# POPULATIONAL AND REPRODUCTIVE ASPECTS OF MACROBRACHIUM ACANTHURUS (WIEGMANN, 1836) (CRUSTACEA: PALAEMONIDAE) FROM NORTH COAST OF SÃO PAULO STATE, BRAZIL

### TAMBURUS, A. F.; MOSSOLIN, E. C. & MANTELATTO, F. L.\*

Laboratory of Bioecology and Crustacean Systematics Postgraduate Program in Comparative Biology, Department of Biology Faculty of Philosophy, Sciences and Letters of Ribeirão Preto (FFCLRP) University of São Paulo (USP), Av. Bandeirantes 3900, CEP 14040-901, Ribeirão Preto (SP), Brazil. \*Corresponding author: flmantel@usp.br;

#### ABSTRACT

Tamburus, A. F.; Mossolin, E. C. & Mantelatto, F. L. 2012. Populational and Reproductive Aspects of Macrobrachium acanthurus (Wiegmann, 1836) (Crustacea: Palaemonidae) from north coast of São Paulo State, Brazil. Braz. J. Aquat. Sci. Technol. 16(1): 9-18. elSSN 1983-9057. Macrobrachium acanthurus has a wide geographic distribution in America, mainly in rivers that flow into the Atlantic Ocean. Considering the economic interest in the Brazilian freshwater shrimp culture and its potential as a living resource, this study addresses the population and reproductive information of *M. acanthurus* that inhabit the north coast of São Paulo State. Individuals (N: 466,164 males and 302 females, with size ranging from 3.96 to 35.14 mm of carapace length) were captured with sieves (two people during 30 minutes) and traps (four hours after the nightfall) in April and October/2008 and in March/2009. Females were predominant in all sampled months; their ovaries showed changes in color and their size increased according to the developmental stage. The presence and percentage of ovigerous females in all sampled months indicated the possibility that the reproductive activity was continuous. The average fecundity (2299  $\pm$  1653 eggs) found was directly related to the female's size. The ovarian development occurred concomitantly with the eggs' development, indicating successive spawning. It was observed that the eggs changed color and increased their volume independently of the female size. The absence of embryo loss during the incubation process may be speculated to be an efficient strategy developed by the ovigerous females, as a mechanism of parental care against the most common causes of egg loss.

Keywords: Decapoda, egg production, fecundity, parental care, successive spawning

### INTRODUCTION

The genus Macrobrachium Bate, 1868 has a worldwide distribution that includes the Americas, with more than 55 recognized species, 17 of which are distributed in Brazil on basins of the inland, the coast and in Amazonia (Mantelatto et al., 2008; Pileggi & Mantelatto, 2010). Macrobrachium acanthurus (Wiegmann, 1836) is endemic to America, with a wide geographic distribution in rivers, estuaries and small lagoons that flow into the Atlantic Ocean. It is known from the U.S.A. (North Carolina, Georgia, Florida, Mississippi, Louisiana, Texas), Mexico, Cuba, Haiti, the Antilles, Dominican Republic, Puerto Rico, Nicaragua, Panama, Colombia, Venezuela, Surinam to Brazil (from Pará to Rio Grande do Sul) (Holthuis, 1952; Valenti et al., 1989; Ramos-Porto & Coelho 1998; Melo, 2003; Almeida et al., 2008).

This species has the ability to adapt to different salinities from fresh to brackish waters, and needs marine conditions to complete its developmental cycle (Hughes & Richard, 1973; Dugger & Dobkin, 1975; Albertoni et al., 2002; Melo, 2003). It is omnivorous and feeds mainly during the night (Coelho, 1963; Carvalho, 1973).

Although the entire life cycle of this species is still under investigation, the knowledge of its biological aspects in Brazil is being accumulated over the recent years: population structure (Carvalho et al., 1979; Valenti, 1984; Müller et al., 1999), fecundity (Paiva & Costa, 1962; Valenti et al., 1989; Müller et al., 1992; Albertoni et al., 2002), geographical distribution (Coelho & Ramos-Porto, 1985), embryonic development (Müller et al., 2007) and molt cycles (Carvalho et al., 1979).

Considering that *M. acanthurus* represents a potential economic resource in Brazilian freshwater shrimp culture and that the knowledge of its life history remains fragmented, complementary studies on the reproductive biology of this species from different areas of its known geographical range are necessary. On this basis, this study was conducted to evaluate the reproductive features of populations from the north coast of São Paulo State.



Figure 1 - Location of the Guaecá River (São Sebastião County) and the Siriúba River (Ilhabela County), São Paulo State, Brazil.

#### MATERIAL AND METHODS

Individuals were captured in three months' samples (April/2008, October/2008 and March/2009), from two distinct sites: one in the Guaecá River (23°48'54.3"S / 045°27'03.6"W) in São Sebastião county, at the continent, and another at the Siriúba River (23°45'20.5"S / 045°20'57.5"W) in Ilhabela county, at the island, both sites located in the north coast of São Paulo State (Figure 1), the distance between these points being about 13 km.

At the Guaecá River sampling site, the water is relatively clear and rarely exceeds 30 cm depth, the vegetation on the margins is low and the river bottom is composed mainly of gravel and thick sand. The sampled point is under anthropic pressure, with the presence of workers maintaining a pipeline in the nearby areas. At the Siriúba River, the sampling site is approximately 1.20 m deep, with dark water, large amounts of vegetation in one of the margins (grasses) and the river bottom is composed by sand with different grain sizes and organic material. The anthropic pressure in this point is due to garbage dump and domestic sewage.

On these points, two sampling methods were used: (1) sieving (50 cm diameter and 2 mm mesh) was conducted with fast movement under submerged marginal vegetation by two people, during 30 min; (2) trapping (30 cm length, 20 cm width, 15 cm height) composed by a closed plastic box, with one access that connects to the environment and the bottom of the trap by a funnel fixed inside in an angle that does not allow the exit of the animal. Six submerged traps with animal ration as bait were used in each sample for a period of 4 hours. In the laboratory of CEBIMar (University of São Paulo), in São Sebastião county (SP), individuals were frozen inside plastic bags (ovigerous females were individualized in containers to avoid possible egg loss) and subsequently transported to the Laboratory of Bioecology and Crustacean Systematics (LBSC) of FFCLRP/USP, in Ribeirão Preto county (SP), where the analyses were completed.

Sex was checked based on the presence (males) or the absence (females) of masculine appendix in the endopodit of the second pair of pleopods. The carapace length (CL = post-orbital margin to posterior dorsal margin of carapace) was obtained with a caliper (accuracy: 0.01 mm).

Ovaries were assessed macroscopically through carapace transparency and their size and color were used to establish the developmental stages as initial, intermediate or final (based on Mossolin & Bueno, 2002).

The egg development stage was characterized by the color of the fresh material. In addition, the presence or the absence of the embryo ocular spot was considered (based on Wehrtmann, 1990 and Mossolin & Bueno, 2002). The egg volume was determined by measuring the short and long axes of the egg (Odinetz-Collart & Rabelo, 1996). These measures were established under stereomicroscope in 20 eggs that were chosen randomly from each female, after the developmental stage had been observed.

Fecundity was estimated based only on females with eggs in early (initial) embryonic development. The eggs were removed and the total mass was counted with a manual counter.

Analysis of the population and the reproductive data followed the procedures described by Zar (1996), using Sigma Program Stat® Windows version 2.03. The  $\chi^2$  test was used to check the sex-ratio. One Way Analysis of Variance test (ANOVA) was applied to analyze the variation between fecundity and carapace length and in eggs' volume among development stages. Mann-Whitney Rank Sum test was used to compare the fecundity and relate it with CL of the individuals. Correlation test was used to assess the relationship between egg quantity and CL, and between CL and egg volume.

Voucher specimens of each population were deposited in the Crustacean Collection of Department of Biology (CCDB) of FFCLRP/USP, under number access CCDB 2698 (Guaecá River) and CCDB 2699 (Siriúba River).

### RESULTS

Despite the abiotic differences found in the two areas of sampling, the population features did not show significant differences. In this way, we grouped the results from both areas.

### Population and reproductive aspects

In total, 466 individuals (mean of  $12.03 \pm 6.77$  mm of CL) were obtained using the two sampling methods, of which 164 were males (35.2%; ranged from 4.10 to 35.14 mm of CL; mean:  $13.29 \pm 8.80$  mm) and 302 females (64.8%; ranged from 3.96 to 23.11 mm; 11.35  $\pm$  5.26 mm).

The total sex-ratio was in favor of females (0.55;  $\chi^2$ : 40.19). Analyzing the three samples separately, a significant deviation of 1:1 was observed in all months: April/08 (0.62;  $\chi^2$ : 8.03), October/08 (0.56;  $\chi^2$ : 18.12) and March/09 (0.43;  $\chi^2$ : 15.68).

From the 302 females collected, 117 females were found carrying eggs (38.7%). The size of the ovigerous females ranged from 6.07 to 23.11 mm of CL, with mean size of  $15.89 \pm 3.00$  mm of CL. The percentage of ovigerous females was 46.1% (N: 89) in April/08, 13.8% (N: 145) in October/08 and 82.4% (N: 68) in March/09.

# **Ovaries' development stages**

In total, 132 females collected in April and October/08 were used for this analysis. Individuals caught in March/09 were discarded because they had been frozen before the gonads' observation, restraining this information. Three developmental stages were established:

- Stage I (initial): colorless, white or light green (Pantone ®/376C), beginning in the dorsal posterior margin of the carapace and extending until the half of the hepatopancreas.

- Stage II (intermediate): light green (Pantone ®/376C) or green (Pantone ®/362C), from the dorsal posterior margin of the carapace until the anterior limit of the hepatopancreas.

- Stage III (final): green (Pantone ®/362C) or dark green (Pantone ®/357C), from the dorsal posterior margin of the carapace exceeding the hepatopancreas, up to the limit of the later tooth rostrum.

Table 1 - *Macrobrachium acanthurus* comparison between egg development stages and ovary development stages of females collected in April and October/08, in São Paulo State.

|                        |         | Eggs' Stages |       |
|------------------------|---------|--------------|-------|
| <b>Ovaries' Stages</b> | Initial | Intermediate | Final |
| Initial                | 33      | 3            | 2     |
| Intermediate           | 2       | 6            | 5     |
| Final                  | 0       | 5            | 5     |

# Egg development stages

Eggs were classified in three embryonic stages, according to the presence or absence of ocular spots and coloration:

- Stage I (initial): absence of ocular spots; color ranging between light green (Pantone ®/376C) and dark green (Pantone ®/357C).

- Stage II (intermediate): presence of ocular spots in trace or elliptical format; light yellow (Pantone ®/397C) or light green color (Pantone ®/376C).

- Stage III (final): presence of large and circular ocular spots and the embryos in some eggs are recognizable; colorless, light yellow (Pantone ®/397C) or dark yellow color (Pantone ®/3985C).

The egg volume had no significant relationship with the female size (Figure 2) (N: 56; r: 0.001). There was a significant variation in the egg volume during the incubation period in two populations ( $P \le 0.001$ ). Average egg volume increased significantly during embryogenesis, from 0.078 ± 0.013 mm<sup>3</sup> (Stage I; 15.65 ± 3.14 mm CL), 0.094 ± 0.018 mm<sup>3</sup> (Stage II; 15.69 ± 2.87 mm CL) to 0.108 ± 0.020 mm<sup>3</sup> (Stage III; 16.51 ± 2.85 mm CL), representing an overall increase of 38.8%.

# Fecundity

Fecundity varied from 171 (CL: 6.43 mm) to 7034 eggs (CL: 20.40 mm), presenting an average of 2299  $\pm$  1653 eggs. Changes in fecundity between size classes of 3 mm were significant (P: 0.007). Fecundity had direct and positive relation with the females' size (N: 56; r: 0.635), and this condition was sustained by r<sup>2</sup> value (Figure 3).

# **Successive Spawning**

Egg development stages were compared with the ovaries' development stages to observe the capacity of this species to maintain a continuous cycle of reproduction. When the eggs of the female were in the initial stage, ovaries were often also in the first stage (Table 1). Regarding the eggs in the intermediate stage, most ovaries observed were in stage II. When the eggs were in the final stage of development, more ovaries were observed to be in stages II and III. Considering the concomitant development of ovary and eggs, it is possible to infer that *M. acanthurus* has the ability to process successive spawning.

# DISCUSSION

Information on the reproductive biology of *M. acanthurus* is quite insufficient, considering the wide geographic distribution along the western Atlantic. This paper represents the first comparative informa-

Figure 2 - *Macrobrachium acanthurus*. Relationship between egg volume and carapace length of ovigerous females collected in April/08, October/08 and March/09 in São Paulo State, Brazil (r: 0.001).



tion on some reproductive aspects of western Atlantic *Macrobrachium* species, which demonstrates a large plasticity of this species that is summarized in the Table 2.

#### **Population features**

Most of the smaller individuals were captured under marginal vegetation that forms dense, partially immersed tufts. On the other hand, the largest ones were captured in the deeper areas, where there are more twigs and detritus serving as refuge. Even so, in our study were not observed a significant difference between the size of individuals of two sites sampled. For some authors there are signs that environmental characteristics can influence the population dynamics and individuals' sizes (Ammar et al., 2001), and so can the sampling method used. The presence of partially submerged vegetation along the river banks serves as a natural shelter for some species of caridean shrimps (Mossolin & Bueno, 2003; Mortari & NegreirosFransozo, 2007), corroborating the assertion made by Carvalho (1973), that these areas are the optimal place to observe and obtain these animals.

The size of the ovigerous females obtained in São Sebastião followed the pattern observed in other populations. The minimum size of the ovigerous females of *M. acanthurus* was found to be 6.07 mm CL (total length = 31.30 mm; eggs in Stage II). On the other hand, other authors reported a minimum ovigerous female size larger of this species in different regions, suggesting that *M. acanthurus* in the Southern region attained the maturity earlier than those from other populations, and/or that problems with the female capture method in the past studies could have occurred. For example, to Albertoni et al. (2002) the smaller female was 76.18 mm of total length, to Müller et al. (1992) the smallest ovigerous female was 48 mm, and Mejía-Ortiz et al. (2001) founded one with 42 mm.

A predominance of females was observed on *M. acanthurus* populations. Several non-exclusive

Figure 3 - *Macrobrachium acanthurus'* relationship between fecundity and carapace length of ovigerous females collected in April/08, October/08 and March/09 in São Paulo State, Brazil (r<sup>2</sup>: 0.4029).



| Species         | z   |       | TL (mm            |                | o                | (mm)          |       |              | Fecundity  |        | V (mm <sup>3</sup> ) | Locality (City/Country) | Reference                      |
|-----------------|-----|-------|-------------------|----------------|------------------|---------------|-------|--------------|------------|--------|----------------------|-------------------------|--------------------------------|
|                 |     | Min   | Мах               | Mean           | Min              | Max 1         | Mean  | Min          | Max        | Mean   |                      |                         |                                |
| M. acanthurus   | 56  | 1     |                   | 1              | 6.08             | 23.11         | 15.65 | 171          | 7034       | 2299   | 0.078                | São Sebastião/Brazil    | Present study                  |
| M. acanthurus   | 65  | 79.3  | 107.5             | 94.1           | ı                | ı             | ı     | 1054         | 17093      | 8438** | 0.071*               | Macaé/Brazil            | Albertoni et al., 2002         |
| M. acanthurus   | ı   | 10.7  | 53.5              | ı              | ı                | ı             | ı     | 440 (N=29) 3 | 042 (N=29) | ı      | 0.124*(N=15)         | São Sebastião/Brazil    | Anger & Moreira, 1998          |
| M. acanthurus   | 87  | 67*   | 141*              | ı              | ı                | ı             | ı     | 740          | 17769      | 8929   | ı                    | Registro/Brazil         | Valenti et al., 1989           |
| M. acanthurus   | 25  | 48.0  | 84.7              | ı              | ı                | ı             | ı     | 15           | 5670       | 1932   | ı                    | Florianópolis/Brazil    | Müller et al., 1992            |
| M. acanthurus   | 36  | 42.0  | 110.4             | 71.1           | ı                | ı             | ı     | 113          | 5568       | 1886** | ı                    | Veracruz/Mexico         | Mejía-Ortíz et al ., 2001      |
| M. amazonicum   | 32  | I     | I                 | I              | 7.0              | 21.0          | ı     | 150          | 2165       | ı      | ı                    | Central Amazon/Brazil   | Odinetz-Collart, 1991;         |
| M. amazonicum   | 75  | ı     | ı                 | ı              | 9 <sup>.</sup> 0 | 19.50         | ı     | I            | I          | ı      | 0,208*               | Tocantins/Brazil        | Odinetz-Collart & Rabelo, 1996 |
| M. amazonicum   | 246 | 27.40 | 63.50             | 36.09          | 7.65             | 19.50         | 10.49 | 16           | 1630       | 211    | 0.186*               | Itacoatiara/Brazil      | Hattori et al., 2009           |
| M. amazonicum   | 77  | 33.1  | 69 <sup>.</sup> 9 | ı              | ı                | ı             | ı     | I            | I          | ı      | 0.228*               | Apure/Venezuela         | Gamba, 1997                    |
| M. carcinus     | 22  | 100.0 | 150.0             | 122.0          | ı                | ı             | ı     | 7000         | 54000      | 27000  | ı                    | Sucre/Venezuela         | Graziani et al., 1993          |
| M. carcinus     | 35  | 120.0 | 190.0             | 161 <u>.</u> 2 | 52.9             | 82.5          | 70.3  | 14420        | 242437     | 98749  | 0.065                | Costa Rica              | Lara & Wehrtmann, 2009         |
| M. carcinus     | 2   | ı     | ı                 | ı              | ı                | ı             | ı     | 7728         | 10186      | 8957   | ı                    | Florianópolis/Brazil    | Müller et al., 1999            |
| M. carcinus     | 16  | 46.4  | 127.7             | 6.06           | ı                | I             | ı     | 502          | 23852      | 7892   | ı                    | Veracruz/Mexico         | Mejía-Ortíz et al., 2001       |
| M. heterochirus | 34  | 51.7  | 153.1             | 71.8           | ı                | ı             | ı     | 293          | 28512      | 3659** | ı                    | Veracruz/Mexico         | Mejía-Ortíz et al., 2001       |
| M. jelskii      | 248 | 34.5  | 45.3              | ı              | ı                | ı             | ı     | I            | I          | ı      | 2.026*               | Apure/Venezuela         | Gamba, 1997                    |
| M. ohione       | 12  | ı     | ı                 | ı              | 11.9             | 18 <u>.</u> 2 | 16.2  | 3577         | 14353      | 11051  | 0.080                | Louisiana/USA           | Corey & Reid, 1991             |
| M. ohione       | 5   | 54.0  | 80.0              | ı              | ı                | ı             | ı     | 6273         | 24800      | ı      | ı                    | Louisiana/USA           | Truesdale & Mermilliod, 1979   |
| M. olfersi      | 49  | 8.0   | 50.5              | ı              | ı                | ı             | ı     | 170          | 8960       | ı      | 0.086*               | São Sebastião/Brazil    | Anger & Moreira, 1998          |
| M. olfersi      | 100 | ı     | ı                 | 40.0           | ı                | ı             | ı     | I            | I          | 1227   | 0.047*               | São Sebastião/Brazil    | Mossolin & Bueno, 2002         |
| M. olfersi      | 22  | 33.2  | 64.0              | 47.6           | I                | I             | I     | 1029         | 6320       | 2210   | 0.035                | Santa Catarina/Brazil   | Nazari et al., 2003            |
| M. olfersi      | 8   | ı     | ı                 | ı              | 9.4              | 12.3          | 11.1  | 1966         | 4683       | 3099   | 0.076                | Florida/USA             | Corey & Reid, 1991             |
| M. olfersi      | 5   | ı     | ı                 | 46.7           | ı                | ı             | ı     | I            | I          | 1917   | 0.023                | Santa Catarina/Brazil   | Müller et al., 2003            |
| M. olfersi      | 16  | I     | I                 | I              | ı                | I             | ı     | 380          | 9577       | 3514   | 0.049*               | Florianópolis/Brazil    | Müller et al., 1999            |
| M. potiuna      | 102 | 28.5  | 38.2              | ı              | 6.1              | 12.4          | ı     | ю            | 47         | 24     | 2.649*               | Mangaratiba/Brazil      | Antunes & Oshiro, 2004         |
| M. potiuna      | 22  | 27.3  | 48.6              | 34.6           | ı                | ı             | ı     | 19           | 65         | 40.2   | 1.789                | Santa Catarina/Brazil   | Nazari et al., 2003            |
| M. potiuna      | 28  | I     | ı                 | ı              | ı                | ı             | ı     | 7            | 87         | 43     | 1.481*               | Florianópolis/Brazil    | Müller et al., 1999            |

Table 2 - Revision of the specimen's size and the egg number of Western Atlantic Macrobrachium species (N: number of individuals analyzed; TL: total body length; CL: carapace length; V: mean egg volume; Min: minimum; Max: maximum). \*: calculated from the data of the author; \*\*: all stages of egg development.

hypotheses may explain this pattern: (1) predation and environmental differences, which can act differently on sexes (Souza & Fontoura, 1996), (2) reproductive strategies, involving the migration of one of the sexes, looking for better conditions to hatch, and (3) human action, since these shrimps can be used for fishing or consumption and are selected by size. Particularly regarding the prevalence of females in March, this can be related to the reproductive season, which was also cited by Carvalho (1978). Migration of females to estuaries can occur in the posture season, while they are incubating the eggs, or/and during the hatching of the larvae and it can also be influenced by the rainy season (Carvalho et al., 1979). The ability to regulate the osmotic pressure in low and high salinities (Carvalho, 1973; Ismael & Moreira, 1997; Anger & Moreira, 1998) is responsible for their survival in estuarine systems and makes the migration of M. acanthurus possible during the breeding season.

# **Reproductive period**

Ovigerous females with embryos at different developmental stages were present in all samples during the study period. Furthermore, the ovaries development was concomitant with egg development. This result with the high percentage of ovigerous females in these 3 months (46.1% in April, 13.8% in October and 82.4% in March) suggests that the spawning and hatching of *M. acanthurus* take place throughout the year. A similar reproductive pattern was reported by Valenti et al. (1986), using the frequency of ovigerous females in each sample month. They noted that *M. acanthurus* reproduced every month of the year on the south coast of São Paulo State, although this species presented reproductive peaks during the summer (December and January).

Continuous reproduction pattern was also observed by other congener species in the Brazilian territory: Sampaio et al. (2007) noted the presence of ovigerous females of M. amazonicum every month in the Jaguaribe River (Ceará State, Brazil); Boss Jr. & Althoff (2002), Antunes & Oshiro (2004), and Mattos & Oshiro (2009) observed a similar pattern in the M. potiuna studied in a different region; Fransozo et al. (2004) detected an annual reproductive cycle of M. iheringi. There is certainly a variety of proximate and ultimate factors, e.g., water quality, water temperature, rainfall or water flow, availability of larval food, which may influence the reproductive period. Temperature is considered an important environmental factor in shaping reproductive traits of caridean shrimps (see Bauer, 1992; 2004). In tropical waters, the reproductive period is extended and year round, because of the relatively stable high temperature (Orton, 1920; Sastry, 1983). In Mexico, Guzmán et al. (1982) suggested that the freshwater populations respond more widely to own factors and environmental characteristics common to the sampled points, such as the photoperiod and precipitation; and respond less intensely to local features such as salinity and temperature. According to this comment and to the previous studies on reproduction aspects (see introduction), we state that *M. acanthurus* present a continuous reproductive period.

# Egg development

In the present study, egg sizes were independent of the body size at all developmental stages. However, in *M. acanthurus*, egg volume increases by 38% on average during embryogenesis. This value is similar to those reported in other *Macrobrachium* species: *M. amazonicum* (Heller, 1862): 33.4% (Odinetz-Collart & Rabelo, 1996); *M. olfersii*: 30.7% (Mossolin & Bueno, 2002); *M. potiuna*: 28.0% (Nazari et al., 2003); *M. carcinus*: 34.0% (Lara & Wehrtmann, 2009). This trend, based on the data set available, seems to corroborate the observation made by Lara & Wehrtmann (2009), that the egg volume increase in species of *Macrobrachium* is independent of the female size.

The size of eggs in decapods is a result of gradual water uptake during incubation and is associated with several variables, such as environment conditions and type of larval development (Herring, 1974; Odinetz-Collart & Rabelo, 1996). It was noted that the eggs changed color and increased in size and volume according to the vitellus consumed by the embryo. These growth and development inside the egg, increasing the occupied space, make the development along the egg long axis possible (Bressan & Müller, 1999) and the increasing egg volume during development can occur due to water increment (Balansundaram & Pandian, 1982).

Macrobrachium acanthurus has a reproductive strategy that priorizes a large number of small eggs (Coelho & Ramos-Porto, 1985; Valenti et al., 1989; Müller et al., 1999), a characteristic of the species that require an estuarine environment to complete their reproductive cycle. Furthermore, small eggs do not have enough vitellus to enable a prolonged embryonic development; they hatch as zoea (Müller et al., 1992) and have a brief development. According to Hancok (1998), species that inhabit brackish waters can produce small and abundant eggs because the salts' concentrations of these environments reduce the water quantity in the eggs through osmosis. The investment in the production of more eggs can also be due to the availability of the resources in the environment and to a lack of competition for them.

Different analysis methods can assist more detailed knowledge for embryonic proposes and con-

tribute to more robust information. Müller et al. (2007) established 12 embryonic development stages based on macro and microscopic observations of the cell division, the egg and the larva format of *M. acanthurus* during the development. García-Guerrero & Hendrickx (2009), established 10 development stages for *M. americanum* (Bate, 1868), based on external observations of growing live embryos and without cytological analyses. Despite these very detailed methodologies of classification, our decision on using only 3 development stages (initial, intermediate and final) was a very fast and efficient method to assess the developmental stage of the eggs.

# **Spawning and Fecundity**

Macrobrachium acanthurus presented a synchrony between the ovary and the egg developments. Females incubating early stage embryos had no mature ovary, while all females carrying nearly hatching embryos had mature ovary to release new eggs, indicating a continuous and successive egg production. This reproductive pattern has been illustrated for other tropical congener species. Carvalho (1978) verified that the same female of *M. acanthurus* could spawn several times during the reproductive season and more intense spawning episodes were noticed under higher temperatures (Valenti et al., 1986). In M. olfersii, shortly after spawning, the ovary started a new development (Mossolin & Bueno, 2002); in M. amazonicum, the observation of mature ovaries and eggs in late developmental stages in the same female indicated a possibility of new spawning (Gamba, 1997), and some ovigerous females of *M. amazonicum* (Sampaio et al., 2007) were found with mature ovaries, which indicated that females could start a new reproductive cycle even when carrying eggs, immediately after spawning.

Fecundity in *M. acanthurus* populations is very variable (Table 2). Unfortunately, some of the information available in the literature does not permit an accurate comparison due to different methodologies of analysis (i.e., fecundity was calculated by previous studies using all stages of egg development, which is not recommended - see Mantelatto & Fransozo, 1997). Excluding these uncertain data, we observed that the mean number of embryos produced by the population of M. acanthurus studied here is on average three times lower than another close population (Registro county/ São Paulo State) studied by Valenti et al. (1989), but similar to that one evaluated in Florianópolis county/ Santa Catarina State by Müller et al. (1992). These intra-specific differences in fecundity are influenced by the female's size variability as well as by temperature and food quality and quantity, which may vary along the latitudinal range of the species distribution (Odinetz-Collart and Rabelo, 1996; Mejía-Ortíz et al., 2001; Fransozo et al., 2004). In particular, female sizes have considerable influence on this aspect (Graziani et al., 1993; Da Silva et al., 2004) serving as an important factor, among many others, that can influence the number of eggs exteriorized (Paiva & Costa, 1962; Shakuntala, 1977; Valenti et al., 1989; Müller & Carpes, 1991; Nazari et al., 2003), and so do the abdomen volume (Corey & Reid, 1991), the weight (García-Dávila et al., 2000) and/or the place where the animals were sampled (Valenti et al., 1989). We observed that the fecundity was intermediate within a latitudinal gradient. In sites closer to the studied area, females carried a greater number of eggs and, when the latitude of the other places increases, the number of transported eggs decreases (Table 2). It can be a tendency similar to some marine caridean species (Bauer, 1992; 2004) and, in our study, the female size was important and influenced the observed differences.

Our comparative analysis evidenced that *M. acanthurus* shares significant similarities in terms of reproductive pattern with other species as *M. amazonicum* and *M. jelskii*. This reproductive positioning in the genus agrees with two recent molecular phylogenetic analysis of American *Macrobrachium* species (Pileggi & Mantelatto, 2010) and Brazilian populations of *M. amazonicum* (Vergamini et al., 2011), in which *M. acanthurus* and *M. jelskii* appear as related taxa, and that *M. acanthurus* shares significant morphological similarities with coastal populations of *M. amazonicum*.

Finally, we cannot refute the possibility of intraspecific population variability in function of different genetic stocks. Therefore, further detailed studies on population genetics are needed to compare other populations in detail along their range of distribution, and those will undoubtedly contribute to the further understanding of the biological variability in this species.

# ACKNOWLEDGMENTS

This work is part of a bachelor thesis by AFT and was supported by Scientific Initiation Fellowships from the Program CNPq/PIBIC/USP (118772/2009-0; 138453/2010-1). ECM thanks to CAPES (Program of Qualification in Taxonomy 563934/2005-0) for financial support. Additional support for this project was provided to FLM by CNPq (472746/2004-9, 471794/2006-6 and 473050/2007-2; Research Scholarships PQ 301261/04-0; 301359/07-5) and FAPESP (Coleções Cientificas 2009/54931-0). We gratefully acknowledge the Department of Biology and Postgraduate Program in Comparative Biology of the FFCLRP/USP for partial financial support, the CEBIMar/USP and IO/USP for logistical support during field and laboratory work, the IBAMA and Instituto Florestal for collection permits (02027.000101/2006-10), Ivana Miranda and anonymous reviewer for her help and suggestions, and Julia Hetem for the English revision. All experiments conducted in this study complied with current applicable state and federal laws of Brazil.

# REFERENCES

- Albertoni, E.F.; Palma-Silva, C. & Esteves, F.A. 2002. Fecundity of *Macrobrachium acanthurus* Wiegmann, 1836 (Decapoda: Palaemonidae) in a tropical coastal lagoon subjected to human impacts (Macaé, Brazil). Acta Limnol. Bras. 14(1): 71-80.
- Almeida, A.O.; Coelho, P.A.; Luz, J.R.; Santos, J.T.A. & Ferraz, N.R. 2008. Decapod crustaceans in fresh waters of southeastern Bahia, Brazil. Rev. Biol. Trop. 56(3): 1225-1254.
- Ammar, D.; Müller, Y.M.R. & Nazari, E.M. 2001. Biologia reprodutiva de *Macrobrachium olfersii* (Wiegmann) (Crustacea, Decapoda, Palaemonidae) coletados na Ilha de Santa Catarina, Brasil. Rev. Bras. Zool. 18(2): 529-537.
- Anger, K. & Moreira, G. 1998. Morphometric and reproductive traits of tropical caridean shrimps. J. Crust. Biol. 18(4): 823-838.
- Antunes, L.S. & Oshiro, L.M.Y. 2004. Aspectos reprodutivos do camarão de água doce *Macrobrachium potiuna* (Müller) (Crustacea, Decapoda, Caridea, Palaemonidae), na Serra do Piloto, Mangaratiba, Rio de Janeiro, Brasil. Rev. Bras. Zool. 21(2): 261-266.
- Balasundaram, C. & Pandian, T.J. 1982. Egg loss during incubation in *Macrobrachium nobilii* (Henderson & Mathai). J. Exp. Mar. Biol. Ecol. 59: 289-299.
- Bauer, R.T. 1992. Testing generalization about latitudinal variation in reproduction and recruitment patterns with sicyoniid and caridean shrimp species. Invert. Reprod. Develop. 22(1-3): 193-202.
- Bauer, R.T. 2004. Remarkable Shrimps: Adaptations and Natural History of the Carideans. University of Oklahoma Press, Norman, U.S.A., 282p.
- Boss Jr, H.B. & Althoff, S.L. 2002. Biologia reprodutiva de *Macrobrachium potiuna* (Müller, 1880) (Crustacea, Decapoda, Palaemonidae), no Parque Natural Municipal São Francisco de Assis, Blumenau, SC. Estud. Biol. 24(48): 45-50.
- Bressan, C.M. & Müller, Y.M.R 1999. Postnaupliar embryonic development of *Macrobrachium acanthurus* (Crustacea, Decapoda). Braz. J. Morphol. Sci. 16(16): 155-260.
- Carvalho, H.A. 1973. Fisioecologia do Pitu Macrobrachium acanthurus (Wiegmann, 1836)

- Crustacea, Decapoda - Comportamento, Consumo de Oxigênio e Resistência a Variações de Salinidade. Master Thesis. University of São Paulo - USP. 92p.

- Carvalho, H.A. 1978. Ciclo Sexual de Macrobrachium acanthurus (Wiegmann, 1836) (Decapoda, Palaemonidae): Relações com Fatores Abióticos e Ciclo de Intermudas. Doctoral Thesis. University of São Paulo - USP. 199p.
- Carvalho, H.A.; Gomes, M.G.S.; Gondim, A.Q. & Pereira, M.C.G. 1979. Sobre a biologia do pitu - *Macrobrachium acanthurus* (Wiegmann, 1836) em populações naturais da Ilha de Itaparica. Universitas 24: 25-45.
- Coelho, P.A. 1963. Observações preliminares sobre a biologia e a pesca dos camarões do gênero *Macrobrachium* Bate, 1868 (Decapoda, Palaemonidae) no Estado de Pernambuco, Brasil. Trabs. Inst. Oceanogr. Univ. Rur. PE 3(1): 75-81.
- Coelho, P.A. & Ramos-Porto, M. 1985. Camarões de água doce do Brasil: distribuição geográfica. Rev. Bras. Zool. 2(6): 405-410.
- Corey, S. & Reid, D.M. 1991. Comparative fecundity of decapod crustaceans 1. The fecundity of thirtythree species of nine families of caridean shrimp. Crustaceana 60(3): 270-294.
- Da Silva, R.R.; Sampaio, C.M.S. & Santos, J.A.
   2004. Fecundity and fertility of *Macrobrachium amazonicum* (Crustacea, Palaemonidae). Braz.
   J. Biol. 64(3A): 489-500.
- Dugger, D.M. & Dobkin, S. 1975. A contribution to knowledge of the larval development of *Macrobrachium olfersii* (Wiegmann, 1836) (Decapoda, Palaemonidae). Crustaceana 29(1): 1-30.
- Fransozo, A.; Rodrigues, F.D.; Freire, F.A.M. & Costa, R.C. 2004. Reproductive biology of the freshwater prawn *Macrobrachium iheringi* (Ortmann, 1897) (Decapoda: Caridea: Palaemonidae) in the Botucatu region, São Paulo, Brasil. Nauplius 12(2): 119-126.
- Gamba, A.L. 1997. Biología reproductiva de *Macrobrachium jelski*i (Miers, 1877) y *Macrobrachium amazonicum* (Heller, 1862) en Venezuela (Crustacea, Decapoda, Palaemonidae). Acta Cient. Venez. 48: 19-26.
- García-Dávila, C.R.; Alcantára, B.F.; Vasquez, R.E. & Chujandama, S.M. 2000. Biologia reprodutiva do camarão *Macrobrachium brasiliense* (Heller, 1862) (Crustacea: Decapoda: Palaemonidae) em igarapés de terra firme da Amazônia Peruana. Acta Amazon. 30(4): 653-664.
- García-Guerrero, M.U. & Hendrickx, M.E. 2009. External description of the embryonic development of the prawn, *Macrobrachium americanum* Bate,

1868 (Decapoda, Palaemonidae) based on the staging method. Crustaceana 82(11): 1413-1422.

- Graziani, C.A.; Chung, K.S. & Donato, M.D. 1993. Comportamiento reproductivo y fertilidad de *Macrobrachium carcinus* (Decapoda: Palaemonidae) en Venezuela. Rev. Biol. Trop. 41(3): 657-665.
- Guzmán, A.M.; Galaviz, J.L.R. & González, L.D.G. 1982. Ciclo anual de maduración y reproducción del "chacal" *Macrobrachium tenellum* y su relación con factores ambientales en las lagunas costeras de Mitla y Tres Palos, Guerrero, México (Decapoda: Palaemonidae). An. Inst. Cienc. Mar Limnol. Univ. Nal. Autón. México 9(1): 67-80.
- Hancok, M.A. 1998. The relationship between egg size and embryonic and larval development in the freshwater shrimp *Paratya australiensis* Kemp (Decapoda: Atyidae). Fresh. Biol. 39: 715-723.
- Hattori, G.Y; Barros, C.A.; Barbosa, J.G.O. & Magalhães, C. 2009. Fecundity of *Macrobrachium amazonicum* (Heller, 1862) (Crustacea, Decapoda, Palaemonidae) at medium Amazonas region, close to Itacoatiara (AM), Brasil. Anais do IX Congresso de Ecologia do Brasil, São Lourenço (MG) 1: 1-3.
- Herring, P.J. 1974. Size, density and lipid content of some decapod eggs. Deep. Sea. Res. 21: 91-94
- Holthuis, L.B. 1952. A general revision of the Palaemonidae (Crustacea, Decapoda, Natantia) of the Americas. II. The Subfamily Palaemonidae. Occasional Papers of the Allan Hancock Foundation 12: 1-396.
- Hughes, D.A. & Richard, J.D. 1973. Some current directed movements of *Macrobrachium acanthurus* under laboratory conditions. Ecology 54(4): 927-929.
- Ismael, D. & Moreira, G.S. 1997. Effect of temperature and salinity on respiratory rate and development of early larval stages of *Macrobrachium acanthurus* (Wiegmann, 1836) (Decapoda, Palaemonidae). Comp. Biochem. Physiol. 118A(3): 871-876.
- Lara, L.R. & Wehrtmann, I.S. 2009. Reproductive biology of the freshwater shrimp *Macrobrachium carcinus* (L.) (Decapoda: Palaemonidae) from Costa Rica, Central America. J. Crust. Biol. 29(3): 343-349.
- Mantelatto, F.L. & Fransozo, A. 1997. Fecundity of the crab *Callinectes ornatus* Ordway, 1863 (Decapoda, Brachyura, Portunidae) from the Ubatuba region, São Paulo, Brazil. Crustaceana, 70(2): 214-226.
- Mantelatto, F.L.; Pillegi, L.G.; Suárez, H. & Magalhães, C. 2008. First record and extension of the known distribution of the inland prawn, *Macrobrachium aracamuni* Rodríguez, 1982 (Decapoda, Palaemonidae) in Brazil. Crustaceana 81(2): 241-246.

- Mattos, L.A. & Oshiro, L.M.Y. 2009. Estrutura populacional de *Macrobrachium potiuna* (Crustacea, Palaemonidae) no Rio do Moinho, Mangaratiba, Rio de Janeiro, Brasil. Biota Neotrop. 9(1): 81-86.
- Mejía-Ortíz, L.M.; Alvarez, F.; Román, R. & Viccon-Pale, J.A. 2001. Fecundity and distribution of freshwater prawns of the genus *Macrobrachium* in the Huitzilapan river, Veracruz, Mexico. Crustaceana 74(1): 69-77.
- Melo, G.A.S. 2003. Manual de Identificação dos Crustacea Decapoda de Água Doce do Brasil. Edições Loyola: Centro Universitário São Camilo: Museu de Zoologia, Universidade de São Paulo. São Paulo. 430p.
- Mortari, R.C. & Negreiros-Fransozo, M.L. 2007. Composition and abundance of the caridean prawn species in two estuaries from the northern coast of São Paulo State, Brazil. Acta Limnol. Bras. 19(2): 211-219.
- Mossolin, E.C. & Bueno, S.L.S. 2002. Reproductive biology of *Macrobrachium olfersi* (Decapoda, Palaemonidae) in São Sebastião, Brazil. J. Crust. Biol. 22(2): 367-376.
- Mossolin, E.C. & Bueno, S.L.S. 2003. Relative growth of the second pereiopod in *Macrobrachium olfersi* (Wiegmann, 1836) (Decapoda, Palaemonidae). Crustaceana 76(3): 363-376.
- Müller, Y.M.R.; Bressan, C.M. & Nazari, E.M. 1992. Dados de fecundidade de *Macrobrachium acanthurus* (Decapoda, Palaemonidae) do rio Capivari, Praia dos Ingleses, Florianópolis, SC. Biotemas 5(1): 123-132.
- Müller, Y.M.R. & Carpes, S. 1991. *Macrobrachium potiuna* (Müller): aspectos do ciclo reprodutivo e sua relação com parâmetros ambientais (Crustacea, Decapoda, Palaemonidae). Rev. Bras. Zool. 8(1/2/3/4): 23-30.
- Müller, Y.M.R.; Nazari, E.M.; Ammar, D.; Ferreira, E.C.; Beltrame, I.T. & Pacheco, C. 1999. Biology of Palaemonidae (Crustacea, Decapoda) from the Ratones Hidrografic Basin, Florianopolis, Santa Catarina, Brazil. Rev. Bras. Zool. 16(3): 629-636.
- Müller, Y.M.R.; Nazari, E.M. & Simões-Costa, M.S. 2003. Embryonic Stages of the freshwater prawn *Macrobrachium olfersi* (Decapoda, Palaemonidae). J. Crust. Biol. 23(4): 869-875.
- Müller, Y.M.R.; Pacheco, C.; Simões-Costa, M.S. & Nazari, E.M. 2007. Morphology and chronology of embryonic development in *Macrobrachium acanthurus* (Crustacea, Decapoda). Invertebr. Reprod. Develop. 50(2): 67-74.
- Nazari, E.M.; Simões-Costa, M.S.; Müller, Y.M.R.; Ammar, D. & Dias, M. 2003. Comparisons of fecundity, egg size, and egg mass volume of the

freshwater prawns *Macrobrachium potiuna* and *Macrobrachium olfersi* (Decapoda, Palaemonidae). J. Crust. Biol. 23(4): 862-868.

- Odinetz-Collart, O. 1991. Strategie de reproduction de *Macrobrachium amazonicum* en Amazonie Centrale (Decapoda, Caridea, Palaemonidae). Crustaceana 61(3): 253-270.
- Odinetz-Collart, O. & Rabelo, H. 1996. Variation in egg size of the fresh-water prawn *Macrobrachium amazonicum* (Decapoda: Palaemonidae). J. Crust. Biol. 16(4): 684-688.
- Orton, J.H. 1920. Sea temperature, breeding and distribution of marine animals. J. Mar. Biol. Assoc. U. K. 12(2): 339-366.
- Paiva, M.P. & Costa, R.S. 1962. Sobre os ovos de Macrobrachium acanthurus (Wiegmann, 1836) Pearse, 1911. Bol. Soc. Agron. 3: 37-40.
- Pileggi, L.G. & Mantelatto, F.L. 2010. Molecular phylogeny of the freshwater prawn genus *Macrobrachium* (Decapoda, Palaemonidae) with emphasis on the relationships among American species. Invert. Syst. 24: 194-208.
- Ramos-Porto, M. & Coelho. P.A. 1998. Malacostraca
  Eucarida. Caridea (Alpheoidea Excluded). In: Young, P.S. (ed.). Catalogue of Crustacea of Brazil. Rio de Janeiro: Museu Nacional. (Série Livros n. 6). p. 325-350.
- Sampaio, C.M.S.; Silva, R.R.; Santos, J.A. & Sales, S.P. 2007. Reproductive cycle of *Macrobrachium amazonicum* females (Crustacea, Palaemonidae). Braz. J. Biol. 67(3): 551-559.
- Sastry, A.N. 1983. Ecological aspects of reproduction. In: F.J. Vernberg & Vernberg, W.B. (eds.) The Biology of Crustacea, vol. 8. Environmental Adaptations. Academic Press, New York. 179-270pp.
- Shakuntala, K. 1977. The relation between body size and number of eggs in the freshwater prawn, *Macrobrachium lamarrei* (H. Milne Edwards) (Decapoda, Caridea). Crustaceana 33(1): 17-22.
- Souza, G.D. & Fontoura, N.F. 1996. Reprodução, longevidade e razão sexual de *Macrobrachium*

*potiuna* (Müller, 1880) (Crustacea, Decapoda, Palaemonidae) no arroio Sapucaia, município de Gravataí, Rio Grande do Sul. Nauplius 4: 49-60.

- Truesdale, F.M. & Mermilliod, W.J. 1979. The river shrimp *Macrobrachium ohione* (Smith) (Decapoda, Palaemonidae): its abundance, reproduction, and growth in the Atchafalaya River basin of Louisiana, USA. Crustaceana 36(1): 61-73.
- Valenti, W.C. 1984. Estudo populacional dos camarões de água doce *Macrobrachium acanthurus* (Wiegmann, 1836) e *Macrobrachium carcinus* (Linnaeus, 1758) do Rio Ribeira de Iguape (Crustacea, Palaemonidae). Master Thesis. University of São Paulo - USP. 149p.
- Valenti, W.C.; Melo, J.T.C. & Lobão, V.L. 1986. Dinâmica da reprodução de Macrobrachium acanthurus (Wiegmann, 1836) e Macrobrachium carcinus (Linnaeus, 1758) do Rio Ribeira de Iguape (Crustacea, Decapoda, Palaemonidae). Cienc. Cult. 38(7): 1256-1262.
- Valenti, W.C.; Melo, J.T.C. & Lobão, V.L. 1989. Fecundidade em *Macrobrachium acanthurus* (Wiegmann, 1836) do Rio Ribeira de Iguape (Crustacea, Decapoda, Palaemonidae). Rev. Bras. Zool. 6(1): 9-15.
- Vergamini, F.G.; Pileggi, L.A. & Mantelatto, F.L. 2011. Genetic variability of the Amazon River prawn *Macrobrachium amazonicum* (Decapoda, Caridea, Palaemonidae). Contrib. Zool. 80(1): 67-83.
- Wehrtmann, I.S. 1990. Distribution and reproduction of *Ambidexter panamense* and *Palaemonetes schmitti* in Pacific Costa Rica (Crustacea, Decapoda). Rev. Biol. Trop. 38(2A): 327-329.
- Zar, J.H. 1996. Biostatistical Analysis. 3rd ed. Prentice Hall, Upper Saddle River, New Jersey. 662p.

Submetido: Janeiro/2011 Revisado: Agosto/2011 Aceito: Novembro/2011