ABSTRACT

This study was developed to evaluate the population structure of *Uca thayeri* in the Rio Formoso estuary, state of Pernambuco, northeastern Brazil. Samplings of the specimens were performed monthly (April 2009 to March 2010), and 2,124 individuals were collected (1,014 males, 1,110 females, and 237 of these were ovigerous). The males had a mean body size (carapace width) (15.3 mm) similar to that of females (15.0 mm). Males and females (50% of the population) reached morphological sexual maturity with 12.7 and 13.8 mm CW, respectively. The total frequency distribution in size classes of males and females was unimodal. The overall sex ratio was skewed in favor of females (0.91:1.0). The ovigerous females and juveniles were continuous throughout the year, but the ovigerous females were more frequent in summer and juveniles in winter and summer. The mean fecundity was 8,859 eggs, ranging from 1,400 to 23,850 eggs. These results show that the population of *U. thayeri* is well established in the Rio Formoso mangrove, where environmental conditions appear to be sufficient to accomplish its vital functions such as feeding and reproduction. However, when compared to other populations in southeastern Brazil, there are some distinct population aspects, especially the reproductive period that was continuous and lower fecundity, probably due to the latitudinal variation.

Key words: *Uca thayeri*, population biology, reproduction, mangrove.

RESUMEN

Este proyecto fue realizado para evaluar la estructura poblacional de la especie *Uca thayeri* en el estuario del Río Formoso, estado de Pernambuco, nordeste de Brasil. Los espécimes fueron colectados mensualmente (Abril 2009 a Marzo 2010) y totalizaron 2.124 individuos (1.014 machos, 1,110 hembras siendo 237 ovígeras). Los machos presentaron una media de tamaño corporal (ancho del caparazón) de 15.3 mm similar al de las hembras (15.0 mm). Machos y hembras (50% de la población) alcanzaron la madurez sexual con 12.7 y 13.8 mm respectivamente. La frecuencia total de distribución de clases de tamaño de machos y hembras fue unimodal. La razón sexual total fue sesgada en favor de las hembras (0.91:1.0). La aparición de hembras ovígeras y juveniles fue continua a lo largo del año, pero las primeras fueron más frecuentes en el verano y los juveniles en el invierno y en el verano. La fecundidad media fue 8.859 huevos, con una variación de 1.400 a 23.850 huevos. Estos resultados muestran que la población de *U. thayeri* está bien establecida en los manglares del Río Formoso, donde las condiciones ambientales parecen ser adecuadas para acompañar las funciones vitales tales como reproducción y alimentación. Sin embargo, cuando comparados con otras poblaciones del sudeste de Brasil, existen algunos aspectos poblacionales diferentes, especialmente el periodo reproductivo que, en el presente estudio, fue continuo y con baja fecundidad, probablemente debido a una variación latitudinal.

Palabras clave: *Uca thayeri*, estructura poblacional, reproducción, mangle.
INTRODUCTION

Structural characterization of natural populations is considered basic information to understand the ecological stability of populations within a given environment. Several studies carried out on populations of marine and estuarine crabs on the Brazilian coast have investigated the seasonal abundance, population density and frequency distribution in size classes, birth rate and mortality, migration, sex ratio, reproductive period, fecundity, recruitment, among others (Castiglioni & Negreiros-Fransozo, 2005; Masunari, 2006; Castiglioni & Negreiros-Fransozo, 2006, Castiglioni et al., 2006, Benetti et al., 2007; Ripoli et al., 2007; Bedê et al., 2008; Costa & Soares-Gomes, 2009, Castiglioni et al., 2010).

Crabs of the genus *Uca* Leach, 1814, popularly known as fiddler crabs (Crane, 1975), are among the most characteristic inhabitants of the intertidal mangrove forests and estuaries in the tropics and subtropics, playing an important role in structural and functional ecology (Genoni, 1985). The activities of the fiddler crabs are closely related to the tidal cycle, as the individuals remain in their burrows during flood tide periods and usually get food, fight or copulate during ebb tides (Crane, 1975; Caravello & Cameron, 1987; Backwell et al., 1999). These burrows protect the crabs from temperature extremes and predators, variations in salinity and are also used for reproduction and molt (Crane, 1975; Macintosh, 1988; Koga et al., 2000). Fiddler crabs are an important component of mangrove ecosystems, because they transfer energy to marine and terrestrial habitats, are consumed by many variety of fish, birds and invertebrates (Skov & Hartnoll, 2001; Skov et al., 2002; Litulo, 2004) and promote turnover of nutrients because of their burrowing habits (Araújo & Maciel, 1977; Aveline, 1980; Macintosh, 1988).

The fiddler crab *U. thayeri* is one of the most abundant species of the genus *Uca*, living in burrows in muddy and sandy mangrove areas (Melo, 1996). This species is distributed throughout the western Atlantic: Florida, Gulf of Mexico, Antilles, Guatemala, Panama, Venezuela and Brazil (from Maranhão to Santa Catarina) (Melo, 1996). Relative growth, population structure and reproductive biology of this species have been evaluated by some authors especially in populations in the southeast of Brazil (Costa & Negreiros-Fransozo, 2003; Negreiros-Fransozo et al., 2003; Costa et al., 2006; Masunari, 2006), and only one study was published about population dynamics by Bezza & Matthews-Cascon (2007) from a population of state of Ceará, northeast Brazil, which characterizes the present study as a pioneering for the Rio Formoso mangrove, state of Pernambuco. Furthermore, since latitude and the habitat can affect life history traits of intertidal crabs (Simons & Jones, 1981; Jones & Simons, 1983; Hines, 1989), we characterized the population dynamics of *U. thayeri* in a mangrove area of the Rio Formoso, south coast of the state of Pernambuco, northeast Brazil. The population was analyzed during a one-year period with regards to the following aspects: body size, size at morphological sexual maturity, size-frequency distribution, sex ratio, reproductive period, fecundity, and frequency of juveniles.

MATERIALS AND METHODS

**Samplings**

Specimens of *Uca thayeri* were collected in the Rio Formoso mangrove (8°41’00 .68 “S and 35°06’09 .49” W), south coast of the state of Pernambuco, northeast Brazil. Sampling was conducted by one person monthly from April 2009 to March 2010 by means of capture per unit effort during low tide (full moon) by digging the sediment (15 cm) around the burrows in three distinct areas during 20 minutes in each area (about 100 m²). All captured crabs were put into labeled plastic bags, kept on crushed ice in an insulated container and transported to the laboratory. Each ovigerous females sampled were placed into plastic bags individually to avoid loss of eggs to estimate the minimum, maximum and mean number of eggs produced by the species.

**Data analysis**

The crabs were sexed and measured (with a precision caliper to the nearest 0.01 mm) for carapace width (CW) of males and females, major cheliped propodus length (CPL) of males, and abdomen width (AW) of females (width corresponding to the fifth abdominal somite).

The minimum, maximum and mean carapace width of males and females were determined. The mean body size (carapace width) of males and females was compared by t test ($\alpha = 0.05$) (Zar, 1996).

The determination of morphological sexual maturity was based on the relationships between the CPL vs. CW structures for males and AW vs. CW for females. These relationships were selected for analysis because of the importance of the dependent variables (CPL and AW) in the reproductive processes of males and females, respectively. A principal component analysis (PCA) was carried out with the above variables ($\log_{10}$ CPL and $\log_{10}$ CW for males, and $\log_{10}$ AW and...
The degree of association between ovigerous females proportions (MANAP) (α = 0.05) (Curi & Moraes, 1981). The proportion of ovigerous females in relation to adult females in each month and season was calculated. Subsequently, the ratio found for sexual crabs sampled and placed in a solution of sodium hypochlorite (NaClO) 5% (PA) in 100 ml of water and then agitated for 5 minutes to separate the eggs. After separation, the eggs were carefully homogenized in 50 ml of deionized water, and three samples were taken from every 1.0 ml. The eggs were examined with a dissecting microscope, characterized as the stages of embryonic development, and counted (Costa et al., 2006; Litulo, 2005a). Three stages of embryonic development were distinguished and characterized based on Rabalais (1991), Rodriguez et al. (1997), Yamaguchi (2001) and Litulo (2005b) as follow: stage I (initial) – with little or no cleavage, yellow coloration, and yolk occupying the entire egg space; stage II (intermediate) – the beginning of the cellular cleavage is visible, but the body parts are not defined, the mass has a light orange color tending to brown, and the embryo occupies 1/3 of the volume of the egg; III (final) – the yolk is consumed, reduced to a tiny spot on the embryo, the eyes are easily visible and the eggs shows a dark brown color. Linear regression was used to analyze the relationship between the number of eggs in each embryonic developmental stage and female’s carapace width. The analysis of variance (ANOVA) complemented by the Tukey test (α = 0.05) (Zar, 1996) was used to compare the number of eggs between different stages of embryonic development.

To estimate the frequency of juveniles, crabs with carapace width lower than the values determined for the morphological sexual maturity of males and females were considered juveniles. The frequency of juveniles determined by the proportion of juveniles in relation to all crabs sampled monthly and seasonally and compared by testing for multinomial proportions (MANAP) (α = 0.05) (Curi & Moraes, 1981).

**Abiotic factors**

During the sampling of crabs, the air and burrow (10 cm of depth) temperatures, and river and burrow-water salinity were monitored monthly with three replicates (beginning, middle and end of each sample). The temperature was measured with a digital thermometer and salinity with a digital refractometer. To estimate the burrow-water salinity, the same is taken from a depth of 10 cm with a pipette and river water was sampled from the closest point on the sample area of crabs. Then, a comparison was performed between seasons by analysis of variance (ANOVA; α = 0.05; Zar, 1996).

RESULTS

We collected 2,124 individuals of *U. thayeri*, including 1,014 males (396 juveniles and 618 adults) and 1,110 females (313 juveniles, 797 adults - 560 non-ovigerous and 237 ovigerous females) (Table 1).

The carapace width (CW) of males of *U. thayeri* ranged from 2.7 mm to 28.4 mm (mean ± Sd: 15.3 ± 4.1 mm) and females from 5.9 mm to 21.2 mm (15.0 ± 3.5 mm). Males showed similar size of females (*t* = 0.33, *p* > 0.05).

The morphological sexual maturity of males was estimated at 13.8 mm CW (50% of males) (Fig. 1), with the smallest mature male measuring 14.73 mm, and the largest immature male 17.73 mm CW (Fig. 2A). Females reached morphological sexual maturity (50%) at 12.7 mm CW, with the smallest mature female at 11.35 mm CW and the largest immature female at 15.02 mm CW (Fig. 2B).

The total size-frequency distributions of carapace width of male and females were not normally distributed (*W* = 0.99 Males, Females *W* = 0.99, *p*<0.05), but were unimodal for both males and females (Fig. 3).

<table>
<thead>
<tr>
<th>Months</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>J</td>
<td>A</td>
<td>J</td>
</tr>
<tr>
<td>Apr/09</td>
<td>13</td>
<td>22</td>
<td>7</td>
</tr>
<tr>
<td>May/09</td>
<td>25</td>
<td>58</td>
<td>24</td>
</tr>
<tr>
<td>Jun/09</td>
<td>23</td>
<td>91</td>
<td>30</td>
</tr>
<tr>
<td>Jul/09</td>
<td>29</td>
<td>58</td>
<td>24</td>
</tr>
<tr>
<td>Aug/09</td>
<td>48</td>
<td>47</td>
<td>31</td>
</tr>
<tr>
<td>Sep/09</td>
<td>43</td>
<td>31</td>
<td>32</td>
</tr>
<tr>
<td>Oct/09</td>
<td>39</td>
<td>22</td>
<td>22</td>
</tr>
<tr>
<td>Nov/09</td>
<td>32</td>
<td>42</td>
<td>24</td>
</tr>
<tr>
<td>Dec/09</td>
<td>39</td>
<td>58</td>
<td>23</td>
</tr>
<tr>
<td>Jan/10</td>
<td>39</td>
<td>63</td>
<td>21</td>
</tr>
<tr>
<td>Feb/10</td>
<td>30</td>
<td>72</td>
<td>31</td>
</tr>
<tr>
<td>Mar/10</td>
<td>36</td>
<td>54</td>
<td>44</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>396</td>
<td>618</td>
<td>313</td>
</tr>
</tbody>
</table>

Table 1: Total number of males and females of *Uca thayeri* sampled at the Rio Formoso mangrove, northeast Brazil, from April 2009 to March 2010. Note: J= juvenile; A= adult; OF= ovigerous females.

Figure 1: Morphological sexual maturity of males and females of *Uca thayeri* sampled in the Rio Formoso mangrove, northeast Brazil. The arrows indicate the size (carapace width CW) and 50% of population is morphologically mature.

The morphological sexual maturity of males was estimated at 13.8 mm CW (50% of males) (Fig. 1), with the smallest mature male measuring 14.73 mm, and the largest immature male 17.73 mm CW (Fig. 2A). Females reached morphological sexual maturity (50%) at 12.7 mm CW, with the smallest mature female at 11.35 mm CW and the largest immature female at 15.02 mm CW (Fig. 2B).
The overall sex ratio did not follow the 1:1 ratio, being skewed in favor of females (0.91 males: 1 female) ($\chi^2 = 4.34$, $p<0.05$). In the analysis of the monthly sex ratio, significant differences were observed in October ($\chi^2 = 10.76$) and November 2009 ($\chi^2 = 3.9$), when females were more abundant than males ($p<0.05$) (Fig. 4A). The analysis of sex ratio of males and females by season showed a significant difference, with males being more numerous in the fall ($\chi^2 = 4.61$) and females more numerous in spring ($\chi^2 = 6.3$) ($p<0.05$) (Fig. 4B).

The sex ratio within carapace width size classes showed significant difference ($p<0.05$) in the intermediate size classes (15.0—16.5 mm and 16.5—18.0 mm), where the females were more frequent than males ($\chi^2 = 5.65$ and $\chi^2 = 20.69$, respectively), and in the three largest size classes (24.0—25.5; 25.5—27.0; 27.0—28.5), where males were predominant ($\chi^2 = 5.56$, $\chi^2 = 5.0$, $\chi^2 = 4.0$, respectively) (Fig. 5). Males were also predominant in smallest classes (1.5—3.0; 3.0—4.5; 4.5—6.0), but there was no significant difference due to the small number of crabs sampled in these classes ("$p>0.05$") (Fig. 5).

The total number of ovigerous females sampled during the period of April 2009 to March 2010 was relatively low (237), representing 30.9% of adult females (797). However, ovigerous females were sampled in all months of the year (Table 1), but more frequently in summer (40.1%) ($p=0.05$) (Fig. 6). Most of ovigerous females sampled bore eggs in initial embryonic developmental stage ($n= 136$, 57.4%), followed by the females that were carrying eggs in the intermediate stage ($n= 88$, 37.1%) and only 13 (5.5%) of the females examined carried eggs in final stage of development. The smallest and biggest ovigerous females sampled measured 9.3 mm to 24.4
mm CW, respectively, and the mean size of the ovigerous females was 16.4 ± 2.47 mm CW. The relative frequency of ovigerous females tended to increase with increasing air temperature ($r^2 = 0.70; p < 0.05$).

The mean size of the females who had eggs counted was 16.2 ± 2.2 mm, ranging from 9.71 to 23.7 mm, and the mean number of eggs produced was 8,859 ± 4,607 eggs, ranging from 1,400 to 23,850 eggs. There was no significant difference in the mean size of females that were carrying eggs at different stages of the embryonic development ($p > 0.05$) (Table 2). Although a decrease in the mean number of eggs during the embryonic development was observed, we found no significant differences among different stages ($p > 0.05$) (Table 2). We observed a positive linear correlation between the carapace width and number of eggs in all stages of the embryonic development ($p < 0.05$) (Fig. 7).

It was observed during one year (Apr 2009 to Mar 2010) that juveniles were continuous in the population, and the highest frequencies of juveniles were obtained in August and September 2009 and March 2010 (Table 1). Juveniles were more abundant in winter (29.2%) and summer (28.3%) (Fig. 8).

The air temperature ranged from 28.6° C (Aug 2009) to 31.9° C (Jan 2010), with an annual mean of 30.5 ± 1.1° C (Fig. 9). The burrow-water temperature of *U. thayeri* ranged from 27.6° C (Aug 2009) to 30.5° C (Jan 2010), with an annual mean of 29.3 ± 1.0° C (Fig. 9). The lowest burrow-water temperatures were observed in August 2009 and the highest in January 2010 (Fig. 9). The air temperature was significantly higher in spring and summer and lower in autumn and winter ($p < 0.05$) (Table 3). However, the burrow-water temperature was significantly lower in winter, when compared to other seasons ($p < 0.05$) (Table 3). The air temperature was significantly higher than that inside the burrows in winter and summer ($p < 0.05$) (Table 3).

Table 2:
Carapace width (CW- mm) and number of eggs of the ovigerous females of *Uca thayeri* which carried eggs in different stages of the embryonic development.

<table>
<thead>
<tr>
<th>Stage of development</th>
<th>CW Min-Max</th>
<th>CW Mean ± Sd</th>
<th>Eggs Min-Max</th>
<th>Eggs Mean ± Sd</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial</td>
<td>10.5 – 25.1</td>
<td>16.5 ± 2.8</td>
<td>1,400 – 23,850</td>
<td>9,852 ± 5,407 a</td>
<td>63</td>
</tr>
<tr>
<td>Intermediary</td>
<td>9.7 – 20.8</td>
<td>16.4 ± 2.3</td>
<td>2,850 – 13,000</td>
<td>7,762 ± 2,700 a</td>
<td>37</td>
</tr>
<tr>
<td>Final</td>
<td>12.4 – 21.5</td>
<td>17.5 ± 2.7</td>
<td>1,500 – 14,150</td>
<td>7,289 ± 4,089 a</td>
<td>13</td>
</tr>
</tbody>
</table>

Note: N= number of ovigerous females, Sd= standard deviation, min= minimum, max= maximum. Values with at least one letter in common do not differ significantly (ANOVA and Bonferroni, $a = 0.05$).
The river-water salinity near the sampling areas ranged from 20 ppt (Aug 2009) to 29 ppt (Jan 2009) (mean ± Sd: 24.9 ± 2.63 ppt) (Fig. 10). The burrow-water salinity ranged from 22 (May 2009) to 31 ppt (Dec 2009) (mean ± Sd: 28.4 ± 2.9 ppt) (Fig. 10). The river-water salinity was lower in autumn and fall (p<0.05) (Table 3). However, the burrow-water salinity was significantly higher in spring (p<0.05) (Table 3). The burrow-water salinity was significantly higher than the river-water salinity in winter and spring (p<0.05) (Table 3).

**DISCUSSION**

Males and females of *U. thayeri* in the present study were similar in size. This result were also found by Negreiros-Fransozo et al. (2003) for a population of the same species in Ubatuba, state of São Paulo, southeast of Brazil, and by Bezerra and Matthews-Cascon (2007) for a population in the Pacoti River mangrove, state of Ceará, northeast of Brazil. Probably the similar size between the sexes may be due to the fact that larger males are more visible and thus become more vulnerable to predation. However, females of *U. thayeri* were bigger than males in the Itacuruçá mangrove, state of Rio de Janeiro (Bedê et al., 2008) and in the Ubatuba, state of São Paulo (Costa & Negreiros-Fransozo, 2003). In most species of *Uca*, the males were larger than females (Litulo, 2005 a, b, c; Litulo, 2006; Castiglioni & Negreiros-Fransozo, 2005; Castiglioni et al., 2006; Mokhtari et al., 2008; Bedê et al., 2008; Hirose & Negreiros-Fransozo, 2008; Costa & Soares-Gomes, 2009). The size difference between males and females in some brachyuran species is because of the higher growth rate in males, or a longer growth period, while females spend a significant amount of energy on the reproductive process (Warner, 1967; Diaz & Conde, 1989; Hartnoll, 2006). Moreover, males that reach larger
sizes have larger chelipeds, thus increasing their chances of success during the pre-copulatory behavior, fighting with other males and for territory defense (Crane, 1975; Christy & Salmon, 1984; Rosenberg, 1997; Backwell et al., 1999; Mariappan et al., 2000; Pope, 2000). Different mortality rates, migration, higher tolerance of one sex to environmental adversities, differential spatial and temporal utilization of resources, differences in foraging efficiency, acquisition or assimilation of food and behavioral patterns differences between sexes are other factors that may influence size differences between male and female crabs (Giesel, 1972; Crane, 1975; Wolf et al., 1974), and thus distinct populations may show different sizes. The intraspecific variation in size observed in *U. thayeri* may be because the populations that live in a region of low latitude (tropical) reach larger sizes than those found at latitudes above 24° (subtropical climate). Low temperature is critical factor for fiddler crabs in warm temperate and subtropical regions, where their activity strongly affect by temperature, and it is known to regulate molting and oogenesis, and thus somatic and gonadic growth in crustaceans (Crane, 1975; Meusy & Peyen, 1988). The variations in temperature and photoperiod can produce latitudinal clines in metabolic rates and somatic growth, resulting in lower rates of growth in larger and older specimens, delaying the size at onset maturity and body size of species living at higher latitudes (Hines, 1989; Jones & Simons, 1983), as observed in different populations of *U. thayeri* along of Brazilian coast. Besides, the abiotic factors in tropical regions vary little, and the temperature remains

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**Table 3: Means of the air and burrow temperatures, and of river- and burrow-water salinity during sampling of the *Uca thayeri* in the Rio Formoso mangrove, northeast Brazil.**

<table>
<thead>
<tr>
<th>Season</th>
<th>Air temperature (°C)</th>
<th>Burrow-water temperature (°C)</th>
<th>River-water salinity (ppt)</th>
<th>Burrow-water salinity (ppt)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fall</td>
<td>30.1 ± 0.7 b A</td>
<td>29.0 ± 1.2 ab A</td>
<td>23.7 ± 2.5 b A</td>
<td>24.4 ± 2.7 c A</td>
</tr>
<tr>
<td>Winter</td>
<td>29.7 ± 1.0 b A</td>
<td>28.3 ± 0.8 b B</td>
<td>22.7 ± 3.1 b B</td>
<td>26.7 ± 2.6 b c A</td>
</tr>
<tr>
<td>Spring</td>
<td>31.2 ± 0.9 ab A</td>
<td>30.0 ± 0.1 a A</td>
<td>26.7 ± 1.5 a B</td>
<td>30.4 ± 0.5 a A</td>
</tr>
<tr>
<td>Summer</td>
<td>32.0 ± 0.3 a A</td>
<td>29.8 ± 0.6 a B</td>
<td>26.7 ± 2.1 a A</td>
<td>28.6 ± 1.6 ab A</td>
</tr>
</tbody>
</table>

Note: Small letters correspond to the comparison within the same environmental variable between seasons, and capital letters correspond to the comparison of temperatures and salinities of the same season. Values with at least one letter in common do not differ significantly (ANOVA, p> 0.05).
high throughout the year, which favors the production and the annual availability of food, and animals grow continuously and at faster rates than those who live in the subtropics (Masunari & Dissenha, 2005). Differences in body size between populations were observed for *U. vocator* (Colpo & Negreiros-Fransozo, 2004), *U. rapax* (Castiglioni & Negreiros-Fransozo, 2005), *U. burgersi* (Benetti et al., 2007) because the populations studied occur in mangrove areas with different levels of organic matter in the substrate.

Sexual maturity is an event often marked by physiological and morphological changes, indicating the transition from juvenile to adult, thereby creating and changing habits and behaviors that make them individuals in a population (Hartnoll, 1982). In species of crabs, the males are considered morphologically mature from the moment they become able to handle or carry the female during pre-copulatory behaviour and successfully transferring the sperm, while females reach maturity when they become able to mate and produce eggs (Hartnoll, 1969). However, morphological sexual maturity was reached asynchronously between males and females of *U. thayeri* in the present study, as also observed in several species of the genus *Uca*, and the females reach maturity at sizes smaller than the males, as observed in *U. thayeri* (Negreiros-Fransozo et al., 2003), *U. leptodactyla* (Cardoso & Negreiros-Fransozo, 2004), *U. burgersi* (Benetti & Negreiros-Fransozo, 2004), *U. rapax* (Castiglioni & Negreiros-Fransozo, 2004), *U. maracoani* (Hirose & Negreiros-Fransozo, 2007) and *U. cumulanta* (Pralon & Negreiros-Fransozo, 2008). Often the lower growth rate observed in female crabs is attributed to the fact that much of their energy is spent in the reproductive process (Warner, 1967; Díaz & Conde, 1989; Johnson, 2003). In crustaceans, reproduction and growth are antagonistic processes in which there is competition for energy resources, which are destined to any process during the life cycle of these animals (Adiyodi & Adiyodi, 1970; Hartnoll, 2006). As previously mentioned, several factors can interfere with the growth rate and size at maturity of crustaceans, such as availability and the amount of food and environmental conditions, like temperature, photoperiod, rainfall (Teissier, 1960; Campbell & Eagles, 1983; von Hagen, 1987). Generally, more favorable habitats, with larger amounts of organic matter in the substrate and high productivity, account for higher growth rates, thus influencing the size of sexually mature crustaceans, as observed in *U. burgersi* (Benetti & Negreiros-Fransozo, 2004), and *U. rapax* (Castiglioni & Negreiros-Fransozo, 2004).

The size-class frequency distribution in a population is a dynamic characteristic that may vary throughout the year as a result of reproduction and recruitment (Thurman II, 1985). The total size-class frequency distribution of carapace width of male and females of *U. thayeri* studied in this study was unimodal. Generally, unimodality is typical of stable populations, which have continued recruitment and mortality rates constant over the life cycle, and the number of individuals entering the population is similar to the number of individuals who leave (Thurman II, 1985; Diaz & Conde, 1989), as observed in *U. thayeri* in the present study. The population of *U. thayeri* studied by Bedê et al. (2008) in the Itacuruçá mangrove, state of Rio de Janeiro, southeast Brazil, showed no defined pattern of size-class frequency distribution. However, populations of *U. thayeri* in Ubatuba, state of São Paulo, southeast Brazil
Figure 7:
Regression between the carapace width (mm) and number of eggs in each stage of the embryonic development of Uca thayeri in the Rio Formoso mangrove, northeast Brazil.
The overall sex-ratio of *U. thayeri* in the present study did not follow the 1:1 ratio, being skewed in favor of females. However, the monthly sex-ratio analysis showed that females were more abundant than males only in October and November 2009, and the seasonal analysis showed that males were more numerous in autumn and spring. Deviations in sex ratio of *U. thayeri* in the present study appear to be related to the reproductive behavior more intense in spring and summer, because males spent more time in moving their major cheliped at the surface to attract females for mating, defending territory or fighting with other males and thus can become more susceptible to predation as also observed by Valiela et al. (1974), Montague (1980), and Emmerson (1994). Thus, the lower frequency of males found in this study may be due to predation as also observed by Väijäla et al. (1974), Montague (1980), and Emmerson (1994). Thus, the lower frequency of males found in this study may be due to differential mortality rates (Wolf et al., 1975; Genoni, 1985) or also due to differential migration patterns of males and females (Montague, 1980). However the differential sex-ratio observed in *U. thayeri* from Ubatuba, state of São Paulo, southeast Brazil was attributed a sampling method used (Costa & Negreiros-Fransozo, 2003), as also observed by Johnson (2003) from others *Uca* species. Deviations of sex ratio in favor of females was observed in *U. thayeri* and *U. victoriana* analyzed by Bedê et al. (2008) in the Itacuruçá mangrove, state of Rio de Janeiro, southeast Brazil. The sex-ratio at the genus *Uca* is often different from 1:1, but with males being generally more abundant than females, as observed in some populations of *Uca* in Brazilian coast: *U. thayeri* (Costa and Negreiros-Fransozo 2003), *U. vocator* (Colpo & Negreiros-Fransozo, 2004), *U. burgeri* (Benetti et al., 2007), *U. rapax, U. mordax, U. cumulanta, U uruguayensis* and *U. vocator* (Bedê et al., 2008), *U. maracoani* (Hirose & Negreiros-Fransozo, 2008), *U. rapax* (Costa & Soares-Gomes, 2009), and *U. victoriana* (Castiglioni et al., 2010).

The species *U. thayeri* showed a predominance of females in the intermediate size classes of carapace width, and males were more abundant in larger size classes, which fit into the anomalous pattern described by Wenner (1972). This may be related to a female’s need to share its energy resources between oocyte production and growth, and therefore having a different growth rate from males, whereas males have a faster growth rate or a period of greater growth (Adiyodi & Adiyodi, 1970; Hartnoll, 1982, 2006). The anomalous pattern has been observed in other Brazilian crab species, such as *Aratus pisonii* (H. Milne Edwards, 1837) (Díaz & Conde, 1989), *U. rapax* (Castiglioni & Negreiros-Fransozo, 2005; Castiglioni et al., 2006), *U. burgeri* (Benetti et al., 2007), *U. maracoani* (Hirose & Negreiros-Fransozo, 2008), and *U. victoriana* (Castiglioni et al., 2010).

For brachyuran species that live in tropical regions, patterns of continuous reproduction can be observed with a constant occurrence of individuals in reproductive stage during the year and/or with peaks during certain months (Pinheiro & Fransozo, 2002; Colpo & Negreiros-Fransozo, 2004; Castiglioni & Negreiros-Fransozo, 2005,
Table 4:
Comparative size of carapace width (mm) of males and females of Uca thayeri sampled in different mangrove areas in Brazilian coast.

<table>
<thead>
<tr>
<th>Mangrove areas</th>
<th>Min-Max</th>
<th>Mean</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(23°29’S, 45°09’W)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ubatuba, SP</td>
<td>3.7 – 25.6</td>
<td>4.5 – 25.5</td>
<td>Negreiros-Fransozo et al. (2003)</td>
</tr>
<tr>
<td>(23°29’S, 45°09’W)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacoti River mangrove, CE</td>
<td>4.0 – 28.0</td>
<td>4.2 – 24.6</td>
<td>Bezerra and Matthews-Cascon (2007)</td>
</tr>
<tr>
<td>(3°43’02”S, 38°32’35”W)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Itacuruçá mangrove, RJ</td>
<td>4.3 – 25.9</td>
<td>2.6 – 25.8</td>
<td>Bedê et al. (2008)</td>
</tr>
<tr>
<td>(22°55’00”S, 43°05’30”W)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rio Formoso mangrove, PE</td>
<td>2.7 – 28.3</td>
<td>5.9 – 21.2</td>
<td>Present work</td>
</tr>
<tr>
<td>(8°41’68”S, 35°06’09.49” W)</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

Note: SP = state of São Paulo; CE = state of Ceará; RJ = state of Rio de Janeiro; PE = State of Pernambuco.

Castiglioni et al., 2006; Hirose & Negreiros-Fransozo, 2008; Costa & Soares-Gomes, 2009) (Table 5). However, in temperate regions, the crabs usually have seasonal reproduction (Flores & Negreiros-Fransozo, 1999; Castiglioni & Santos, 2001; Costa & Negreiros-Fransozo, 2003; Costa et al., 2006). The ovigerous females of U. thayeri were recorded in all months indicating continuous reproduction throughout the year in the present study, although with a reproductive peak in summer. However, for the population of U. thayeri studied by Costa & Negreiros-Fransozo (2003) in Ubatuba, state of São Paulo, southeast Brazil, reproduction was characterized as seasonal, with considerable reproductive activity from January to March (summer) and an apparent rest period in June and July, when non-ovigerous females were recorded in the population. Seasonal reproduction was also observed in other populations of U. thayeri from Texas, USA (Salmon, 1987) and from state of Ceará, northeast Brazil (Bezerra & Matthews-Cascón, 2007). Reproductive activity concentrated in a particular time of year, usually spring and summer may be related to temperature, photoperiod and greater food availability for larvae that increase in the warmer months of the year (Pillay & Ono, 1978; Sastry, 1983; Costa & Negreiros-Fransozo, 2003). Another factor that may influence the seasonality of reproduction is rainfall, and in some subtropical species, reproduction is influenced by the intensity of precipitation rather than by temperature (Crane, 1975; Litulo, 2004; Litulo, 2006). The spawning in the rainy seasons may provide selective advantages in intertidal crabs since periods of higher rainfall can cause changes in the water salinity and promote an increase in nutrient concentration, which are both essential for the development of larvae (Litulo, 2004; Conde & Díaz, 1989). However, for the population of U. thayeri from Rio Formoso the greatest reproductive intensity was observed during the summer which is considered a dry season in northeastern Brazil and the temperature probably exerted more influence than rainfall on the reproduction of the species in this area. According to Sastry (1983) the temperature may act as a metabolic, biochemical, and hormonal modulator, triggering the processes of ecdysis, mating, and gonad development.

To maximize the probability of larval survival, where their eggs are ripe for hatching, many mangrove female crabs travel the long distance to the water’s edge during the night at the high tides (Gifford, 1962). Probably, the low number of ovigerous females of U. thayeri sampled containing eggs in the final embryonic development stage in this study may be explained by the fact that these females become less active during the day and leave their burrows at night, especially during the larval issue. Christy (1982) suggested that the synchronization of reproduction with tidal cycles in Uca species could be an adaptation to increase the probability that the planktonic larvae are carried back to the adult’s environment by tidal currents.

Reproductive aspects related to the production of eggs play an important role in the evolution of life history strategies, since egg production is a process that requires a high amount of energy in decapod crustaceans. Moreover, the number of eggs produced is species-specific and can vary widely according to latitude, environment structure and food availability (Thurman, 1985; Henmi, 2003). The population of U. thayeri reviewed by Costa et al. (2006) in Ubatuba, state of São Paulo, southeast Brazil had an average fecundity of 31,068 ± 11,185 eggs, whereas
ovigerous females of the population in this study produced an average of 8,859 ± 4,607 eggs. The differences observed in the reproductive potential of the population of *U. thayeri* in Ubatuba and the population of this study suggests a phenotypic plasticity, probably due to the latitudinal variation adaptive strategy, and the population of *U. thayeri* in Ubatuba showed seasonal reproduction and high fecundity, while the population of Rio Formoso reproduced continuously, but with lower fecundity.

For fiddler crabs, the size of the brood has been used to explain the interspecific variation in feeding activity of females during the incubation period, the gap in the production of consecutive broods and the location of mating and incubation (Christy & Salmon, 1984; Salmon, 1987; Henmi, 1989). Thus, the fiddler crabs have two reproductive behaviours: ovigerous females with broad front remain in their burrows during the incubation of eggs without eating (Christy, 1982), and females of those species with narrow front eat actively during incubation (Salmon, 1984). Species that produce small broods (narrow front) can get food on the soil surface because their brood is small and remains covered and protected by their burrow and so these females can produce broods continuously unlike the species that produce large broods (broad front) (Christy & Salmon, 1984). Thus these differences in eating behavior during fiddler crabs hatching can influence the reproductive process. However, according to Salmon (1987), some species do not fit into these patterns, like *U. thayeri*, which exhibits morphology between broad and narrow front, considered “intermediate”, and behaves similar to the kinds of narrow front: offsprings are few, and the females eat during the incubation period. The females of *U. thayeri* analyzed in this study were collected in the interior of the funnel-shaped burrows, each about 10 cm deep and some ovigerous females were sampled out of the burrow. This suggests that ovigerous females of *U. thayeri* may leave the burrows for food and thus are able to get enough energy to reproduce again once the eggs hatch. However, in a study on *U. thayeri* in Ubatuba, southeast Brazil by Costa et al. (2006), ovigerous females were sampled in deep burrow and the authors suggested that they do not feed during the incubation period. The eggs mass produced by the population of *U. thayeri* from Rio Formoso is lower than Ubatuba and thus can come out of burrows to feed and with less risk of losing the eggs by friction with the substrate, since the eggs are fully protected by the abdomen. This may explain why *U. thayeri* in Ubatuba reproduces only in summer, and the population of this study reproduces continuously - a population produces more eggs, but only when environmental conditions are favorable (summer) and other population produces fewer eggs, but these can be released throughout the year.

We observed a positive linear correlation between the carapace width and number of eggs in all stages of the embryonic development in *U. thayeri* in this study. Similar results were found for this species by Bezerra & Matthews-Cascón (2007), in *U. urvillei* by Litulo (2005c), in *U. vocans* by Litulo (2005b), in *U. chlorophthalmus* by Litulo (2006), and in *U. rapax* by Costa & Soares-Gomes (2009). The frequency of juveniles in the population of *U. thayeri* was continuous, and the highest frequencies of juveniles were seen in August and September 2009 (winter) and March 2010 (summer), so there are peaks in the frequency of juveniles in two distinct periods of the year. It can be inferred that the dominance of juveniles in winter can be attributed to higher reproductive activity in summer (January-March 2010) and the dominance of juveniles in
summer corresponds to another peak of ovigerous females in winter and spring. Continuous rate of juveniles, but with a peak in the winter because of higher reproductive intensity in the summer months was also observed in *U. urvillei* (Litulo, 2005c), *U. rapax* (Castiglioni & Negreiros-Fransozo, 2005), *U. burgersi* (Benetti et al., 2007) and *U. chlorophthalmus* (Litulo, 2006).

In this study, we observed that the burrows temperature was lower than the air temperature in winter and summer. The species of fiddler crabs and other ocypodoids generally increase the frequency of visits to their burrows to offset the high temperatures, because the water inside the burrows cools the body temperature by evaporation (Smith & Miller, 1973; Crane, 1975; Macintosh, 1978). This evidence suggests that the more land-crab species of mangroves are adapted physiologically and behaviorally to deal successfully with this environmental stress (Macintosh, 1988). Moreover, the river-water salinity was lower in autumn and winter, probably because these are the rainiest seasons in northeast Brazil. The burrow-water salinity was higher than the river-water salinity in the Rio Formoso probably due to the high evaporation rate of the water contained in the substrate during low tides, and consequently, increasing salinity in both the substrate and inside the burrows (Smith & Miller, 1973; Crane, 1975; Macintosh, 1978). The variations in temperature and salinity are the two biggest problems faced by crabs that live in estuaries and these environmental factors seem to affect crab reproduction and larval development timing (Edney, 1961; Macintosh, 1982; O’Connor, 1993; Rodrigues & Jones, 1993).

The results obtained in the present study shows that the population of *U. thayeri* is well established in the estuary of Rio Formoso, where environmental conditions (mainly temperature, photoperiod and availability and quantity of food resources) are probably enough to perform their vital functions such as feeding and reproduction. However, when compared to other populations in southeastern Brazil, there are some distinct population aspects, especially the reproductive period that was continuous and lower fecundity, probably due to the latitudinal variation.

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