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Original article

Population and reproductive biology of the fiddler crab *Uca thayeri* Rathbun, 1900 (Crustacea: Ocypodidae) in a tropical mangrove from Northeast Brazil

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ABSTRACT

Population and reproductive biology of *Uca thayeri* Rathbun, 1900 were studied for the first time in a tropical mangrove. Absolute density, sex ratio, population structure, handedness, breeding season and fecundity were investigated. Seven transects were delimited in a mangrove area of the Pacoti River, Northeast of Brazil (3° 43′ 02″ S/38° 32′ 35″ W). On each transect, ten 0.25 m^2 squares were sampled on a monthly basis during low tide periods from September 2003 to August 2004. A total of 483 crabs were obtained, of which 250 were males, 219 non-ovigerous females, and 14 ovigerous females. The *U. thayeri* population presented bi-modal size frequency distribution, with males and non-ovigerous females not differing significantly size-wise. Ovigerous females were larger than males and non-ovigerous females. The overall sex ratio (1:1.07) did not differ significantly from the expected 1:1 proportion. The major cheliped was the right one in 50% of the males. The observed density was of 8.5 individuals/m^2, with the specimens being found mostly in shaded areas. Ovigerous females were found in 5 months of the year, coinciding with the rainy season, suggesting that the population of *U. thayeri* presents seasonal reproductive events. Juvenile crabs were more abundant during the dry period, while larger crabs were found mainly during the rainy period. The fecundity of the studied population was much smaller than that of subtropical populations of this species. The regression analysis shows that the number of eggs increases linearly with the increase of carapace width.

1. Introduction

The fiddler crabs (Genus *Uca*), which are distributed along tropical and subtropical mangroves of the Old and New World, are a well diversified group inhabiting various biotopes. Their adaptive radiation is considered to be related to the extension of the habitat and food sources through modifications of their own morphology, behavior, ecology and physiology (Crane, 1975; Christy and Salmon, 1984; Takeda and Murai, 2003).

In recent years, the number of studies on fiddler crab populations has increased, revealing informations on density, size frequency distribution, spatial dispersion, sex ratio,

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handedness, juvenile recruitment and reproductive season, among others (Thurman, 1985; Diaz and Conde, 1989; Leme and Negreiros-Fransozo, 1998; Costa, 2000; Litulo, 2005a,b). Most studies already carried out on fiddler crab population structure and reproduction were conducted for subtropical species (Spivak et al., 1991; Mouton and Felder, 1995), while much remains unknown about the tropical ones (Litulo, 2005a,b).

The fiddler crab *Uca thayeri* Rathbun, 1900 is a common resident of mangrove forests along the West Atlantic coast (Crane, 1975; Melo, 1996). Aspects of its courtship (Kellmeyer and Salmon, 2001; Weaver and Salmon, 2002), physiology (Vernberg and Costlow, 1966; Vernberg and Tashian, 1959), allometric growth and handedness (Negreiros-Fransozo et al., 2003) have been studied. In Southeast Brazil, the population dynamics of this fiddler crab was studied in a subtropical mangrove by Costa (2000) and Costa and Negreiros-Fransozo (2002).

Eight species of *Uca* have been recorded in the tropical mangroves of Northeast Brazil: *Uca burgersi* (Holthuis, 1967); *Uca cumulanta* (Crane, 1943); *Uca leptodactyla* (Rathbun, 1898); *Uca maracoani* (Latreille, 1802–1803); *Uca mordax* (Smith, 1870); *Uca rapax* (Smith, 1870); *U. thayeri* Rathbun, 1900 and *Uca vocator* (Herbst, 1804) (Coelho, 1994–1995; Melo, 1996). Although those species are very common in the tropical mangroves of Northeast Brazil, little attention has been directed at understanding the factors concerning their population dynamics.

No previous work has yet been published on the population structure and breeding season of *U. thayeri* in tropical areas. Comparisons between populations may constitute an important strategy in verifying differences among them, as well as in understanding the environment and biological constraints that are shaping them (Oshiro, 1999; Litulo, 2005b).

In the present study, some aspects of population biology of *U. thayeri* were investigated, such as density, size structure, sex ratio, breeding season, fecundity, and handedness in a tropical mangrove of the Pacoti River, Northeast Brazil.

2. Materials and methods

2.1. Site description

The fieldwork took place at the Pacoti River mangrove, Ceará State, Northeast of Brazil (3° 43′ 02″ S/38° 32′ 35″ W) (Fig. 1). The climate is tropical with a maximum temperature of 34 °C, and a minimum of 22 °C. The rainy season is concentrated within a few months of the year with an annual average rainfall of 600–1000 mm. Tides are semidiurnal with maximum tidal amplitude of about 3.1 m and a minimum of 0.9 m (Freire, 1989). The mangrove vegetation of this area is dominated by *Avicennia schaueriana* Stapf and Leechman, *Avicennia germinans* Linnaeus, *Laguncularia racemosa* Gaerth and *Rhizophora mangle* Linnaeus (Miranda et al., 1988).

2.2. Sampling methods

Seven transects were delimited in a mangrove area of the Pacoti River, comprising an area of 1.2 km^2. On each transect, ten 50 × 50 cm (0.25 m^2) squares equally spaced, were sampled on a monthly basis during spring low tide periods from September 2003 to August 2004. At each month, the same squares were sampled. The transects ran from the edge of mangrove vegetation to mud flats in the river in order to sample the whole habitat and not only the *U. thayeri* burrow's area. The squares were excavated with a corer to a depth of 30 cm and all fiddler crabs presented in the areas limited by the squares were bagged, labelled and preserved in 70% ethanol until further analysis.

The salinity of the Pacoti River was measured with a refractometer, using the Practical Salinity Scale, and the pluviometric indices from September 2003 to August 2004 were gathered by ''Fundação Cearense de Meteorologia e Recursos Hídricos'' (FUNCEME).

2.3. Laboratory analysis

In the laboratory, specimens were identified, sexed, checked for the presence of eggs on female pleopods and, in the case of males, had registered which of the chelipeds were enlarged. The carapace width (CW) was measured using a vernier caliper (±0.01 mm accuracy). The number of crabs was recorded for each transect.

The population size structure was analyzed in function of the size frequency distribution of all individuals collected during the study period. Specimens were grouped in 3 mm size class intervals from 4 to 28 mm CW. The period of time when ovigerous females were found in the population was considered as the breeding season.

To estimate fecundity, 20 ovigerous females with eggs at stage I were selected for egg counting according to the methodology proposed by Litulo (2005b), with some modifications. Pleopods were removed from the females, placed in petri dishes filled with seawater, and had their eggs detached by gradually adding a solution of sodium hypochlorite. Bare pleopods were then discarded by being gently stirred in a beaker filled with 50 ml of seawater. With a pipette, five sub-samples of 1 ml were taken from the seawater with eggs. The eggs in each sub-sample were counted under a dissecting microscope. The average value obtained was extrapolated for the whole suspension in order to estimate the number of eggs.

2.4. Statistical procedures

The chi-square test (χ^2) and the Fisher test (*z*) were used to evaluate the sex ratio and the enlarged cheliped ratio. Overall size frequency distributions were tested for normality using Kolmogorov–Smirnov (KS) test (Zar, 1984), and mean size of males and females was compared using the Student's *t*-test. For fecundity analysis, data were analyzed using the power function ($Y = aX + b$) of egg number (EN) vs. CW.

3. Results

3.1. Population structure

A total of 483 crabs were sampled during the study period, of which 250 were males (51.77%), 219 non-ovigerous females (45.35%), and 14 ovigerous females (2.88%) (Table 1). Males ranged from 4.0 to 28.0 mm CW (mean ± SD: 11.98 ± 6.18 mm); non-ovigerous females from 4.2 to 24.6 mm CW

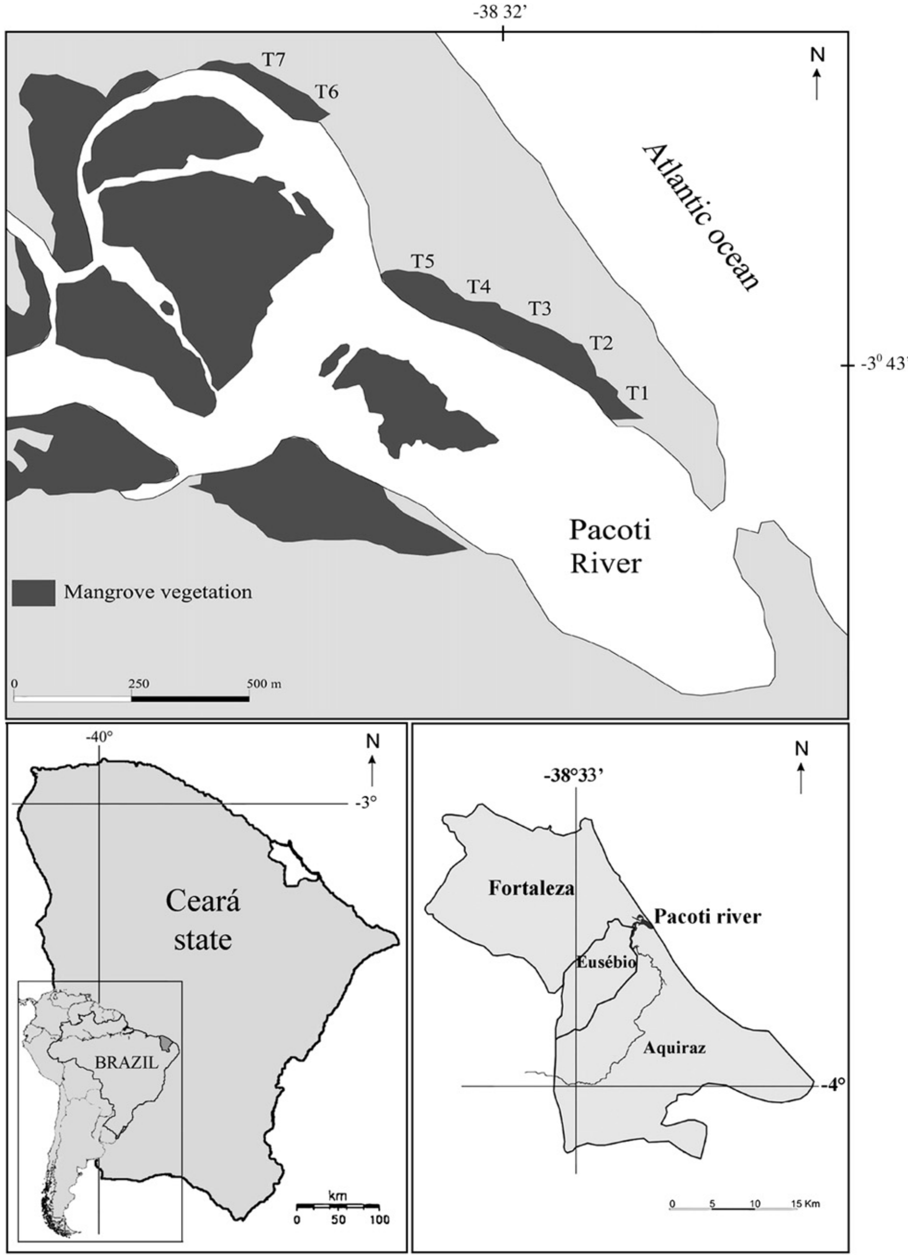

Fig. 1 – Map indicating the sampling area at Pacoti River mangrove, Northeast Brazil. T: transect.

(mean ± SD: 11.83 ± 5.82 mm); and ovigerous females from 18.5 to 26.5 mm CW (mean ± SD: 22.08 ± 2.35 mm). Ovigerous females were significantly larger than non-ovigerous females ($t = 13.82$, $p < 0.001$) and males ($t = 11.58$ $p < 0.001$). Male and non-ovigerous females did not differ significantly in size ($t = 0.78$, $p > 0.05$). Figure 2 shows the mean size for all sampled crabs.

Figure 3 shows the yearly size frequency distributions for males and ovigerous and non-ovigerous females. There was a non-conspicuous bi-modal size distribution for each sex, with non-normal distributions for males (KS = 0.1463, $p < 0.0001$), and females (KS = 0.2116, $p < 0.0001$). Both males and females were more abundant in the smallest size classes (4–7 mm, 7–10 mm). The males and females were also abundant in larger size classes (16–19 mm and 19–22 mm, respectively).

The monthly number of crabs sampled throughout the year is listed in Table 1. Monthly sex ratio and the handedness results were calculated. The overall sex ratio was 1:1.07 and did not differ significantly from the expected 1:1 proportion (χ^2 test, $p > 0.05$). The monthly sex ratio also did not differ from the Mendelian proportion (z test, $p > 0.05$). The proportion of males having the right (126 individuals) or left (124 individuals) chelae hypertrophied did not differ significantly from an expected 1:1 ratio (χ^2, $p > 0.05$). Furthermore, no adult male having either two giant chelipeds or two small chelipeds was collected (Table 1).

3.2. *Density*

Table 2 shows the fiddler crab densities in each transect. The mean yearly density was 8.5 individuals/m^2. The higher

Table 1 – *Uca thayeri* Rathbun, 1900 – total number, handedness and sex ratio of individuals collected monthly at Pacoti River mangrove, Northeast Brazil

Month	Males					Non-ovigerous females		Ovigerous females		Males and females		Sex ratio
	Right	Left	Ratio	Total	%	Total	%	Total	%	Total	%	
September	5	10	1:0.5	15	3.1	18	3.73	–	–	33	6.83	1:0.83
October	18	13	1:1.38	31	6.42	25	5.18	–	–	56	11.6	1:1.24
November	15	9	1:1.66	24	4.97	23	4.76	–	–	47	9.73	1:0.66
December	9	11	1:0.81	20	4.14	23	4.76	–	–	43	8.9	1:0.86
January	18	16	1:1.12	34	7.04	24	4.97	1	0.2	59	12.21	1:1.36
February	8	10	1:0.8	18	3.73	19	3.94	4	0.83	41	8.5	1:0.75
March	3	4	1:0.75	7	1.45	6	1.24	2	0.41	15	3.1	1:1
April	7	13	1:0.53	20	4.14	21	4.35	6	1.24	47	9.73	1:0.74
May	15	13	1:1.15	28	5.8	18	3.73	–	–	46	9.53	1:1.55
June	12	11	1:1.09	23	4.77	19	3.93	1	0.2	43	8.9	1:1.15
July	7	3	1:2.33	10	2.07	6	1.24	–	–	16	3.31	1:1.66
August	9	11	1:0.81	20	4.14	17	3.52	–	–	37	7.66	1:1.05
Total	126	124	1:1.04	250	51.77	219	45.35	14	2.88	483	100	1:1.07

values were found in the transect 5 (13.8 individuals/m^2) and transect 1 (13.7 individuals/m^2), while lower values were found in the transect 6 (2.8 individuals/m^2) and transect 2 (5.8 individuals/m^2).

3.3. *Reproductive biology*

3.3.1. *Breeding season*

During the study period, 14 ovigerous females were collected, between January and June 2004 (Table 1), corresponding to the months of maximum rainfall at the Pacoti River mangrove (Fig. 4). During that period it was also observed that the fiddler crabs were more abundant in the largest size classes, while in the dry period they were more concentrated in the smallest ones (Fig. 5). Ovigerous females were more abundant in the 19–22 mm size class, and the mean CW size was 22.08 ± 2.35 mm.

3.3.2. *Fecundity*

Fecundity ranged from 19120 (CW = 18 mm) to 25012 (CW = 26.5 mm) eggs. Egg number was positively correlated with female size and the resulting scatter plot shows a linear trend (Fig. 6), expressed by the function $EN = 774.46 \times CW + 4465.4$ ($r^2 = 0.80$, $n = 20$).

4. Discussion

4.1. *Population structure*

The population structure of *U. thayeri* at the Pacoti River mangrove is characterized by the simultaneous presence of two cohorts, mainly in the rainy period, therefore showing bi-modal size frequency distribution. The ovigerous females were collected only during the rainy season, suggesting seasonal breeding. In general, unimodal populations show breeding seasons that may occur at any time of the year, with continuous recruitment and constant larval mortality rates, a common pattern found in tropical fiddler crab populations (MacIntosh, 1989; Litulo, 2005a,b); while bi-modal populations show seasonal reproductive events (Rabalais and Cameron,

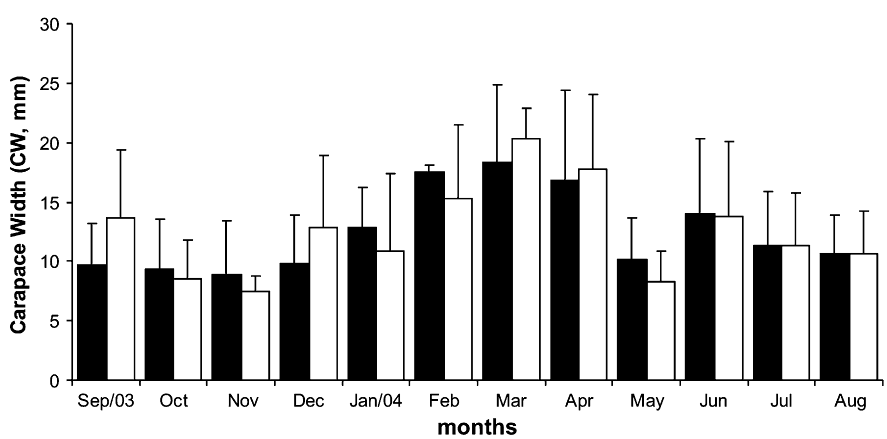

Fig. 2 – *Uca thayeri* Rathbun, 1900. Mean size of individuals collected at Pacoti River mangrove, Northeast Brazil, among September 2003 and August 2004. Black bars: males; white bars: females (ovigerous and non-ovigerous).

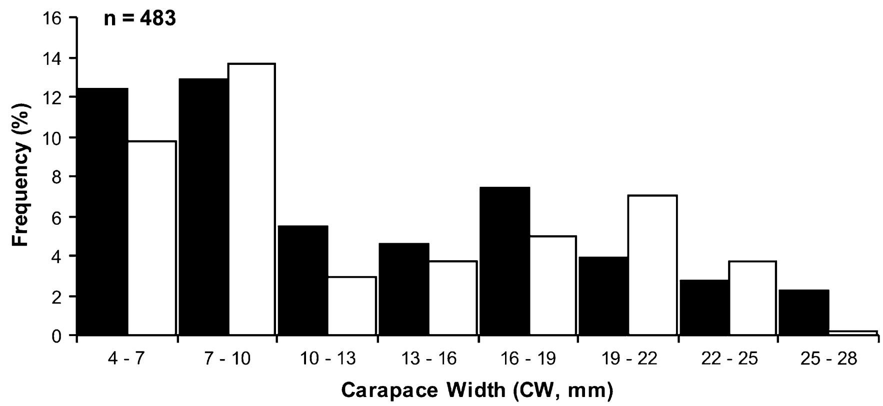

Fig. 3 – Overall size frequency distribution of *Uca thayeri* collected at Pacoti River mangrove, Northeast Brazil, from September 2003 to August 2004. Black bars: males; white bars: females (ovigerous and non-ovigerous).

1983; Thurman, 1985; Spivak et al., 1991; Mouton and Felder, 1995; Yamaguchi, 2001; Costa and Negreiros-Fransozo, 2002).

The difference between male and female carapace width was not greatly significant in the population studied and the overall size frequency distribution was non-normal, with a greater abundance of males and females in the smallest size classes. Similarly, Costa (2000), studying a *U. thayeri* population in a subtropical mangrove of Southeast Brazil, did not find significant differences between male and female size. However, fiddler crab populations have been reported to show sexual size dimorphism, where males are larger than females (Spivak et al., 1991; Johnson, 2003; Litulo, 2005a,b). According to Johnson (2003), *Uca* females may have reduced growth rates because they concentrate their budget on gonad development, a fact that may lead to a lower somatic growth than the observed amongst males. On the other hand, larger males have greater chances of obtaining females for copulation and of winning intra-specific fights (Christy and Salmon, 1984; Litulo, 2005a).

In crustacean populations, sexual differences in distribution and mortality may be responsible for unbalanced sex ratios (Johnson, 2003). Moreover, fiddler crab populations have been recorded historically with significant deviations from 1:1 proportions (Frith and Brunenmeister, 1980; Spivak et al., 1991; Costa, 2000; Jaroensutasinee and Jaroensutasinee, 2004; Litulo, 2005a,b). Differences between male and female spatial distributions, mortality rates, sampling methods (Montague, 1980), and differential predation on crab sex ratio (Wolf et al., 1975; Spivak et al., 1991) have been reported as causes of such biases.

According to Geisel (1972), physiologic and behaviorally homeostatic populations, living in constant environments, present a 1:1 sex ratio, or slightly male-biased; while populations that inhabit variable environments will present deviations toward the females, in order to maximize the evolutionary potential due to unequal selection between males and females. Fisher (1930) predicted that in random mating populations the evolutionary stable sex ratio would be 1:1. In this study, the overall sex ratio did not differ significantly from the expected 1:1 ratio, showing that *U. thayeri* population at the tropical mangrove of Pacoti River is physiologic and behaviorally adapted to the habitat, besides also being evolutionary stable.

Crane (1975) made the general statement that large claws on *Uca* males occur about equally often on the right as well as the left side, but reports of predominantly right-handed specimens have been stated for some Indo-West Pacific *Uca* species (Williams and Heng, 1981; Jones and George, 1982;

Table 2 – Density of each transect and total (number of individuals/m^2) of *Uca thayeri* collected at Pacoti River mangrove, Northeast Brazil from September 2003 to August 2004

Transects	Density (individuals/m^2)		Total density (males/females)
	Males	Females	
Transect 1	8.4	5.3	13.7
Transect 2	3	2.8	5.8
Transect 3	6.4	7	13.4
Transect 4	4.8	5.8	10.6
Transect 5	6.4	7.4	13.8
Transect 6	1.2	1.6	2.8
Transect 7	6.8	6.5	13.3
Average (individuals/m^2)			8.5

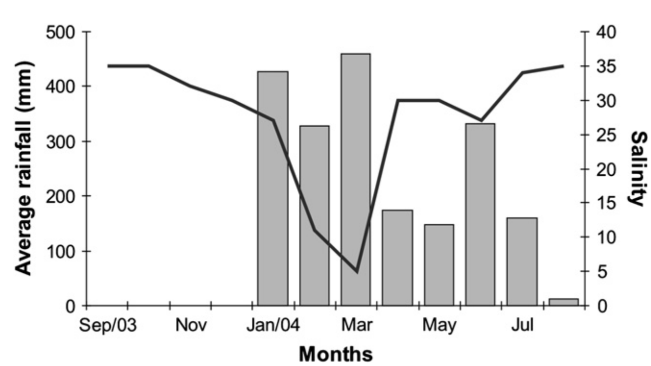

Fig. 4 – Monthly average rainfall (bars) of the Pacoti River mangrove from September 2003 to August 2004 and salinity (line) of Pacoti River, Northeast Brazil.

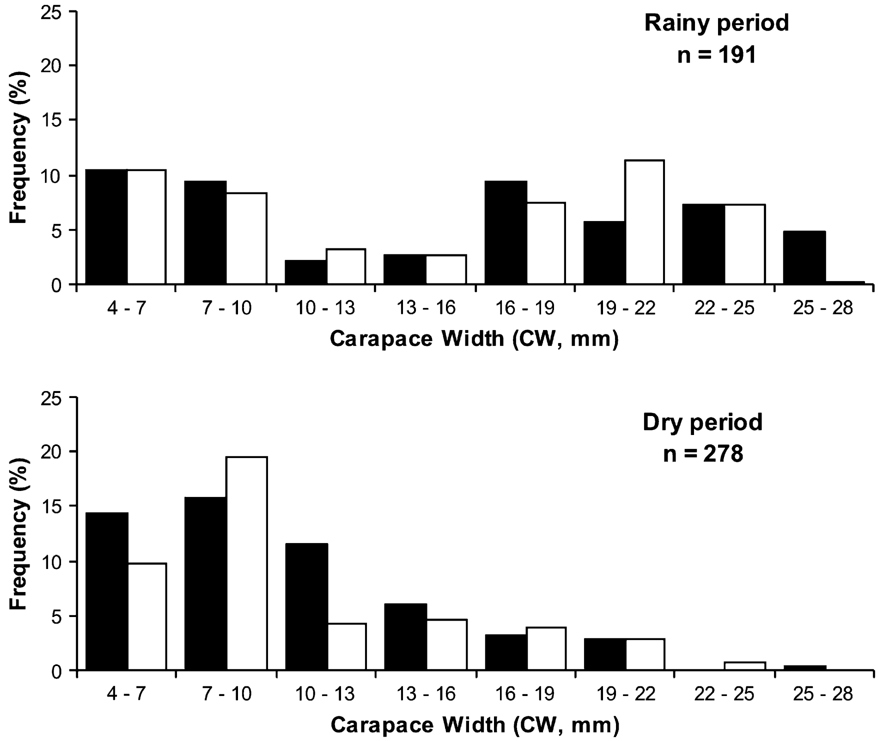

Fig. 5 – Overall size frequency distribution of *Uca thayeri* collected at Pacoti River mangrove, Northeast Brazil in the rain and dry periods. Black bars: males; white bars: females (ovigerous and non-ovigerous).

Jaroensutasinee and Jaroensutasinee, 2004) and left-handed for *U. burgersi* population from Barbuda Island, West Indies (Gibbs, 1974). The study of handedness in *U. thayeri* populations is very important; considering that handedness might be useful as an indicator of taxonomic grouping of the genus *Uca*, as is "broad-front" or "narrow-front" (Jones and George, 1982).

In the *U. thayeri* population analyzed in this study, the proportion of males having the right or left chelae hypertrophied did not differ significantly from an expected 1:1 ratio. This result suggests that in the young *U. thayeri* males, both chelipeds have an equal potential of growing into the giant one found on adults. In fact, Negreiros-Fransozo et al. (2002) did not find a predominance of the left or the right side regarding enlarged chelipeds in a subtropical *U. thayeri* population.

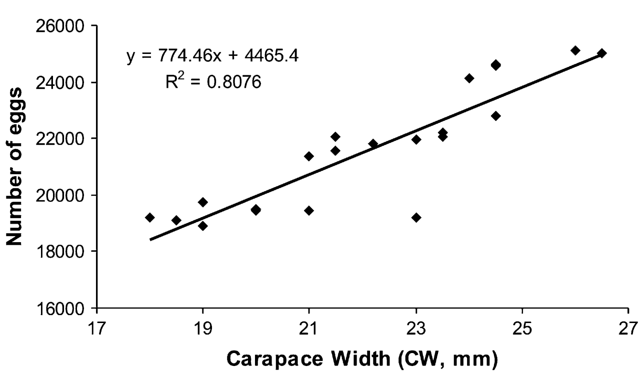

Fig. 6 – Scatter plot for the relationship between egg number (EN) and female size (CW) in *Uca thayeri* Rathbun, 1900 from Pacoti River mangrove, Northeast Brazil.

4.2. *Density*

Concerning the density of *U. thayeri* among the transects, transects 1–7 were composed of muddy substratum with a high content of humidity and organic matter and by a dense *R. mangle* vegetation. Coelho et al. (1973) and Costa (2000) state that *U. thayeri* prefer shaded areas with high contents of organic matter and humidity. However, some portions of the transect 2 were composed by coarse sediments, and the transect 6 was, in large extension, an open mud flat, inhabited by an *U. maracoani* (Latreille, 1801–1802) population. Due to these facts, the *U. thayeri* density was smaller in those transects.

4.3. *Reproductive biology*

The study of the breeding season in Crustacea can facilitate the understanding of the adaptive strategies and reproductive potential of a species and also its relationship with the environment and other species (Litulo, 2005a). In brachyuran crabs, different reproductive strategies have been reported. Specifically regarding tropical and subtropical fiddler crab populations, this has also been found to be true (Hines, 1982).

Tropical species present a continuous breeding season throughout the year, because near the tropics environmental conditions are generally favorable for gonad development, while subtropical species have seasonal breeding periods (Mouton and Felder, 1995). However, both seasonal and continuous breeding periods can be found in tropical and subtropical regions (Litulo, 2005b). In fact, Costa and Negreiros-Fransozo (2002) found ovigerous females only during 7 consecutive months in a subtropical *U. thayeri* population in Southeast Brazil, indicating the seasonal nature of the reproductive effort, being more pronounced in the warmer months. Juveniles occurred all over the year, although more numerous in the colder months. However, in the study accomplished by Costa (2000) also in a subtropical *U. thayeri* population in Southeast Brazil, the ovigerous females were present during 12 months, showing the continuous reproductive event.

Peaks of breeding season may be associated with abiotic and biotic factors such as temperature, photoperiod, rainfall, and food availability (Pinheiro and Fransozo, 2002). The occurrence of ovigerous females only in the rainy season suggests that in the Pacoti River mangrove the *U. thayeri* population has a breeding season closely associated with the rainy period. The fact that this period is also the time of the highest river discharges may yield evidence to a relation between increase in nutrient availability and success of planktotrophic larvae development (Christy and Morgan, 1998). Litulo (2005a) found a close association between the rainy period and breeding season in a tropical *Uca annulipes* (H. Milne Edwards, 1837) population.

Costa (2000) found 16 ovigerous females among 258 collected females in a 1-year-period. According to Christy (1987), ovigerous female fiddler crabs prefer to inhabit deep burrows because they provide a stable thermal environment that yields constant embryonic developmental rates. In fact, Litulo (2005a) found ovigerous females of *U. annulipes* inhabiting burrows at depths of about 30 cm and ovigerous females of *Uca inversa* (Hoffman, 1874) were mostly found in burrows of about 50 cm (Litulo, 2005b). Therefore, the low number of ovigerous females collected by Costa (2000) in this study may be due to the fact that ovigerous females hide inside deep burrows in order to incubate their eggs.

Negreiros-Fransozo et al. (2003), studying the relative growth of *U. thayeri* in a subtropical mangrove population of Southeast Brazil, found that for males the relative-growth analysis rendered an estimation of 13.8 mm of CW for the size at the onset of sexual maturity, while for females it had a wider puberty size ranging from 10.7 to 16.8 mm of carapace width. In our study, crabs smaller than 10 mm of CW, which were more abundant during the dry period, were considered juveniles. Fiddlers in the larger size classes were found, mainly, in the rainy season, showing that in the Pacoti River *U. thayeri* populations attain sexual maturity during this period. However, the CW size in which *Uca* populations attain sexual maturity can vary with latitude (Masunari and Swiech-Ayoub, 2003; Cardoso and Negreiros-Fransozo, 2004; Masunari et al., 2005; Masunari and Dissenha, 2005). Therefore, allometric growth studies with *U. thayeri* at Pacoti River mangrove must be done in order to determine the size of CW in which this fiddler attains sexual maturity.

According to Thurman (1985), the fecundity of *Uca* species in temperate and tropical areas can vary greatly, where the size and the amount of eggs are in close association with the environmental conditions. In this contribution, the greatest egg amount (25012) was registered for a female with 26.5 mm of CW. Costa (2000) recorded for a subtropical *U. thayeri* population that females from 23 to 26 of CW carried more than 45000 eggs, showing that in *U. thayeri* fecundity is correlated with environmental conditions. Levin and Bridges (1995) state that species inhabiting lower latitudes are less fertile than species which inhabit high latitudes.

The number of eggs in *U. thayeri* increased in accordance with CW, as found in other brachyurans. Some females with the same CW size showed differences in the amount of eggs carried. This fact may be related to food availability, individual variation of eggs production, and natural loss of eggs (Hines, 1982).

This study constitutes the first account on the population ecology and reproduction of *U. thayeri* in a tropical area. Further research on allometric growth, reproductive output and larval ecology will be necessary in order to understand its life cycle.

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