler Crabs of the World. Ocypodidae: Genus *Uca*. Princeton University, Princeton, New Jersey, USA. 736 p.

Croll, G.A. & J.B. McClintock. 2000. An evaluation of lekking behavior in the fiddler crab *Uca* spp. J. Exp. Mar. Biol. Ecol. 254: 109-121.

Curi, P.R. & R.V. Moraes. 1981. Associação, homogeneidade e contrastes entre proporções em tabelas contendo distribuições multinomiais. Ciên. Cult. 33: 712-722.

Drach, P. & C. Tchernigovtzeff. 1967. Sur la méthode de détermination des stades d'intermue et son application générale aux crustacés. Vie Milieu 18: 595-610.

Emmerson, W.D. 1994. Seasonal breeding cycles and sex ratios of eight species of crabs from Mgazana, a mangrove estuary in Transkei, southern Africa. J. Crust. Biol. 14: 568-578.

Flores, A.A.V. & M.L. Negreiros-Fransozo 1998. External factors determining seasonal breeding in a subtropical population of the shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura: Grapsidae). Invertebr. Reprod. Dev. 34:149-155.

Flores, A.A.V. & M.L. Negreiros-Fransozo. 1999. On the population biology of the mottled shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae) in a subtropical area. Bull. Mar. Sci. 65: 59-73.

Flores, A.A.V., J. Saraiva & J. Paula. 2002. Sexual maturity, reproductive cycles, and juvenile recruitment of *Perisesarma guttatum* (Brachyura, Sesarmidae) at Ponta Rasa mangrove swamp, Inhaca Island, Mozambique. J. Crust. Biol. 22: 143-156.

Fontelles-Filho, A.A. 1989. Recursos pesqueiros: biologia e dinâmica populacional. Imprensa Oficial do Ceará, Fortaleza, Brazil. 296 p.

Frith, D.W. & S. Brunenmeister. 1983. Fiddler crab (Ocypodidae: Genus *Uca*) size, allometry and male major chela handedness and morphism on a Thailand mangrove shore. Phuket Mar. Biol. Cent. Res. Bull. 29: 1-16.

Fukui, Y. 1990. Breeding and molting of *Gaetice depressus* (De Haan) (Brachyura: Grapsidae) under laboratory conditions. Res. Crust. 19: 83-90.

Genoni, G.P. 1985. Food limitation in salt marsh fiddler crab *Uca rapax* (Smith) (Decapoda, Ocypodidae). J. Exp. Mar. Biol. Ecol. 87: 97-110.

Gibbs, P.E. 1974. Notes on *Uca burgersi* from Barbuda, Leeward Islands. Crustaceana 27: 84-91.

Gibbs, P.E. & G.W. Bryan. 1972. A study of strontiun, magnesium, and calcium in the environment and exoskeleton of decapod crustaceans, with special reference to *Uca burgersi* on Barbuda, West Indies. J. Exp. Mar. Biol. Ecol. 9: 97-110.

González-Gurriarán, E. 1985. Reproducción de la nécora *Macropipus puber* (L.) (Decapoda, Brachyura) y ciclo reproductivo en la Ría Arousa (Galicia, NW España). Bol. Inst. Ocean. 2: 10-32.

Greenspan, B.N. 1982. Semi-monthly reproductive cycles in male and female of fiddler crabs, *Uca pugnax*. Anim. Behav. 30: 1084-1092.

Haefner Jr., P.A. 1976. Distribution, reproduction and moulting of the rock crab, *Cancer irroratus* Say, 1917, in the Mid-Atlantic Bight. J. Nat. Hist. 10: 377-397.

Hartnoll, S.R. 1985. Growth, sexual maturity and reproductive output, p.121-128. *In* A.M. Wenner (ed.). Factors in Adult Growth. A.A. Balkema, Rotterdam, The Netherlands. 362 p.

Henmi, Y. 1989. Reproductive ecology of three ocypodid crabs. II. Incubation sites and egg mortality. Ecol. Res. 4: 261-269.

Henmi, Y. 1992. Annual fluctuation of life-history traits in the mud crab *Macrophthalmus japonicus*. Mar. Biol. 113: 569-577.

Henmi, Y. 2003. Trade-off between brood size and brood interval and the evolution of underground incubation in three fiddler crabs (*Uca perplexa, U. vocans* and *U. dussumieri*). J. Crust. Biol. 23: 46-54.

Hines, A.H. 1989. Geographic variation in size at maturity in brachyuran crabs. Bull. Mar. Sci. 45: 356-368.

Hutchinson, G.E. 1981. Introducción a la Ecologia de Poblaciones. Blume, Barcelona, Spain. 492 p.

Hyatt, G.W. & M. Salmon. 1978. Combat in the fiddler crabs *Uca pugilator* and *U. pugnax*: a quantitative analysis. Behaviour 65: 182–211.

Johnson, P.T.J. 2003. Biased sex ratios in fiddler crabs (Brachyura, Ocypodidae): a review and evaluation of the influences of sampling method, size class, and sex specific mortality. Crustaceana 76: 559–580.

Jones, M.B. & M.J. Simons. 1983. Latitudinal variation in reproductive characteristics of a mud crab, *Helice crassa* (Grapsidae). Bull. Mar. Sci. 33: 656-670.

Koch, V. & M. Wolff. 2002. Energy budget and ecological role of mangrove epibenthos in the Caeté estuary, North Brazil. Mar. Ecol. Prog. Ser. 228: 119–130.

Koga, T., M. Murai, S. Goshima & S. Poovachiranon. 2000. Underground mating in the fiddler crab *Uca tetragonon*: the association between female life history traits and male mating tactics. J. Exp. Mar. Biol. Ecol. 248: 35–52.

Leme, M.H.A. 2002. A comparative analysis of the population biology of the mangrove crabs *Aratus pisonii* and *Sesarma rectum* (Brachyura, Grapsidae) from the north coast of São Paulo state, Brazil. J. Crust. Biol. 22: 553–557.

Litulo, C. 2005. Breeding season of the hermit crab *Dardanus deformis* H. Milne Edwards, 1836 (Anomura, Diogenidae) in Maputo Bay, southern Mozambique. J. Nat. Hist. 39: 2137–2144.

Macintosh, D.J. 1988. The ecology and physiology of decapods of mangrove swamps. Symp. Zool. Soc. Lond. 59: 315–341.

Melo, G.A.S. 1996. Manual de Identificação dos Brachyura (Caranguejos e Siris) do Litoral Brasileiro. Plêiade, São Paulo, Brazil. 604 p.

Mouton, E.C.J. & D.L. Felder. 1995. Reproduction of the fiddler crabs *Uca longisignalis* and *Uca spinicarpa* in a Gulf of Mexico salt marsh. Estuaries 18: 469–481.

Mouton, E.C.J & D.L. Felder. 1996. Burrow distributions and population estimates for the fiddler crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico salt marsh. Estuaries 19: 51-61.

Murai, M., S. Goshima & Y. Henmi. 1987. Analysis of the mating system of the fiddler crab, *Uca lactea*. Anim. Behav. 35: 1334–1342.

Negreiros-Fransozo, M.L., A. Fransozo & G. Bertini. 2002. Reproductive cycle and recruitment period of *Ocypode quadrata* (Decapoda: Ocypodidae) at a sandy beach in southeastern Brazil. J. Crust. Biol. 22: 157–161.

Negreiros-Fransozo, M.L., F.L.M. Mantelatto & A. Fransozo. 1999. Population biology of *Callinectes ornatus* Ordway, 1863 (Decapoda, Portunidae) from Ubatuba (SP), Brazil. Sci. Mar. 63: 157–163.

O'Connor, N.J. 1990. Morphological differentiation and molting of juvenile fiddler crabs (*Uca pugilator* and *Uca pugnax*). J. Crust. Biol. 10: 608-612.

Odum, W.E. & E.J. Heald. 1972. Trophic analyses of an estuarine mangrove community. Bull. Mar. Sci. 22: 671–738.

Pillay, K.K. & N.B. Nair. 1971. The annual reproductive cycles of *Uca annulipes, Portunus pelagicus* and *Metapenaeus affinus* (Decapoda, Crustacea) from the south-west coast of India. Mar. Biol. 11: 152–166.

Pillay, K.K. & Y. Ono. 1978. The breeding cycles of two species of grapsid crabs (Crustacea: Decapoda) from the north coast of Kyushu, Japan. Mar. Biol. 45: 273–288.

Rieger, P.J. 1998. Desenvolvimento larval de *Uca (Minuca) burgersi* Holthuis (Crustacea, Decapoda, Ocypodidae) em laboratório. Rev. Bras. Zool. 15: 727–756.

Rodríguez, A., P. Drake & A.M. Arias. 1997. Reproductive periods and larval abundance patterns of the crabs *Panopeus africanus* and *Uca tangeri* in a shallow inlet (SW Spain). Mar. Ecol. Prog. Ser. 149: 133–142.

Salmon, M. 1987. On the reproductive behavior of the fiddler crab *Uca thayeri*, with comparisons to *U. pugilator* and *U. vocans*: evidence for behavioral convergence. J. Crust. Biol. 7: 25-44.

Santos, S., M.L. Negreiros-Fransozo & A. Fransozo. 1995. Morphometric relationships and maturation in *Portunus spinimanus* Latreille, 1819 (Crustacea, Brachyura, Portunidae). R. Bras. Biol. 55: 545–553.

Sastry, A.N. 1983. Ecological aspects of reproduction, p. 179-270. *In* J. Vernberg & W.B. Vernberg (eds.). The Biology of Crustacea. Vol. 8. Environmental Adaptations. Academic, New York, USA.

Snowden, R.J., D.A. Clayton & E.Y. Taher. 1991. Population biology of *Ilyoplax stevensi* (Brachyura: Ocypodidae) on a Kuwait mudflat. Mar. Ecol. Prog. Ser. 71: 219–225.

Sokal, R.R. & F.J. Rohlf. 1987. Introduction to Biostatistics. Freeman, New York, USA. 363 p.

Somerton, D. 1980a. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquat. Sci. 37: 1488-1494.

Somerton, D. 1980b. Fitting straight lines to Hiatt growth diagrams: a re-evaluation. J. Cons. Int. Explr. Mer. 39: 15-19.

Spivak, E.D., M.A. Gavio & C.E. Navarro. 1991. Life history and structure of the world's southernmost *Uca* population: *Uca uruguayensis* (Crustacea, Brachyura) in Mar Chiquita Lagoon (Argentina). Bull. Mar. Sci. 48: 679-688.

Thurman II, C.L. 1985. Reproductive biology and population structure of the fiddler crab *Uca subcylindrica* (Stimpson). Biol. Bull. 169: 215-229.

Thurman II, C.L. 1987. Fiddler crabs (Genus *Uca*) of eastern Mexico (Decapoda, Brachyura, Ocypodidae). Crustaceana 53: 94-105.

Trott, T. 1996. On the sex ratio of the painted ghost crab *Ocypode gaudichaudii* H. Milne Edwards and Lucas, 1843 (Brachyura, Ocypodidae). Crustaceana 71: 47-56.

Twilley, R.R. 1985. The exchange of organic carbon on basin mangrove forests in a southwest Florida estuary. Estuar. Coast. Shelf Sci. 20: 543-57.

von Hagen, H.O. 1982. Visual and acoustic display in *Uca mordax* and *U. burgersi* sibling species of neotropical fiddler crabs I: waving display. Behaviour 83: 229-250.

von Hagen, H.O. 1984. Visual and acoustic display in *Uca mordax* and *Uca burgersi,* sibling species of neotropical fiddler crabs II: vibration signals. Behaviour 91: 204-228.

Warner, G.F. 1977. The Biology of Crabs. Elek Science, New York, USA. 202 p.

Watson, J. 1970. Maturity, mating and egg laying in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 27: 1607-1616.

Wenner, A.M. 1972. Sex-ratio as a function of size in marine Crustacea. Am. Nat. 106: 321-350.

Wenner, A.M. 1989. Incidence of insemination in female blue crabs, *Callinectes sapidus*. J. Crust. Biol. 9: 587-594.