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Research Article

**Reproductive biology of *Macrobrachium amazonicum* (Heller, 1862)
(Decapoda: Palaemonidae) in a reservoir situated in Minas
Gerais State, southeastern Brazil**

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ABSTRACT. The palaemonid shrimp *Macrobrachium amazonicum* is widely distributed in coastal rivers, estuaries and inland waters of South America. Despite this, little is known regarding its biology in the natural environment. Furthermore, this species is economically important because it is the main freshwater shrimp commercially exploited by artisanal fisheries in northern and northeastern Brazil, besides showing great potential for aquaculture. Considering this, the present study aimed to analyze aspects of the reproductive biology of *M. amazonicum*. A total of 251 females were analyzed, 102 of these being ovigerous. The carapace length ranged from 6.03 to 10.06 mm (average \pm standard deviation: 7.52 ± 0.84 mm). Reproduction was continuous with a gradual increase from April to June 2012. No significant relationship between frequency of ovigerous females and environmental variables was observed. The fecundity showed a positive linear relation with the carapace length and the number of eggs varied from 33 to 389 (average \pm standard deviation: 203 ± 78.06 eggs/female). A dominance of eggs at an early stage was observed in most months. There was an increase in the size/volume of eggs from early to late embryonic stage. Ovigerous females produced eggs at the same development stage, with the same size and volume regardless of their body size. The results demonstrated higher similarity of this population to other continental *M. amazonicum* populations than from estuarine ones, showing the environment influence in the life-history of individuals.

Keywords: *Macrobrachium amazonicum*, decapod, reproduction, tropical crustaceans, Brazil.

INTRODUCTION

Decapod crustaceans are essential components in aquatic environments (Magalhães, 2003). They represent an important group not only by the ecological aspect, because they form an important link between producers and consumers of higher trophic levels (Albertoni *et al.*, 2003a, 2003b), but also by economic and social aspects, especially for communities that use them as fishery resource and food (Valenti *et al.*, 1989).

Shrimps are a diverse group of decapod crustaceans, and the genus *Macrobrachium* (Bate, 1868) is one of the most important of freshwater Palaemonidae. Currently this genus includes 243 species which have a worldwide distribution in tropical waters (De Grave & Franssen, 2011), with 17 species recorded in Brazil (Pileggi & Mantelatto, 2010, 2012).

Macrobrachium amazonicum is one of the most widespread species in water bodies of the Neotropical region (Pileggi & Mantelatto, 2010; Vergamini *et al.*, 2011). Its occurrence covers all the main South American river basins, including the Orinoco, Amazon, Araguaia-Tocantins, São Francisco, Paraná and Paraguay, as well as the smaller rivers along the South Atlantic, in the northern and northeastern coasts of Brazil (Bialetzki *et al.*, 1997; Magalhães, 2000; Melo, 2003; Vergamini *et al.*, 2011; Pileggi *et al.*, 2013).

At least two different kinds of life cycle in populations of *M. amazonicum* are known: those living in coastal regions, which inhabit rivers close to estuaries and depend on brackish water to complete their life cycle and continental populations, living in rivers, lakes and other water bodies without contact with the coast (Moraes-Valenti & Valenti, 2010). As a

result, there will be variations between populations with regard to ecological, behavioral and life history traits (Hayd & Anger, 2013), beyond the physiological and morphological characteristics necessary for adaptation in different habitats (fresh or brackish water) (Charmantier & Anger, 2011; Boudour-Bouchecker *et al.*, 2013).

There are records that populations that inhabit different geographical regions have biological variations (Maciel & Valenti, 2009; Pantaleão *et al.*, 2011; Vergamini *et al.*, 2011), such as reproductive adaptations, especially those that were observed in species belonging to the genus *Macrobrachium* that have adjusted to freshwater environments. These adjustments include females with lower fertility, production of larger eggs and with a greater amount of yolk, larger larvae with benthic habit and an abbreviated larval development in terms of duration and stages (2-3 stages), besides smaller adults (Rabalais & Gore, 1985; Anger, 2001; Bauer, 2011). However, *M. amazonicum* is a notable exception because it has an extended larval development in freshwater (9-11 stages) (Magalhães, 1985; Walsh, 1993) and according to Anger (2013), this pattern is an indication of recent evolutionary transition from coastal marine to freshwater habitats.

According to Maciel & Valenti (2009) and Meireles *et al.* (2013), *M. amazonicum* presents a wide phenotypic plasticity, probably in response to several environmental conditions found by the species. For example, their reproductive strategies, egg size and larval development are strongly dependent of the region in which they live, being the particular hydrological and geographical environmental characteristics the main factors that influence these aspects. According to Odinetz-Collart & Rabelo (1996), egg size increases as the distance from the ocean also increases. Fecundity is related to several factors and may be proportional to female body size (Silva *et al.*, 2004), to length and volume of abdomen (Corey & Reid, 1991), to length of pleopods, to rate mortality of eggs (Annala, 1991) and to female age (Sastry, 1983).

The construction of hydroelectric plants causes damage to the ecosystem modifying the entire area. According to Tundisi (2003), the barriers formed and reservoirs themselves are the main reasons of threat to organisms that live in Brazilian aquatic ecosystems. Therefore, the conservation of *M. amazonicum* populations should be considered a priority in face of intense change that has been going in places of occurrence of this species.

Thus, the aim of this study was to analyze the reproductive biology of *M. amazonicum* in a hydroelectric reservoir, on Araguari River, Minas Gerais

State (MG), to improve knowledge about this species and to allow comparisons with populations in other regions.

MATERIALS AND METHODS

Samples of *M. amazonicum* were collected monthly from April 2012 to May 2013 in the reservoir of Miranda hydroelectric dam located in the region of Triângulo Mineiro and Alto Paranaíba, Minas Gerais State, southeast Brazil (19°03'13.0"S, 047°59'25.5"W). A sampling section of 100 m length and 5 m wide was defined on a shore of reservoir with abundant aquatic vegetation. This place was selected due to the abundance of shrimps recorded in a previous evaluation, because it has easy and safe access and it is an area that allowed an efficient use of hand sieves.

To standardize the capture effort, collections were made by two people during a period of 1 h in the early evening (except in May 2012 when the sample was taken during the day time). At each sampling period, water temperature was recorded with a mercury thermometer at a depth of 15 cm. Rainfall data for the sampling period was obtained at the Laboratory of Climatology and Hydric Resources of the Institute of Geography at Federal University of Uberlândia (UFU).

Captured specimens were immediately transferred to a plastic box containing water from the collecting site and transported to the Aquatic Ecosystem Ecology Laboratory (UFU). Shrimps were stored in labeled vials containing 70% EtOH until reproductive analysis.

Sex of shrimps was determined by examination of the endopodite morphology of the second pair of pleopods (Ismael & New, 2000). Total length (TL - from the anterior portion of the rostrum to the posterior portion of the telson) (mm) and carapace length (CL - from the posterior portion of the orbit to the posterior extremity of the carapace) (mm) were obtained using a caliper ruler (0.1 mm).

Eggs were classified in three stages according to their embryonic development: Stage I: Initial Stage (eggs mostly occupied by yolk, no eye pigments visible); Stage II: Intermediate Stage (yolk occupying about 50-75% of egg volume, eggs with eye pigment visible as a line or elliptical) and Stage III: Final Stage (yolk occupying about 25-50% of egg volume, eye fully developed).

The relationship between the frequency of ovigerous females and environmental factors (temperature and rainfall) during the sampling period was evaluated by Spearman's correlation.

For fecundity analysis, only the females with eggs at the initial stage (Stage I) were selected to avoid egg

loss during incubation (see Anger & Moreira, 1998). From each female, eggs were carefully removed from the pleopods using tweezers and counted under a stereomicroscope.

The relationship between fecundity and size of ovigerous females was determined by linear regression ($Y = a + bX$), considering the number of eggs as dependent variable and the carapace length as independent variable. Regression coefficients were tested for significant deviations from zero (ANOVA).

In order to evaluate size and volume of the eggs, five females were used in each embryonic development stage (initial, intermediate and final stages), totaling 15 ovigerous females. A sample of 20 eggs per female was randomly inspected and the long and short axes of eggs were measured under stereomicroscope equipped with a micrometric eyepiece.

The egg volume was calculated from the formula $V = \pi \cdot l \cdot h^2 / 6$, where l = long axis and h = short axis (Odinetz-Collart & Rabelo, 1996). Differences in mean size and volume of the eggs among the three developmental stages was tested using ANOVA and Tukey's test. The relationship between the size of females and the volume and size of eggs was tested by Spearman's correlation in order to verify whether females with different body sizes, but with eggs in the same stage of embryonic development, also had eggs of different sizes.

Statistical analyzes were performed using Systat software (version 10.2) and the significance level was set at $P < 0.05$ (Zar, 1996).

RESULTS

Specimens of *M. amazonicum* were recorded in 13 of the 14 months of collection, except in May 2012. The carapace length of females ranged from 6.03 to 10.06 mm, with a mean of 7.52 ± 0.84 mm SD (Table 1).

Ovigerous females were found in almost all months, with the exception of May 2012 in which no individuals were collected, and in May 2013 in which females with eggs were not collected. The percentage of ovigerous females in relation to total females was 40.1% (102 ovigerous females in 251 females collected). The lowest monthly relative frequencies of females with eggs were found in July 2012 (14.3%) and August 2012 (25%), while the highest percentages were observed in April (67.8%) and June 2012 (66.7%) (Fig. 1).

Reproductive peaks were recorded in some periods amongst the months of April and June 2012. In the other months, mainly between September 2012 and April 2013, the frequency of ovigerous females remained between 34 and 50% (Fig. 1).

Table 1. Number of individuals (N), minimum (Min), maximum (Max), mean and standard deviation (Mean \pm SD) carapace length of *M. amazonicum* specimens sampled from April 2012 to May 2013 in the reservoir of Miranda Dam, Minas Gerais, State.

Sex	Carapace length (mm)			
	n	Min	Max	Mean \pm SD
Non-ovigerous females	149	6.03	10.03	7.18 ± 0.75
Ovigerous females	102	6.03	10.06	8.04 ± 0.69

During the sampling period, rainfall ranged from 0 (August) to 313 mm (January), with an average of 128 mm month⁻¹. Although there has been an upward trend in the frequency of ovigerous females with increasing rainfall in September and October 2012, no relationship between these two variables was found ($R = 0.174$; $P > 0.05$) (Fig. 2).

Water temperature was recorded from July 2012 to April 2013 and ranged between 21°C and 29°C, with an average of 25.7 ± 3.2 °C. In some months (September, October and December 2012) there was an increased in water temperature and a correspondent increase in the frequency of ovigerous female but there was no significant correlation between these variables ($r = 0.437$; $P > 0.05$) (Fig. 3).

For fecundity analysis 58 ovigerous females were used with carapace length between 6.03 and 9.08 mm and fecundity ranging from 33 to 389 eggs (average of 203 ± 78.06 eggs/female). The number of eggs ranged from 118 (June 2012) to 297 (March 2013), resulting in an average of 209 ± 79.00 eggs/female per month.

Regression analysis between female body size and the number of eggs indicated a significant correlation between these two variables ($P < 0.001$), that is, there was an increase in fecundity with the growth of females, given that for each increase of the female body unit, the number of eggs increased by ~73 times (Fig. 4).

The stage of embryonic development was evaluated for all eggs from 102 ovigerous females and it was found that 58 females (56.1%) had eggs at the initial stage, 35 females (34.0%) had eggs at the intermediate stage and 9 females (8.1%) were observed with eggs at the final stage. There was a dominance of eggs at an early stage in most months analyzed, except for June 2012, March and April 2013 (Fig. 5). Data from October 2012 was not evaluated because only one ovigerous female with a reduced sample of eggs was collected, being these eggs considered a remnant of a recent larvae hatching.

Considering the size of the eggs, there was a significant difference for the short axis among the three stages ($F = 90.175$; $df = 2, 397$; $P < 0.001$), as well as

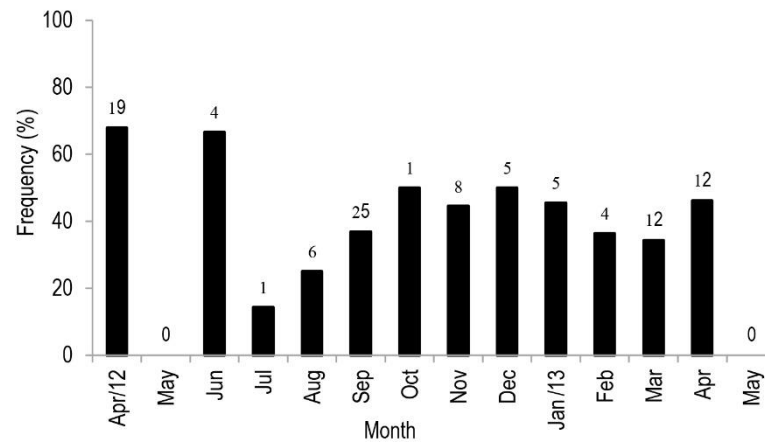


Figure 1. Relative frequency of ovigerous females in relation to total females of *M. amazonicum* sampled from April 2012 to May 2013 in the reservoir of Miranda Dam Minas Gerais State, Brazil. (The value above the bars represents the number of females with eggs used to obtain the frequency).

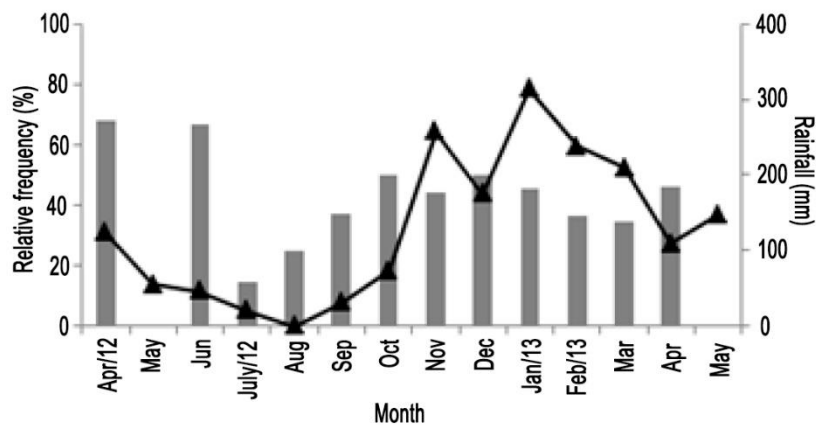


Figure 2. Relative frequency of *M. amazonicum* ovigerous females according to mean rainfall (mm) sampled from April 2012 to May 2013 in the reservoir of Miranda Dam, Minas Gerais, State, Brazil.

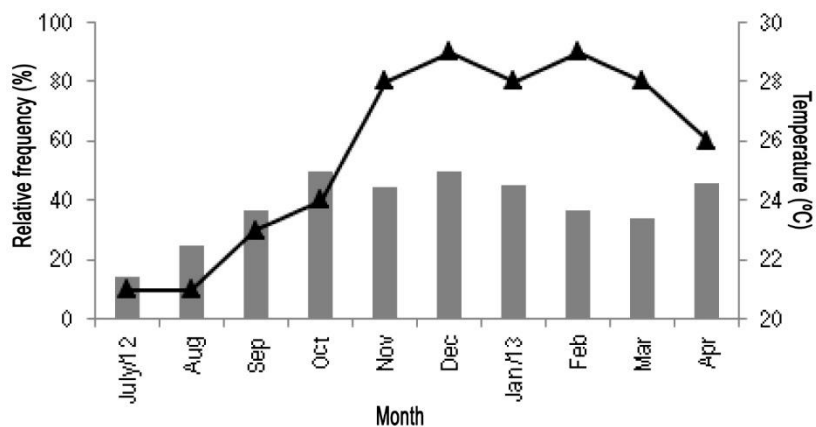


Figure 3. Relative frequency of *M. amazonicum* ovigerous females according to mean temperature (°C) sampled from April 2012 to May 2013 in the reservoir of Miranda Dam, Minas Gerais, State, Brazil.

for the long axis ($F = 728.060$; $df = 2, 397$; $P < 0.001$). The mean volume of the eggs also differed significantly

between the stages of embryonic development ($F = 228.413$; $df = 2, 397$; $P < 0.001$) (Table 2).

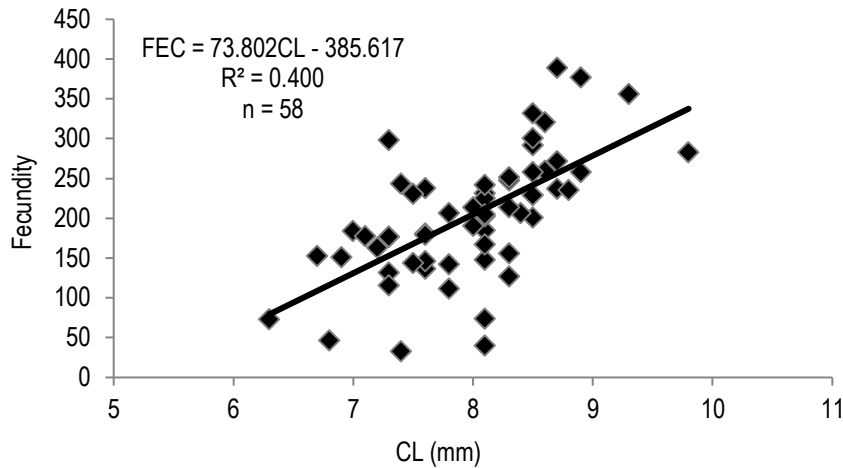


Figure 4. Relationship between fecundity (FEC) and carapace length (CL) of *M. amazonicum* ovigerous females sampled from April 2012 to May 2013 in the reservoir of Miranda Dam, Minas Gerais, State, Brazil.

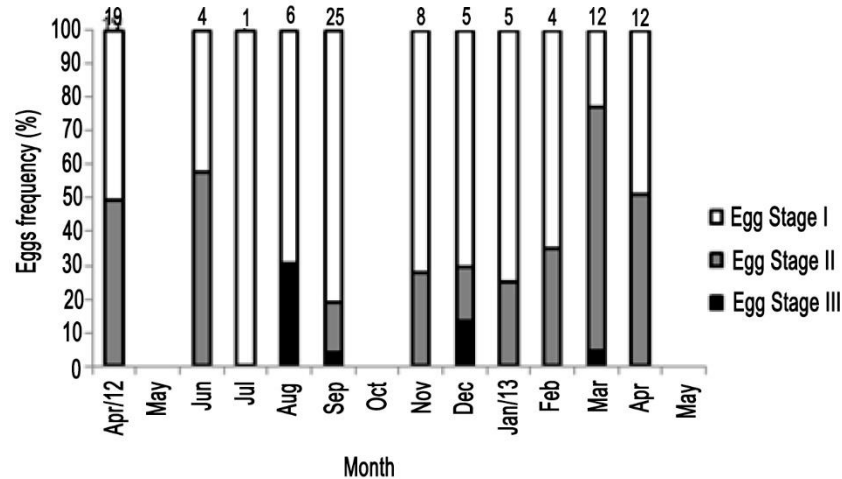


Figure 5. Relative frequency (%) of eggs obtained monthly related to their respective stage of embryonic development: I Initial stage; II Intermediate stage and III Final stage of *M. amazonicum* sampled from April 2012 to May 2013 in the reservoir of Miranda Dam, Minas Gerais, State. (The value above the bars represents the number of ovigerous females used to obtain the frequency).

Table 2. Egg measures in three different stages of embryonic development (I-III) of *M. amazonicum* females sampled from April 2012 to May 2013 in the reservoir of Miranda Dam, Minas Gerais, State. Mean \pm SD ($n = 300$), numbers in parentheses are the lowest and highest values found. Means \pm SD in the same column followed by different letters, differ in such ($P < 0.001$) by Tukey's Test.

Stage	Short axis (mm)	Long axis (mm)	Volume of the egg (mm ³)
I	0.57 \pm 0.04 (0.42-0.67) ^a	0.70 \pm 0.05 (0.53-0.82) ^a	0.12 \pm 0.02 (0.05-0.18) ^a
II	0.62 \pm 0.04 (0.51-0.73) ^b	0.81 \pm 0.04 (0.73-0.91) ^b	0.16 \pm 0.03 (0.11-0.24) ^b
III	0.67 \pm 0.06 (0.53-0.87) ^c	0.97 \pm 0.06 (0.84-1.16) ^c	0.23 \pm 0.05 (0.13-0.44) ^c

The relationship between the average volume of the eggs in initial, intermediate and final stages with female body size (CL) was not significant ($r = -0.273$; $P >$

0.05) (Fig. 6), as well as the average size of the eggs ($r = -0.309$; $P > 0.05$) (Fig. 7).

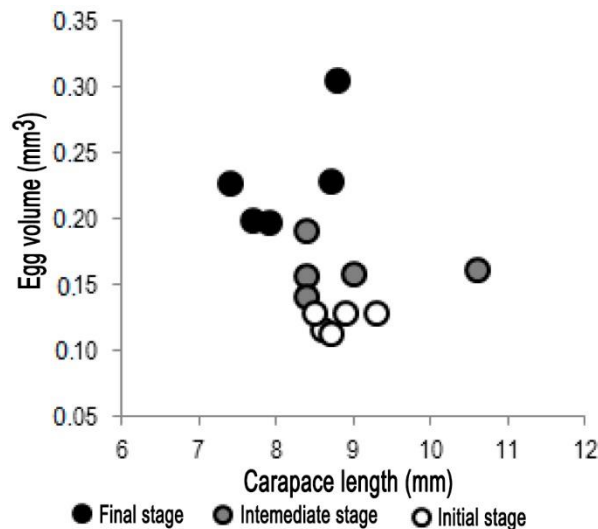


Figure 6. Relationship between the average egg volume in its three development stages and the size of *M. amazonicum* females sampled from April 2012 to May 2013 in the reservoir of Miranda Dam, Minas Gerais, State.

DISCUSSION

According to Bialetzki *et al.* (1997), *Macrobrachium amazonicum* has rapid development and high capacity for colonization, which gives a great plasticity degree for this species with high adaptability to different environmental conditions (Vergamini *et al.*, 2011). In May 2012, no individuals of *M. amazonicum* were found and we have two assumptions for this event. The first is that there was a heavy rain on the sampling site few days before collection. It may have expanded the wetlands and, consequently, afforded the formation of more protected environments, which collaborate for the dispersal of specimens. The second assumption is related to the period of sampling in this month. The collection was performed during the day due to logistic reasons. According to Coelho (1963) species of the genus *Macrobrachium* are crepuscular, with more pronounced activities at the end of the day when they come out to feed. This night movement, namely, vertical migration performed by organisms, occurs in response to predation by fish on the water surface during the day (Zaret & Suffern, 1976).

The species showed a continuous reproductive pattern, with higher proportions of females with eggs in April and June 2012. Studies conducted with the same species also demonstrated the occurrence of ovigerous females during all sampling months, but with peaks in some of them. Freire *et al.* (2012) found a greater abundance of females with eggs in January and February. They reported that the peaks refer to better physiological conditions, *i.e.*, higher accumulation of

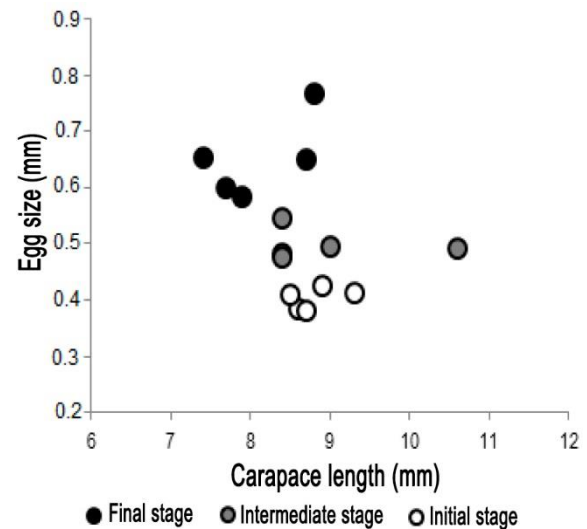


Figure 7. Relationship between the average egg size in its three development stages and the size of *M. amazonicum* females sampled from April 2012 to May 2013 in the reservoir of Miranda Dam, Minas Gerais, State.

energy during reproductive periods; while Silva (2011) observed a higher frequency of ovigerous females from September to November and in January, pointing out that this occurred in raining periods.

Pinheiro & Hebling (1998) observed that the reproductive period of freshwater decapod crustaceans is associated with the rainy season, thermal variations and photoperiod in the region. Collart (1991) found ovigerous females all over the year, with peaks related to hydrological cycles, and Gamba (1997) noted the oviposition period decreasing in the dry season. Valenti (1984) confirms this fact, noting that freshwater prawns of the genus *Macrobrachium* have continuous or periodic reproduction and in Brazil most species have long reproductive periods with some peaks. Rainfall is an important climatic variable due to its effect in concentration of nutrients, ions and organic matter, changes in river current speed, pH, amount of dissolved oxygen, turbidity and other physical-chemical factors (Maier, 1978). However, in this study it was not detected a relationship between the frequency of ovigerous females and rainfall, since the months in which there were reproductive peaks (April and June 2012) did not coincide with increased rainfall.

Temperature is a physical variable that influences the geographic distribution of species or populations and modulates most physiological and metabolic processes of these individuals (Daoud *et al.*, 2007). The variations in water and air temperature can interfere in the reproductive cycle and create favorable or unfavorable periods for reproduction (Sastri, 1983), since they can affect development and maturation of

gonadal tissues (Erdman & Blake, 1987). In the present study, the highest temperatures did not coincide with peaks of female reproduction. This pattern corroborates most studies dedicated to the determination of reproductive periods of freshwater decapods of tropical areas, in which the periodicity of environmental factors that influences the reproduction of these organisms are less evident when compared to temperate regions. Studies performed in Brazil with *Macrobrachium potiuna* (Müller, 1880) in Rio de Janeiro State (Antunes & Oshiro, 2004) and *Potimirim glabra* (Kingsley, 1878) in São Paulo State (Hoffmann, 2007), did not show any association between frequency of ovigerous females and water temperature.

Macrobrachium spp. have a wide variation of fecundity. For example, Lobão *et al.* (1986) reported for other species of the same genus such as *Macrobrachium potiuna*, *M. iheringi* (Ortmann, 1898), *M. australiense* (Holthuis, 1950), *M. borellii* (Nobili, 1896) and *M. jelskii* (Miers, 1877) absolute fecundities lower than 200 eggs. Although *M. amazonicum* has a relatively high fecundity, with a production of 6,000 to 7,000 eggs in aquaculture tanks (Ribeiro *et al.*, 2012), this is considered low compared to species of greater commercial interest and that reach larger sizes, such as *M. rosenbergii* (De Man, 1879), *M. acanthurus* (Wiegmann, 1836), *M. carcinus* (Linnaeus, 1758) and *M. malcolmsonii* (H. Milne-Edwards) (Coelho *et al.*, 1982; Valenti, 1984; Lobão *et al.*, 1985; Scaico, 1992). According to Ismael & New (2000), *M. rosenbergii*, which is the most used species for aquaculture in Brazil, and *M. carcinus*, present fecundity ranging from 80,000 to 100,000 eggs per female. For *M. acanthurus*, females with 18,000 eggs have already been recorded (Valenti *et al.*, 1986, 1989).

However, the low fecundity of *M. amazonicum* in relation to other species is offset by its continuous reproductive activity. Fecundity of *M. amazonicum* was reported by several authors. Meireles *et al.* (2013) recorded an average of 2237 ± 586 eggs per female, in Pará, while in Mato Grosso do Sul they found females with significantly fewer eggs (271 ± 54 eggs). In Tucuruí hydroelectric reservoir in Pará State (PA), Silva *et al.* (2005) obtained an average of 273 eggs/female, similar to the monthly average of our study (203 ± 78.06 eggs). However, Lucena-Frédou *et al.* (2010) in Combu Island (PA) observed absolute fecundity ranging from 40 to 3,375 eggs/female, with a mean value of 905 ± 590 SD eggs/female. Da Silva *et al.* (2004), found average values between 696 (females with 5.0 to 5.5 cm total length) and 1554 eggs/female (9.5 to 10.0 cm).

The variation in fecundity averages are related to the type of environment in which the samples were taken.

It is known that shrimp species inhabiting estuarine environments produce a large number of small eggs, because salt concentrations in these environments reduce the amount of water from the egg through the osmotic process. Those that inhabit lentic limnetic environments produce eggs with intermediate number and size, while species living next to headwater streams produce a small number of large eggs (Hancock, 1998).

Different populations of *M. amazonicum* can show similar patterns. According to Maciel & Valenti (2009) fecundity of this species is probably influenced by the availability of nutrients and dissolved salts.

The low fecundity obtained in the present study may also be related to accidental egg loss by females in freshwater environments. Antunes & Oshiro (2004) suggested that the apparent egg loss by females might result in a better accommodation of these in the female's body where they are incubated, promoting better water circulation between the eggs mass and consequently, an increase in oxygenation around the embryos. Moreover, these losses may be caused, partly, by parasites and bacterial or fungal infections (Kuris, 1991). It also should be taken into account, in which development stage the eggs were counted to determine fecundity, since only some studies indicate which stage was considered.

In addition to the previously mentioned factors, variations in estimated fecundity may be associated with female age, with an increase when female becomes mature (Graziani *et al.*, 1993). Particular genetic characteristics of populations, changes in environmental conditions such as temperature and food availability, as well as differences in dimensions of the sampled females (Corey & Reid, 1991; Anger & Moreira, 1998) can also result in fecundity differences.

In *Macrobrachium* spp. there is an intrinsic relationship between fecundity and female size. The number of eggs is highly variable in individuals of the same species, but increases in quantity with female size. Thus, a larger abdomen size implies in a greater accommodation of eggs in pleopods (Valenti, 1984; Silva *et al.*, 2004). This positive correlation was observed in this study and in several others with *M. amazonicum* (Silva *et al.*, 2004; Silva, 2006; Oliveira, 2010; Hayd & Anger, 2013; Meireles *et al.*, 2013). For the latter authors, in crustaceans with similar body shapes fecundity depends mainly on the body size.

The low coefficient of linear regression obtained in this study ($R^2 = 0.40$), may be related to the large variation in fecundity for females with similar sizes. According to Leme (2006), variations in the number of eggs within the same size class are related to the intrinsic state of females at the time of allocating energy to egg production.

When analyzing Figure 5, which relates the egg frequency with their development stages each month, it is possible to observe a great amount of eggs at the initial stage (I) and a slightly smaller amount of these at the intermediate stage (II), occurring almost all over the year. With regard to the eggs at the final stage (III), it is evident that there was a considerable month decrease. We believe stage III is much faster than the others, that is, the larvae develop faster in this phase, not allowing sampling of many eggs in the final stage.

The comparison of egg size in relation to the long and short axes, and the volume among the three development stages, demonstrated a significant increase in egg size during incubation. This situation could be explained by water entrance in the egg. The increase in volume could facilitate the rupture of egg membrane and, hence, larval hatching (Lardies & Wehrmann, 1996). In addition, the water absorption also aid in cell mobility, structural organization and in embryo growth (Green, 1965; Kobayashi & Matsuura, 1995). According to Anderson (1982), the increase in length of the egg reflects the growth of embryonic structures in the cephalic-caudal axis.

Available information about egg size in different populations of *M. amazonicum* are relatively scarce and the egg stages considered for this analysis have been little considered in the literature. Odinetz-Collart & Rabelo (1996) collected *M. amazonicum* ovigerous females in seven locations in the Amazon region with different distances from the ocean and found that the average egg volume increased with distance of the sampling site from the estuary. The average egg volume in the initial stage of this study ($0.12 \pm 0.02 \text{ mm}^3$) is the same as that found by Odinetz-Collart & Rabelo (1996) at Cametá, in the lower Tocantins River (0.1207 mm^3), but it is lower than that found by the same authors at Lake Tefé (0.2188 mm^3). However, the average volume of eggs in the final stage of this study ($0.23 \pm 0.05 \text{ mm}^3$), is in an intermediate size compared to the values found in the same article at Cametá (0.1648 mm^3) and at Guaporé River (0.3272 mm^3).

According to Magalhães & Walker (1988), the size of eggs varies on the basis of the ecological characteristics of the aquatic environment. On the other hand, Meireles *et al.* (2013) pointed out that differences in egg size may be due to specific characteristics of the population in each location. Other studies attribute the variations in egg volumes of decapod shrimps to differences in energy allocation per embryo (Clarke, 1993).

The relationship between the size/volume of eggs with the size of *M. amazonicum* females was discussed in some studies. Meireles *et al.* (2013) studied this correlation in estuarine populations in Pará and limnetic

populations in Mato Grosso do Sul, finding that there was no significant differences between the diameter and the average volume of female eggs of different size classes in the same region. Odinetz-Collart & Rabelo (1996) found that egg volume was independent of the carapace length of females in populations from the Amazon region.

The absence of correlation between the volume and size of eggs in their developmental stages (initial, intermediate and final) with female size (Figs. 6-7) is probably related to egg hatching and larvae emerging from one of the five females, thus leading to a large difference in volume and size when compared to eggs of the other females in the same stage.

The results presented here indicate that the reproductive patterns showed higher similarity to other continental *M. amazonicum* populations than to estuarine ones, confirming the influence of the environment on the reproductive biology of individuals. Despite this, the existing references regarding the studied species include mainly coastal environments. Therefore, this study may subsidize future and necessary researches about life-history, biological and ecological traits referred to populations living in continental waters, that will contribute to a better understand of *M. amazonicum*. In addition, this species stands out by its commercial interest and the expansion of research that consider the differences between populations and that assess their relations with the environmental characteristics is important and have significant implications for aquaculture development.

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