Reproductive pattern comparison of *Uca thayeri* Rathbun, 1900 and *U. uruguayensis* Nobili, 1901 (Crustacea, Decapoda, Ocypodidae)

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ABSTRACT

Ovigerous females of *Uca thayeri* and *U. uruguayensis* were used to achieve and compare their reproductive pattern. The females mean size was 6.6 ± 0.8mm for *U. uruguayensis* and 17.3 ± 4.4mm for *U. thayeri*. The mean fecundity obtained for *U. uruguayensis* was 1883 ± 490 eggs (N = 27) and for *U. thayeri* was 31068 ± 11186 eggs (N = 31). The differences observed in reproductive pattern of *U. thayeri* and *U. uruguayensis* suggest an adaptive strategy by each species: *U. thayeri* presented seasonal reproduction with a pronounced intensity from January to March and higher fecundity, while *U. uruguayensis* reproduction was continuous all year round, but with lower fecundity.

Key words: Crustacea, fiddler crab, fecundity, *Uca thayeri*, *U. uruguayensis*, reproductive pattern

INTRODUCTION

Reproduction is the main mechanism that keeps species continuity so that it contributes to regulate the population size. According to Hartnoll and Gould (1988), variability of crustacean reproductive pattern is an adaptive process result determined by evolutionary pressure that increases progeny survival. Sastry (1983) observed that egg number and its production periodicity were species-specific factors that reflected the reproductive strategy of every species, and the fecundity analysis did not only estimate the egg number, but it also represented the rhythms in which eggs were produced. Adaptations on mating systems jointly with environmental conditions are also factors that influence fiddler crab fecundity. In this context, reproduction processes on wide front species occur inside male burrows with large progenies being produced. It did not happen with narrow front females that reproduce inside female burrows and show small progenies (Christy and Salmon, 1991). Koga et al. (2000) analyzed Ocypodidae fecundity and found that the production of big progenies could not be continuous (because of food scarcity, desiccation and egg vulnerability). Females with small progenies, however, reproduced continuously.

The aim of this study was to define reproductive pattern similarities and differences of most abundant species from Comprido and Escuro rivers mangrove in Ubatuba, Brazil: *U. thayeri* Rathbun, 1900 and *U. uruguayensis* Nobili, 1901.
The first one is considered an intermediate as for front-orbital distance because it shows similarities as much with broad (habitat and behavior) as with narrow front species (reproductive physiology) (Crane, 1975; Salmon, 1987; Christy and Salmon, 1991). The latter species, however, is a true representative of broad front species, being considered the allopathic representative of north Atlantic most common group (Crane, 1975).

MATERIAL AND METHODS

The study site is located in Comprido and Escuro rivers mangrove (23° 29'S and 45° 09' W), which flow in the Fortaleza Bay (23° 29'S and 45° 09' W) at Ubatuba, North littoral of São Paulo State. Collection took place monthly throughout the year 1997. Crabs were collected manually during low-tide periods by digging the sediment around the burrows along nine transects (3m vs. 0.20m) with a shovel or a knife. All captured crabs were put into labeled plastic bags. After the total scanning of the transects, collectors searched for additional ovigerous females, which were kept separately. If they were found, they were used only for fecundity study.

Carapace width was taken from each female that were grouped in size classes with 2.5 and 2.0mm of amplitude for U. thayeri and U. uruguayensis, respectively. Breeding intensity was analyzed by relating the number of ovigerous females and the total of adult females obtained. It was named here as ovigerous-ratio. Only initial development eggs were used to determine the fecundity, as eggs in advanced development stages were more suitable to accidental loss and diseases. For eggs removal, pleopods of each female were cut at the articulation point in the abdomen. Afterwards, eggs were detached from pleopods and kept in separated recipients.

As U. uruguayensis show a low number of eggs, its fecundity was estimated by total count of eggs. U. thayeri, however, required another technique due to the higher egg quantity when compared to other Uca species. Each egg mass was transferred for 50ml Becker with alcohol, and homogeneously suspended (using an agitator). Five sub-samples (1 ml each) were removed for egg count under a stereomicroscope. The average value obtained was then extrapolated for the whole suspension to estimate the total number of eggs.

RESULTS

A total of 58 ovigerous females of U. uruguayensis were obtained, which measured a mean size of 6.9 ± 0.9mm CW, ranging from 5.2 to 8.5mm CW. Fig. 1 present ovigerous-ratio. With exception of January and June, 1997 all other months revealed ovigerous females of this species. U. uruguayensis showed a mean fecundity of 1883 ± 490 eggs, of which 27 were used for fecundity (mean size of 6.6 ± 0.8mm CW). Egg number are indicated in table I for each size class. Fecundity variation relative to carapace width was fitted into a power function given by the equation F = -1535 + 518CW and yielded a correlation coefficient of $r^2 = 0.71$. The scatter plot representing this correlation is shown on Fig. 2.

During the study period, 16 ovigerous females of U. thayeri were obtained, which presented a mean size of 17.3 ± 4.4mm CW, ranging from 15.3 to 23.6mm CW. The ovigerous-ratio is presented in Fig. 3. The months with higher occurrence of ovigerous crab were January, February, and March.

A total of 31 ovigerous females of U. thayeri were obtained for fecundity study, which showed a mean fecundity of 31068 ± 11186 eggs. Their carapace width varied from 12.7 to 25.5mm and they were grouped into 5 size classes. Table 2 indicates mean fecundity results for each size class. The scatter plot representing the fecundity equation ($F = - 36135 + 3423CW; r^2 = 0.78$) is shown in Fig. 4.

<table>
<thead>
<tr>
<th>CW Size Class (mm)</th>
<th>X ±SD</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 - 6</td>
<td>1456 ± 199</td>
<td>8</td>
</tr>
<tr>
<td>6 - 7</td>
<td>1823 ± 395</td>
<td>12</td>
</tr>
<tr>
<td>7 - 8</td>
<td>2421 ± 395</td>
<td>6</td>
</tr>
<tr>
<td>8 - 9</td>
<td>2795</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 1 - U. uruguayensis: Mean fecundity (X) and standard deviation (SD) registered for ovigerous females size classes (CW) analyzed throughout 1997, at Ubatuba, SP Brazil (N = 27; CW = carapace width).
Reproductive Pattern Comparison of *Uca thayeri* Rathbun, 1900 and *U. uruguayensis* Nobili, 1901

**Figure 1** - *Uca uruguayensis* Nobili, 1901. Temporal variation of the frequency of ovigerous-females.

**Figure 2** - Relation between egg number and carapace width of *U. uruguayensis*. (F= fecundity; CW= carapace width; $r^2$= determination coefficient).

**Table 2** - *U. thayeri*: Mean fecundity (X) and standard deviation (SD) registered for ovigerous females size classes (CW) analyzed throughout 1997, at Ubatuba, SP, Brazil (N = 31; CW = carapace width)

<table>
<thead>
<tr>
<th>CW Size Class (mm)</th>
<th>X ±SD</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>12.5 - 15.5</td>
<td>16788 ± 3907</td>
<td>2</td>
</tr>
<tr>
<td>15.5 - 18.5</td>
<td>21638 ± 4103</td>
<td>9</td>
</tr>
<tr>
<td>18.5 - 21.5</td>
<td>29555 ± 4242</td>
<td>10</td>
</tr>
<tr>
<td>21.5 - 24.5</td>
<td>39871 ± 6548</td>
<td>8</td>
</tr>
<tr>
<td>24.5 - 27.5</td>
<td>57710 ± 1824</td>
<td>2</td>
</tr>
</tbody>
</table>
DISCUSSION

Reproductive intensity in brachyuran can be measured by quantifying the relative frequency of ovigerous females. According to Sastry (1983), the beginning and the duration of the reproductive period are dependent on the occurrence of favorable environmental conditions. The major controlling factors appear to be latitude, temperature, larval food availability, and intertidal zonation (Thorson, 1950; Sastry, 1983). The breeding period becomes protected from cool to warm subtropical localities (Emmerson, 1994). Since most studies have been conducted in temperate region, seasonal breeding is well reported in the literature (Thurman II, 1985 for *U. subcylindrica* in U.S.A./Mexico; Murai *et al.*, 1987 for *U. lactea* in Japan; Spivak *et al.*, 1991 for...
U. uruguayensis in Argentina; and Mouton and Felder, 1995 for U. longisignalis and U. spincarpa in Mexico). Yet, the majority of tropical crabs breed continuously, i.e., throughout the year, or have prolonged breeding seasons compared to species at higher latitudes (Sastry, 1983). The reproduction in U. thayeri was remarkably seasonal, with a pronounced activity from January to March, and a pause period from April to August, when the ovigerous females were not found. According to Costa and Negreiros-Fransozo (2003), this could be attributed to the higher availability of food resources during warmer months, when conditions for planktonic development of larvae were optimal. Beyond this, the more pronounced reproductive intensity for U. thayeri occurred in the warmer months of the year, also coinciding with a higher feeding activity of ovigerous females (Salmon, 1987).

For U. uruguayensis, ovigerous females were registered all the year round, with exception during January and June. However, the major frequency of ovigerous females occurred in February and July, immediately after the absence of ovigerous crabs in the sampling site. Crustacean adaptations to terrestrial environment have been involved with morphological, physiological and behavioral mechanisms. Not only terrestrial brachyuran, but also those who inhabit the upper littoral have been coming across big problems to remain at this habitat as: keeping the continuity of reproductive and developmental processes, as well as temperature regulation and low water availability (Bliss, 1968). According to Thurman II (1985) as was the low fecundity and egg production frequency, as big egg masses were paralleled adaptations species that inhabited the land. Reproduction frequency per capta was inversely correlated to territoriality.

For many fiddler crab species there is a close association between mating and incubation place and fecundity. Salmon (1987) suggested when mating was underground the female showed highfecundity (like U. pugilator), but when it happened at the surface, a low egg number was produced (like with U. vocans). Henmi and Kaneto (1989) demonstrated the advantages and disadvantages of incubating eggs inside burrows. For species with large egg masses, that are suitable to mechanical losses when females walk, it represents a very advantageous proceeding. In this case, female stop feeding or they rarely do it, like U. pugilator (Christy and Salmon, 1984) and U. lactea (Murai et al., 1987). According to Salmon (1987), ovigerous females defend and build burrows with a chimney shape near river margins, where they stay during incubation period and obtain their food around the burrows. In this study, ovigerous females of U. thayeri were also sampled inside burrows with a chimney shape, and many crabs were collected walking around the burrows, which probably indicated feeding activity. Unlike U. thayeri, all the ovigerous females of U. uruguayensis were collected in deeper burrows, masking their capture difficult, and with eggs in initial embryonic development. This suggested that this species did not feed during incubation period. However, further experimental studies should be carried out to confirm it.

According to Thurman II (1985), the fecundity (size and number of eggs) for species of the genus Uca from tropical and temperate areas could vary according to environmental conditions. Nevertheless, fiddler crabs, which lived very near the rivers, presented larger size and produced higher number of eggs; while semi terrestrial or totally terrestrial species have small size and a low number of progenies. These comparisons are presented in Table 3.

The pattern noted by Thurman II (1985) could be observed for the species analyzed in the present study. The area occupied by U. thayeri was very near the river and were subdued to flood during high tide. As supposed by Thurman II, this species was larger and produced higher number of eggs than U. uruguayensis that inhabited superior intertidal areas that were sandy and dry, where the vegetation was scarce.

An important phenomenon occurring in many Crustacean groups is the tendency of extending embryonic period and jointly, shortening or eliminating larval phases. It is easy to understand considering how critical is the planktonic life for crabs and how protected embryonic is near maternal abdomen, during pleopodial incubation (Rieger, 1996). According to Rieger (1996), species of genus Uca are facing evolutionary process in a sense of diminishing the number of zoeal stages. Similar has been observed by U. uruguayensis that seems to still be defining zoeal number, because this species show a large variation of this stage when reared in the laboratory.
Salmon (1987) suggested *U. thayeri*’s embryonic development must happen in a very fast way, due to the low number of ovigerous females he could collect during egg developmental period. In the present study it was observed only with *U. uruguayensis*, as all collected ovigerous females showed initial development eggs; however, many females with intermediate and final development egg of *U. thayeri* were collected.

### Table 3 - Fecundity comparison on genus *Uca* species (CW = carapace width).

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat (Reference)</th>
<th>Mean CW (mm)</th>
<th>Mean fecundity</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>U. subcylindrica</em></td>
<td>Terrestrial (Thurman II, 1985)</td>
<td>13.4</td>
<td>627</td>
</tr>
<tr>
<td><em>U. burgesi</em></td>
<td>Semi terrestrial (Gibbs, 1974)</td>
<td>10.4</td>
<td>1782</td>
</tr>
<tr>
<td><em>U. triangularis</em></td>
<td>Intertidal (Feest, 1969)</td>
<td>9.6</td>
<td>3990</td>
</tr>
<tr>
<td><em>U. annulipes</em></td>
<td>Intertidal – Brackish (Feest, 1969)</td>
<td>11.3</td>
<td>6400</td>
</tr>
<tr>
<td><em>U. rapax</em></td>
<td>Intertidal (Greenspan, 1980)</td>
<td>15.8</td>
<td>28500</td>
</tr>
<tr>
<td><em>U. thayeri</em></td>
<td>Intertidal Inferior (Present study)</td>
<td>19.6</td>
<td>31067</td>
</tr>
<tr>
<td><em>U. uruguayensis</em></td>
<td>Intertidal superior (Present study)</td>
<td>6.6</td>
<td>1883</td>
</tr>
<tr>
<td><em>U. minax</em></td>
<td>Brackish – Riverine (Gray, 1942)</td>
<td>20.3</td>
<td>184928</td>
</tr>
<tr>
<td><em>U. tangeri</em></td>
<td>Brackish – Riverine (Feest, 1969)</td>
<td>27.4</td>
<td>59000</td>
</tr>
</tbody>
</table>

Fecundity differences were observed as much between both species as between individuals of the species. These differences were related to many factors: the weather during which females were collected; food availability; multiple spawning (1°, 2° or 3° spawning of reproductive cycle); individual variation on egg production and natural egg losses related to female activity on the surface (Hines, 1982; Henmi and Kaneto, 1989; Costa and Negreiros-Fransozo, 1996).

The fact of *U. thayeri* showing a higher egg production when compared with *U. uruguayensis* did not confirm the larval supply of the former species was higher. The probability of mechanical losses, related to feeding activity on the surface was higher for *U. thayeri* than *U. uruguayensis*. These points could be clarified when the fertility study of both species indicated the actual larval number that hatched from each egg mass.

**RESUMO**

Fêmeas ovígeras de *U. thayeri* e de *U. uruguayensis* foram utilizadas para se avaliar e comparar o padrão reprodutivo. O tamanho médio das fêmeas foi de 6,6 ± 0,8mm para *U. uruguayensis*, variando de 17,3 ± 4,4mm para *U. thayeri*. A fecundidade média obtida para *U. uruguayensis* foi 1883 ± 490 ovos (N = 27) e para *U. thayeri* de 31068 ± 11185 ovos (N = 31). As diferenças observadas no padrão reprodutivo de *U. thayeri* e *U. uruguayensis* sugerem estratégias adaptativas: *U. thayeri* apresenta uma reprodução sazonal, com atividade pronunciada de janeiro a março e alta fecundidade, enquanto *U. uruguayensis* reproduz-se continuamente, mas com proles menores.
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