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Research Article

Reproductive variability of the Amazon River prawn, *Macrobrachium amazonicum* (Caridea, Palaemonidae): influence of life cycle on egg production

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ABSTRACT. Diverse reproductive strategies may be adopted by different species of *Macrobrachium* prawns, and even among different populations of the same species. The present study evaluated the influence of differences in the reproductive strategies of two geographically isolated populations of *Macrobachium amazonicum*, upon female fecundity, reproductive output and the chemical content of prawns and eggs. One prawn population from Pará only completes its life cycle in brackish water, whereas another from Mato Grosso do Sul only inhabits freshwater. Pará female prawns exhibited a larger average size and weight and produced more eggs than females from Mato Grosso do Sul. However, the Mato Grosso do Sul population produced eggs that were larger in volume than those of females from the other population. Furthermore, eggs produced by Pará prawns were composed primarily of water (56%), whereas those produced in Mato Grosso do Sul were composed mostly of organic matter (80%). This difference in the eggs' chemical compositions did not apply to the chemical compositions of the females, as individuals from both sites were composed primarily of water. Mato Grosso do Sul females invested a higher amount of energy in brood formation (14% of their wet weight) than individuals from Pará (only 10%). It is possible that *M. amazonicum* populations show a higher degree of plasticity in their reproductive activity due to habitat conditions and genetic differences. Although the brackish population produces larger individuals, and exhibits higher fecundity, the freshwater population exhibited a higher reproductive investment. These results suggest a high reproductive capacity to adapt to different environmental conditions for this species, which should be considered in the context of aquaculture activities.

Keywords: *Macrobrachium amazonicum,* reproductive potential, ecological plasticity, egg production, Brazil.

Variabilidad reproductiva del camarón del río Amazonas, *Macrobrachium amazonicum* (Caridea, Palaemonidae): influencia del ciclo de vida en la fecundidad

RESUMEN. Diversas estrategias reproductivas pueden ser adoptadas por distintas especies de camarones del género *Macrobrachium*, e incluso entre diferentes poblaciones de la misma especie. En el presente estudio se evaluó la influencia de las diferencias en las estrategias reproductivas de dos poblaciones de *Macrobachium amazonicum*, geográficamente aisladas, sobre la fecundidad, rendimiento reproductivo y composición química de los camarones y sus huevos. Una población de camarones de agua dulce de Pará sólo completa su ciclo de vida en agua salobre mientras, que otra de Mato Grosso do Sul sólo habita en aguas dulces. Las hembras de la población de Pará presentaron, en promedio, mayores tamaños y mayor peso y producen más huevos que las hembras de Mato Grosso do Sul. Sin embargo, la población de Mato Grosso do Sul produjo huevos que eran más grandes en volumen que aquellos de las hembras de la otra población. Aún más, los huevos producidos por hembras de la población de Pará contenían mayor cantidad de agua (56%), mientras que aquellos producidos por las hembras de Mato Grosso do Sul se componen sobre todo de materia orgánica (80%). Esta diferencia en la composición química de los huevos no se aplicaba a la composición química de las hembras, ya que individuos de ambos sitios estaban compuestos principalmente de agua. Las hembras de Mato Grosso do Sul invirtieron una mayor cantidad de energía en la puesta (14% de peso húmedo) que las hembras de Pará (solo 10%). Es posible que las poblaciones de *M. amazonicum* muestren un mayor grado de plasticidad en su actividad reproductiva debido a las condiciones del medio y a diferencias genéticas. Aun cuando la población estuarina produce individuos más grandes y presenta mayor fecundidad, la población de agua dulce presenta una inversión reproductiva mayor. Estos resultados sugieren una alta capacidad reproductiva de adaptación a diferentes condiciones ambientales para esta especie, que debe ser considerada en el contexto de las actividades de acuicultura.

Palabras clave: *Macrobrachium amazonicum,* potencial reproductivo, plasticidad ecológica, producción de huevos, Brazil.

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INTRODUCTION

Macrobrachium Spence Bate, 1868 is one of the best examples of a widespread crustacean genus that is distributed globally throughout tropical and subtropical waters. Over 240 species are recognized worldwide (Wowor *et al*., 2009; De Grave & Fransen, 2011); its greatest diversity occurs in the Indo-Pacific region, and the Americas support more than 55 species, of which 17 occur in Brazil (Mantelatto *et al*., 2008; Pileggi & Mantelatto, 2010 and 2012).

The Amazon River prawn, *Macrobrachium amazonicum* (Heller, 1862), is endemic to South America, with a wide geographic distribution: it inhabits inland and coastal waters of different salinities (Vergamini *et al*., 2011) that flow into the Atlantic Ocean (Holthuis, 1952). It is known to inhabit the Amazon and Orinoco river basins and the rivers between them (Holthuis, 1952; Odinetz-Collart & Rabelo, 1996), as well as rivers and estuaries in Venezuela, Colombia, Suriname, Guyana, Peru, Bolivia, the northern and northeastern coasts of Brazil, Paraguay and Argentina (Davant, 1963; Bialetzki *et al*., 1997; Holthuis, 1952; Melo, 2003; Valencia & Campos, 2007; Vergamini *et al*., 2011; Pileggi *et al*., 2013).

The species has a high potential for aquaculture (Kutty *et al*., 2000; New, 2005), reaching large sizes (up to 16 cm and 30 g) and having a firm-textured meat, resulting in a high degree of acceptance by consumer markets (Moraes-Riodades & Valenti, 2001; Moraes-Valenti & Valenti, 2010). Moreover, the species has a continuous reproductive pattern (Romero, 1982; Odinetz-Collart, 1991; Melo, 2003), rapid development and high survival rate throughout larval development from hatching to the appearance of the first juvenile shrimp, may also be considered beneficial for cultivation in large systems (Anger *et al*., 2009). Although the life cycle of *M. amazonicum* is still under investigation, variability has been noted in recent years among populations inhabiting different geographical regions (for review see Maciel & Valenti, 2009; Pantaleão *et al*., 2011; Vergamini *et al*., 2011).

Different reproductive strategies have previously been observed in the *Macrobrachium* group. Although many of the members of this genus have successfully colonized fresh water, not all of these species have become able to reproduce independently from salt water. Inland species usually have abbreviated larval development -ALD (two to three zoeal stages)-, larger larvae that inhabit benthic habitat with low dispersion pattern, low fertility (tens to hundreds of large size eggs), and adults of smaller size. On the other hand, the coastal/estuarine species have high fertility, relatively small egg size, extended larval development -ELD (12 to 13 zoeal stages)- with small-sized planktonic larvae, and adults of medium to large sizes (Kiyohara, 2006; Bauer, 2011).

The members of the genus *Macrobrachium* can be divided into three types according to their life cycle: the first type exhibits ELD that depends on marine access; the second includes species such as *M. amazonicum* with distributions that include both inland and coastal waters, whose larval development is more or less extended; and the third type includes species with ALD that are independent of marine influence, and are restricted to inland waters (Williamson, 1973; Magalhães & Walker, 1988; Bueno & Rodrigues, 1995; Alekhnovich & Kulesh, 2001). In all three types a number of costs/ disadvantages and benefits/advantages can be cited in terms of reproduction (for review see Bauer, 2011).

The number and size of eggs and the egg production rate may be characteristic of a species and plays a significant role in the life history and ecology of the species (Yoshino *et al*., 2002). However, such characteristics may also vary according to a female's age and size and also according to environmental factors (for review see Sastry, 1983). In this context, Anger & Moreira (1998) found significant differences in the amount of reproductive energy invested by carideans from fresh water and from salt water.

The volume of eggs produced by crustacean species may exhibit a general pattern of specific variation, with volume decreasing from cold waters toward warmer waters, over a north-south latitudinal gradient, and from deep water to shallow water (Sastry, 1983). In this context, recently fertilized eggs may reflect various selection pressures, sometimes opposing one another, that influence reproductive investment and larval development (Bauer, 1991).

Egg size has various interrelated ecological implications that may influence the following: 1) size of the species at sexual maturity, 2) timing of juveniles release, 3) number of egg masses produced per unit of time, 4) number of eggs per clutch, 5) stage of development, and 6) juvenile's size when released into the environment (for review see Scaico, 1992). Moreover, large eggs produce large newly hatched juveniles, whose survival ability is generally correlated with their size (Thorson, 1950), since more yolk reserves for the lecithotrophic non-feeding larva in ALD species allow subsisting during larval development.

Thus, considering this scenario with respect to an intriguing target species, the aim of this study was to evaluate the effects of the adoption of different reproductive strategies by inland and coastal *M. amazonicum* populations comparing and characterizing their reproductive potential through fertility studies, the chemical compositions of females and eggs, and reproductive output (RO).

MATERIALS AND METHODS

The study was conducted in the Crustacean Sector of the Aquaculture Center (CAUNESP) at the São Paulo State University, Jaboticabal. *Macrobrachium amazonicum* specimens were obtained from two different populations: one inhabiting a body of water close to the estuary, in northeastern Pará (Furo das Marinhas, Santa Barbara region; salinity = 0-14 ppt), and the other, a fully limnetic population from Mato Grosso do Sul (Aquidauana; salinity = 0 ppt), both in Brazilian territory. The population from Pará was raised in grow-out ponds in Jaboticabal. All females were sized with a caliper (precision: 0.1 mm), on the basis of total length (TL: the distance between the tip of the rostrum and the distal tip of the telson with the animal stretched out) and carapace length (CL: the distance between the posterior margin of the right orbit and the midpoint of the posterior margin of the carapace). The rostrum of some specimens was broken, so the carapace length (CL) was preferred in the majority of the analyses.

The developing embryos of ovigerous females were classified according to the criteria proposed by Mantelatto & Garcia (1999), and modified from Boolootian *et al*. (1959): the Initial Stage, when eyes of larvae are not visible, and eggs mostly filled with yolk; Intermediate Stage, when eyes become visible, beginning of pigmentation and segmentation of the larvae; and Final Stage, when the zoea becomes visible. For the fecundity analysis, only the females with embryos at the initial stage were selected to avoid brood egg loss during incubation (Torati & Mantelatto, 2008) (N = 20 individuals from each population).

The eggs were carefully removed from the pleopods and counted under a light stereomicroscope. The average volume (mm^3) of an egg was calculated from random subsamples of 15 eggs per female, using the formula $1/6\ \pi\ I^3$ (Jones & Simons, 1983), where the parameter "I" stands for the mean of two diameters (longest and shortest), including the chorionic membrane adhering to the embryonic surface. The minimum and maximum diameters of each egg were measured under a stereomicroscope equipped with a camera lucida.

The wet weights of all egg masses were determined to the nearest 1 µg. Eggs were separated from the females, washed, and interstitial water removed by capillary action onto filter paper. The eggs were first dried to a constant dry weight at 50ºC for 24 h and then combusted for 4 h at 500ºC to obtain ash-free dry weights. The content of organic material was estimated by subtracting ash weight from dry weight. Females were treated similarly, except that they were dried and combusted as above for 48 and 12 h respectively (Lardies & Wehrtmann, 1996). The reproductive output index (RO: weight of the total egg mass from a female divided by the weight of that female) was calculated for wet and dry weight for females with eggs at the initial stage, according to Clarke *et al*. (1991).

Statistical analyses were carried out using ANOVA on ranks test to compare the individual sizes and reproductive outputs of different populations. The level of significance was $P < 0.05$ (Zar, 1996). Voucher specimens were deposited at the Crustacean Collection of the Biology Department of FFCLRP, University of São Paulo, Brazil (CCDB/FFCLRP/USP, accession numbers: 1955-1962, 1970, 1971, 2119).

RESULTS

Mean size of *M. amazonicum* collected from Pará and Mato Grosso do Sul (MGS) was 86.9 ± 21.7, 48.8 ±

7.4 mm TL and 19.4 ± 4.8 mm and 8.6 ± 1.6 mm CL, respectively. The ovigerous females varied significantly in size between the areas of study, with larger individuals (*P* < 0.05) collected in Pará (CL = 17.2 ± 1.6 mm; (MGS): CL = 9.9 ± 0.4 mm).

Mean number of eggs per female from Pará was 2237 ± 586 in the initial stage whereas those from (MGS) carried significantly fewer eggs (mean = 271 ± 54) (*P* < 0.05). The eggs of females from both areas were slightly oval, with mean diameter and volume of 0.67 ± 0.04 mm and 0.16 ± 0.03 mm^3 in (MGS), and 0.63 ± 0.06 mm 0.13 ± 0.04 mm^3 in Pará, respectively. Eggs taken from females from (MGS) were significantly larger in diameter and volume than those collected from females from Pará (*P* < 0.05).

Despite the tendency towards an increase in fertility with body size observed in females from Pará, this relationship was not statistically significant (*P* > 0.05) for most size classes. Furthermore, such a tendency was not observed in females collected from (MGS). There was no significant difference (*P* > 0.05) between mean egg diameter and volume of females belonging to different size classes from the same region (Table 1).

The relationships among female size (CL), the average size of each egg and the total egg mass presented an interesting pattern: females from Pará produced larger egg masses with lower egg sizes, whereas in (MGS) the reverse pattern was found, with lower numbers of large volume eggs (Fig. 1).

Regression analysis between dimensions of ovigerous females (CL, WW: wet weight and DW: dry weight) and the number of eggs in early stage of development indicated a significant correlation (*P* < 0.05) only between the size (CL), weight (WW) and fecundity (FEC) of females collected in Pará (Fig. 2).

Females from Pará (WW = 3.36 ± 0.52 g; DW = 1.05 ± 0.18 g) were significantly heavier than those from (MGS) (WW = 0.51 ± 0.10 g; DW = 0.11 ± 0.02 g) (*P* < 0.05). There were also significant differences (*P* < 0.05) in the amount of water, ash and organic matter contents between the females from the two areas studied, with higher values found for females from Pará (Table 2). Despite the difference in weight found between the females from the different study areas, water was the primary body component in both places, representing an average of 68.8% and 78.0% of the body wet weight of females from Pará and (MGS), respectively. Inorganic compounds represented, on the average, 6.7% and 4.6% of females' wet weight from Pará and (MGS), respectively. The average organic content represented 24.5% of females' wet weight from Pará and 17.3% of females from (MGS).

Mean weight of egg mass differed significantly between the two sampling locations (*P* < 0.05). This corroborates the difference found in female fecundity between these localities and could be related to the difference in average wet weight of each individual egg, since females from Pará carried greater number of heavier eggs (Pará = 0.13 ± 0.05 mg; MGS = 0.07 ± $2x10^{-5}$ mg) (*P* < x|0.05).

Eggs also exhibited differences in their chemical composition: those from Pará were primarily composed of water (55.95%), whereas those from Mato Grosso do Sul were primarily composed of organic matter (80.29%). The only similarity between the eggs from both localities was their low percentage of ash (Table 3).

Ovigerous females from Pará invested in egg production, on the average, 7.8% (0.08 ± 0.02) of their wet weight and 10.3% (0.10 ± 0.02) of their dry weight, whereas in (MGS), the same investments were 3.4% (0.03 ± 0.01) and 14.5% (0.14 ± 0.06), respectively. Despite the difference described above, no investment difference was found between females of different sizes from the same population.

DISCUSSION

The reproductive features of *Macrobrachium amazonicum* varies between inland and coastal populations. Individuals of *M. amazonicum* from Pará and Mato Grosso do Sul exhibited a greater size variation. This pattern has also been observed in other *M. amazonicum* populations, whose total length could vary from 35 mm (Scaico, 1992) to over 100 mm (Guest, 1979; Romero, 1982; Pantaleão *et al*., 2011). This size variation is similar to that described for different *M. olfersii* populations (Ammar *et al*., 2001), and might suggest a high degree of plasticity in these species, showing high adaptability to different environmental conditions. Such variations between different populations may be attributed to differences in water flow (Odinetz-Collart & Moreira, 1993) or latitudinal differences (Mashiko, 1983; Bauer, 1992; Gorny *et al.,* 1992; Wehrtmann & Andrade, 1998). However, we attribute such differences primarily to the hydro-geographical particularities of each location that directly influence the life history of each population, because both populations inhabited areas with similar water flow.

Accurate information regarding egg production is of primary importance for the management of

Table 1. Variation in the fecundity, diameter (mm) and volume (mm^3) of *Macrobrachium amazonicum* eggs, according to size classes of ovigerous females (PA: Pará, MS: Mato Grosso do Sul, N: number of ovigerous females analyzed, min/max: minimum and maximum values, $\bar{X}$: average, SD: standard deviation).

Locality	Size Class	N	Fecundity min.	Fecundity max.	Fecundity $\bar{X} \pm$ SD	Egg diameter (mm) min.	Egg diameter (mm) max.	Egg diameter (mm) $\bar{X} \pm$ SD	Volume (mm^3) min.	Volume (mm^3) max.	Volume (mm^3) $\bar{X} \pm$ SD
	11.6 - 13.4	01	-	-	1743	-	-	0.65	-	-	0.14
	13.4 - 15.2	0	-	-		-	-				-
	15.2 - 17.0	06	1341	2372	1814 ± 417.8	0.58	0.69	0.65 ± 0.04	0.10	0.18	0.15 ± 0.03
PA	17.0 - 18.8	11	1362	2956	2444.9 ± 542.3	0.56	0.67	0.61 ± 0.04	0.09	0.16	0.12 ± 0.03
	18.8 - 20.6	01	-	-	2989	-	-	-	-	-	-
	Total	19	1341	2956	2237 ± 585.6	0.56	0.69	0.63 ± 0.06	0.09	0.18	0.13 ± 0.04
	9.2 - 9.8	06	159	300	237.2 ± 50.6	0.64	0.71	0.67 ± 0.03	0.14	0.19	0,16 ± 0.02
MS	9.8 - 10.4	12	170	377	270.9 ± 58.4	0.63	0.72	0.67 ± 0.03	0.13	0.19	0,16 ± 0.02
	10.4 - 11.0	02	261	328	294.5 ± 47.4	0.66	0.67	0.67	0.15	0.26	0.205 ± 0.08
	Total	20	159	377	270.6 ± 54.5	0.63	0.72	0.67 ± 0.04	0.13	0.26	0.16 ± 0.03

commercial species (Caddy, 1989). In the present study, differences were found between the two populations regarding the size of females and the number of eggs. Mean fertility of females from Pará was significantly higher than that observed for females from Mato Grosso do Sul. The female's body size limits eggs production in several crustacean species, including caridean shrimps (Bauer, 1991). Furthermore, our data indicates that female size can also limit fertility in *M. amazonicum* populations, since females from Pará are larger than those from Mato Grosso do Sul and produced a higher number of eggs.

The fecundity of *M. amazonicum* varies widely, reaching more than 7,200 eggs per clutch (Ribeiro *et al*., 2012). However, other studies have reported much lower values (Coelho *et al*., 1982: fecundity = 6,000 eggs; Silva *et al*., 2004: maximum fecundity = 2,193 eggs; Lobão *et al*., 1986: fecundity = 1,344 eggs; Gamba, 1984: fecundity = 1,000 eggs; Scaico, 1992: mean fecundity = 595 eggs). This variation is most likely due to environmental influences and evolutionary characteristics of each population. Notably, mean fertility of females from Mato Grosso do Sul was the lowest reported for *M. amazonicum* so far.

The fecundity described for *M. amazonicum* in the present study is much lower than that observed in other species of commercial interest such as *M. acanthurus* (Wiegmann, 1836) (mean fecundity 18,000 eggs) (Valenti *et al*., 1986, 1989), *M. carcinus* (Linnaeus, 1758), and *M. rosenbergii* (De Man, 1879) (between 80,000 and 100,000 eggs) (Silva *et al*., 2004; Lara & Wehrtmann, 2009). However, despite its low fecundity, *M. amazonicum* exhibits other advantages that could make it eligible for aquaculture, such as monthly spawns, high rates of spawning and larval survival and the production of omnivorous larvae (Guest, 1979; Magalhães, 1985; Scaico, 1992; Araujo & Valenti, 2007).

Significant correlations between carapace length, wet weight and fecundity were only found in females of *M. amazonicum* from Pará. A similar correlation pattern has been found for other *Macrobrachium* species (Bond & Buckup, 1982; Lobão *et al*., 1986; Mashiko, 1990; Mossolin & Bueno, 2002; Tamburus *et al*., 2012). The lack of significant correlations, between female size and fecundity, that was found for the Mato Grosso do Sul population, has also been

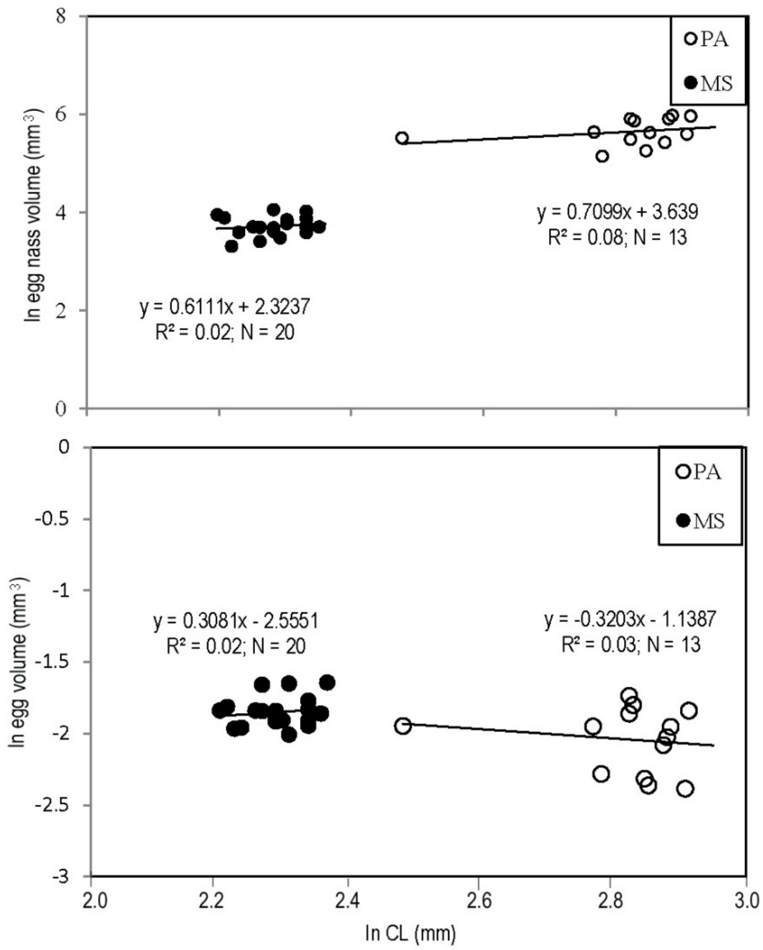

Figure 1. Relationship between the average egg volume and mass and the size of females (CL) from Pará (PA: ○) and Mato Grosso do Sul. (MS: ●), R^2: coefficient of determination, N: number of individuals.

found for other palaemonid species with abbreviated larval development (Mantel & Dudgeon, 2005).

In pleocyemate decapod crustaceans, large eggs appear to be associated with continental species, whereas small eggs are usually produced by brackish water species (Magalhães & Walker, 1988; Odinetz-Collart & Magalhães, 1994). This pattern might explain the results found in the present study, since individuals of *M. amazonicum* from Pará, a brackish water population, spawned smaller-sized eggs than females from Mato Grosso do Sul, inhabitants of freshwater. A similar pattern was described for *M. nipponense*, where larger eggs (0.10 mm^3) were found in freshwater lakes and rivers populations, whereas smaller eggs (0.05 mm^3) were found in estuarine populations (0.06-0.09 mm^3) (Mashiko, 1992; Mashiko & Numachi, 1993).

Egg volumes of both *M. amazonicum* populations studied here (Pará: 0.13 ± 0.04 mm^3 and Mato Grosso do Sul: 0.16 ± 0.03 mm^3) were of intermediate size compared to the values found by Odinetz-Collart & Rabelo (1996) for the same species, collected in two other regions (Low Tocantins: 0.12 mm^3; Tefé: 0.22 mm^3). This difference in egg size might be due to specific population characteristics for each locality, with an average egg size increase with an increasing distance from the sea (Odinetz-Collart & Rabelo, 1996). Analyses of egg production indicate that smaller species invest more resources in reproduction than larger ones by reducing the volume and increasing the number of produced eggs (Hines, 1982). In the present study, females from Mato Grosso do Sul invested more energy in reproduction without reducing the volume of eggs to promote fertility. This pattern is the result of a high energy investment per egg, producing fewer spawns but juveniles that are more capable of surviving. Differences in biomass and chemical composition of newly hatched larvae of *M. amazonicum* populations from the Amazon and from the Pantanal regions were recently reported (Urzúa &

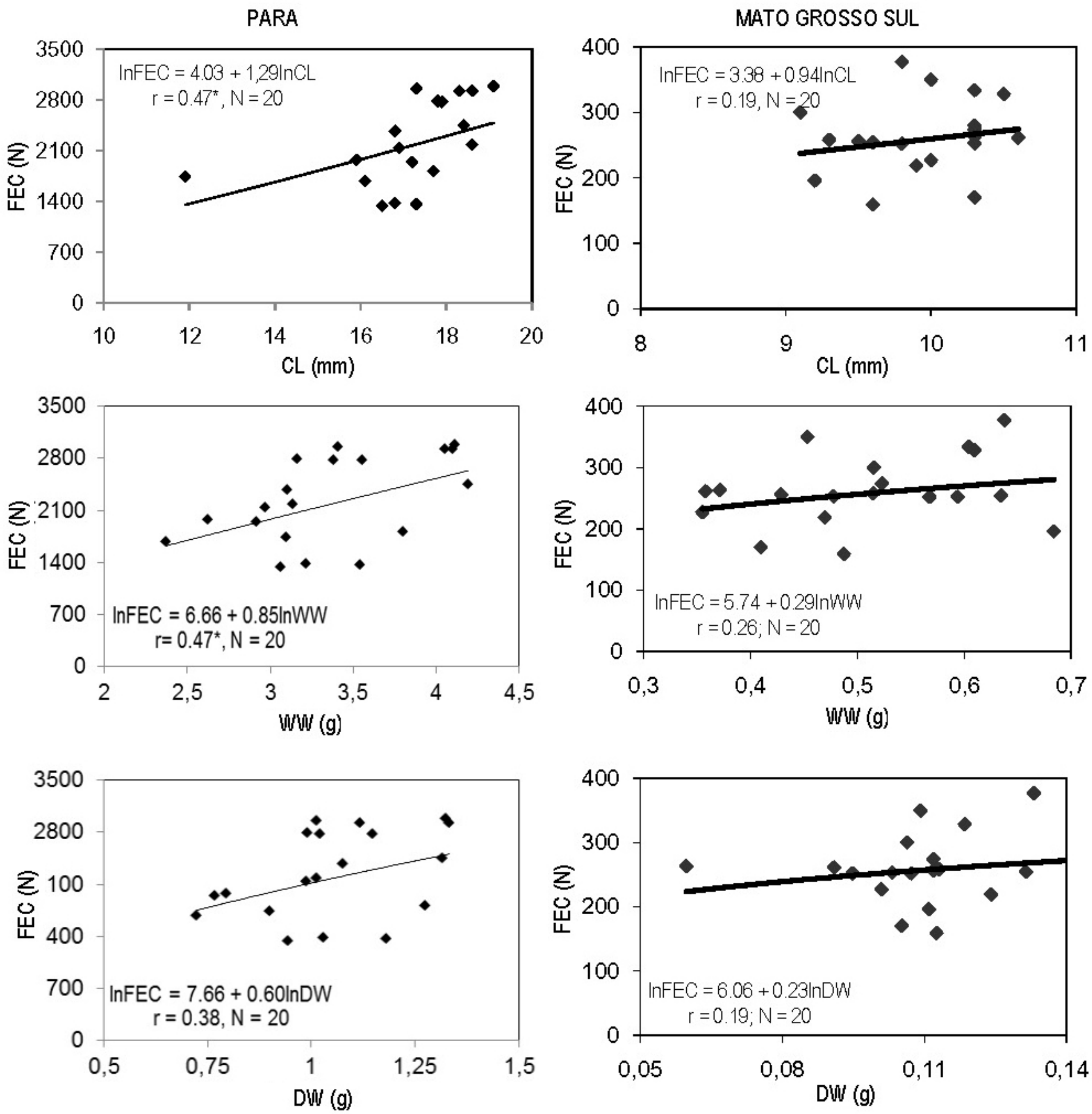

Figure. 2. Correlation and regression analysis between fecundity (FEC) and female size of *Macrobrachium amazonicum* (CL: carapace length, WW: wet weight, DW: dry weight), (PA: Pará, MS: Mato Grosso do Sul), (r: correlation coefficient, N: number of individuals, * significant correlation).

Anker, 2011), corroborating an intimating relationship between egg and larvae.

The adoption of different reproductive strategies may be observed in many *Macrobrachium* species: some carry a great number of small eggs [*Macrobrachium olfersi* (Corey & Reid, 1991); *M. acanthurus* and *M. carcinus* (Müller *et al*., 1999)], whereas others carry fewer but larger eggs [*M. borelli* (Pereira & Garcia, 1995); *M. potiuna* (Müller & Carpes, 1991), *M. nipponense* (Mashiko, 1990), *M. nattereri* (Heller, 1862) (Magalhães & Walker, 1988)]. Our data demonstrated that both strategies were adopted by *M. amazonicum* populations: those from Pará produced many eggs of a smaller size; whereas females from Mato Grosso do Sul produced fewer and larger eggs. The variation in female size and egg volume described above for *M. amazonicum* populations are similar to the pattern described for *M. nipponense* and may be attributed to hydro-geographical site features (Mashiko, 1990, 1992).

The egg diameter is the primary factor responsible for the variation in fertility among same-size

Table 2. Chemical composition (weight and percentage) of *Macrobrachium amazonicum* females from Pará (PA) and Mato Grosso do Sul (MS) ($\overline{X}$: average, SD: standard deviation, min: minimum value, max: maximum value).

Females	PA	MS
	$\overline{X}$ ± SD (min – max)	$\overline{X}$ ± SD (min – max)
Wet weight (g)	3.36 ± 0.52 (2.37 - 4.19)	0.51 ± 0.10 (0.35 - 0.68)
Dry weight (g)	1.05 ± 0.18 (0.72 - 1.33)	0.11 ± 0.02 (0.06 - 0.15)
Water content (g)	2.31 ± 0.35 (1.65 - 2.94)	0.40 ± 0.09 (0.25 - 0.57)
Water content (%)	68.78 ± 2.09 (65.33 - 73.72)	78.04 ± 3.65 (71.58 - 84.03)
Organic matter (g)	0.83 ± 0.22 (0.17 - 1.11)	0.09 ± 0.02 (0.04 -0.12)
Organic matter (%)	24.53 ± 4.87 (5.89 - 28.54)	17.32 ± 3.33 (9.58 - 21.08)
Ash content (g)	0.22 ± 0.14 (0.13 - 0.81)	0.02 ± 0.01 (0.009 - 0.03)
Ash content (%)	6.68 ± 2.09 (65.33 - 73.72)	4.64 ± 1.40 (1.75 - 7.41)

individuals (Hines, 1982) and may vary according to genetic characteristics (Valenti *et al*., 1989). In general, large-egg species have relatively low individual fecundity when compared to small-egg species (Ammar *et al*., 2001). This pattern might explain the difference found in this study since females from Pará produced more eggs of smaller size compared to those produced by females from Mato Grosso do Sul, which attained smaller body size, thereby restricting the available abdomen space to accommodate eggs. The genus *Macrobrachium* probably emerged from a marine habitat and is still adapting to freshwater environment (Tiwari, 1955). This process of adaptation may result in an increase in egg size and a subsequent decrease in egg mass, which are general steps known to occur in that evolutionary change (Rodríguez, 1982; Magalhães & Walker, 1988).

Some studies attribute differences in egg volume of decapod prawn to a real difference in the energy allocation per embryo (Clarke, 1993). In this sense, large eggs would produce large juveniles with greater survival ability (Steele & Steele, 1975). Although this statement may be applied to populations of *M. amazonicum*, it will not always be true, because it is possible that larger eggs are composed of a greater proportion of water rather than organic matter, which is the primary source of metabolic energy for embryos (Pandian, 1970).

Water is also necessary for embryo development, assisting in 1) the flotation process, 2) control of internal egg temperature, and 3) rupture of the membrane at hatch time (Pandian, 1970). However, water has little importance in terms of the embryo's growth and development rates. Thus, we suggest that both chemical composition and reproductive investment should be investigated when making inferences about spawning energy allocation.

Estuarine species generally spawn a large number of small eggs because the salt concentration in the environment reduces the amount of water in the eggs due to osmotic processes (Hancock, 1998). This existing knowledge is based only on observations of egg size, with no data on chemical composition. However, the eggs produced by females from Pará were of small size but had a proportionately larger amount of water than those from Mato Grosso do Sul. This pattern might be attributable to differences in egg membrane permeability (for review see Pandian, 1970), which allows marine or brackish water species to spawn eggs composed primarily of water without the risk of desiccation in different decapods groups

Table 3. Chemical composition (weight and percentage) of the egg masses spawned by females of *Macrobrachium amazonicum* from Pará (PA) and Mato Grosso do Sul (MS) ($\overline{X}$: average, SD: standard deviation, min: minimum value, max: maximum value).

Eggs	PA	MS
	$\overline{X}$ ± SD (min – max)	$\overline{X}$ ± SD (min – max)
Wet weight (mg)	287.35 ± 0.10 (130.77 - 436.10)	17.44 ± 0.01 (1.98 - 26.63)
Dry weight (mg)	120.90 ± 0.03 (68.99 - 160.80)	15.44 ± 0.01 (1.86 - 23.27)
Water Content (mg)	166.45 ± 0.07 (43.50 - 276.90)	1.90 ± 0.01 (0.12 - 6.52)
Water Content (%)	55.95 ± 9.13 (33.26 - 64.52)	10.97 ± 7.90 (4.99 - 40.70)
Organic matter (mg)	116.42 ± 0.03 (64.69 - 153.20)	14.15 ± 0.01 (1.26 - 21.87)
Organic matter (%)	42.43 ± 9.08 (34.03 - 64.75)	80.29 ± 9.06 (53.67 - 91.22)
Ash content (mg)	4.48 ± 0.01 (2.60 - 7.60)	1.43 ± 0.01 (0.60 - 2.10)
Ash content (%)	1.62 ± 0.44 (0.82 - 2.44)	9.76 ± 6.16 (3.64 - 30.33)

[Anomura: Lardies & Wehrtmann (1996); Torati & Mantelatto (2008); Astacidea: Pandian (1970); Brachyura: Gardner (2001); Caridae: Pandian (1967) *apud* Pandian (1970); Lardies & Wehrtmann (1997), among others]. The production of large eggs in high salinity environments may be due to differences between internal and external osmolarity that generate differences in the process of water intake by the egg (see Giménez & Anger, 2001). Moreover, large-egg species generally hatch large larvae with a shorter period of larval development and more rapid larval growth (Hancock, 1998). Thus, producing large eggs could be an ecological strategy, to compensate for the low fertility found in the *M. amazonicum* population from Mato Grosso do Sul.

The reproductive output of *M. amazonicum* varied between study populations. Higher values were found for females from Pará when wet weight was analyzed. On the other hand, higher values were found for females from Mato Grosso do Sul when the dry weight was analyzed. The values of reproductive ouput (RO) found for *M. amazonicum* were similar to those found for *M. hainanense* (RO = 0.11, Mantel & Dudgeon, 2005), *M. nipponense* (RO = 0.06-0.12; Mashiko, 1983), and *M. carcinus* (RO = 0.04-0.21; Lara & Wehrtmann, 2009) and lower than those found for other species of caridean shrimps (*Chorismus antarticus* = 0.171 ± 0.003; *Crangon crangon* = 0.165 ± 0.004; *Notocrangon antarcticus* = 0.118 ± 0.001; *Pandalus montagui* = 0.243 ± 0.006) (Clarke, 1985). Several studies have analyzed wet weight as a proxy for the reproductive output of a species (Clarke, 1985; Galeotti *et al*., 2006). Other studies have used both dry weight and wet weight to estimate this parameter (Pinheiro & Terceiro, 2000; Miranda *et al*., 2006; Torati & Mantelatto, 2008). However, according to the results described here, we suggest the use of dry weight to provide a more accurate estimate of the amount of energy invested in reproduction, since weight or volume of the egg mass may be influenced by the amount of water in the eggs, which is quite variable between different populations of the same species.

The higher investment of reproductive energy made by females from Mato Grosso do Sul is probably a way to compensate for the low fertility observed in this population. We speculate that larvae of this population probably do not have an adequate nutritional source, so they are endowed with food (yolk) to help them subsist during larval development.

Moreover, females from Pará compensate for the low energy invested in reproduction by producing a higher number of eggs in each spawn. Thus, both populations, independently and according to environmental conditions, have methods for maintaining high population fitness through efficient but different reproductive strategies. This reproductive flexibility observed in *M. amazonicum* populations is most likely the primary explanation for the success of this species in the colonization of a variety of environments over a wide geographical scale in South America (Odinetz-Collart, 1991). In addition, the significant intraspecific genetic variability among Brazilian populations reinforces this potentiality for environmental adaptation (Vergamini *et al*., 2011).

Based on the data presented here, we can affirm that *M. amazonicum* populations exhibit a high degree of plasticity in terms of reproductive activity. The coastal population produced significantly larger individuals, a higher total egg biomass and higher fecundity despite their low reproductive output, whereas the inland population produced smaller individuals and exhibited a lower fecundity. Because *M. amazonicum* is a species of commercial interest, such differences may be important in the selection of a population for aquaculture purposes.

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