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The influence of environmental variables in the reproductive performance of *Macrobrachium amazonicum* (Heller, 1862) (Caridea: Palaemonidae) females in a continental population

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ABSTRACT

Macrobrachium amazonicum is a commercially important freshwater prawn with a high degree of reproductive plasticity. The species is classified into two groups: coastal populations, with larger individuals exhibiting high fecundity and needing brackish water for larval development; and continental populations, with smaller specimens exhibiting low fecundities and completing metamorphosis in freshwater. The objective of this study was to investigate the influence of environmental factors in the fecundity, egg size and volume, and reproductive output in females of *M. amazonicum* from a continental population during a two-year period. We also compared our results with those obtained for other continental and coastal populations. Reproductive parameters differed markedly between continental and coastal populations in most cases. The continental population studied here, however, exhibited reproductive characteristics similar to those of coastal populations. The present study found a correlation between the reproductive parameters and the environmental variables analyzed. This result corroborates the hypothesis that wide variation in reproductive parameters in the geographical distribution of *M. amazonicum* is related to the environmental characteristics in which populations are inserted. We suggest that further studies could investigate the potential of continental populations for aquaculture, which could significantly reduce production costs.

Key words: Amazon river prawn, shrimp, Tietê, abiotic factors, reproductive output.

INTRODUCTION

Reproduction is one of the most important life history events of all organisms (Yoshino et al. 2002). For crustaceans, the number and size of eggs, together with reproductive output, are important variables with several ecological implications, such as in size of newly hatched larvae; in size of sexual maturity; number of egg masses produced and whether the brood mass is partitioned into many small or few large eggs (Hines 1982, Scaico 1992, Meireles et al. 2013).

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The Amazon River prawn *Macrobrachium amazonicum* (Heller, 1862) is widely distributed in South America, from Venezuela to Argentina; it inhabits lacustrine, flood-plain, and lotic environments in tropical and subtropical flatlands (Maciel and Valenti 2009). The species is present in all main eastern river basins (Orinoco, Amazon, Araguaia-Tocantins and São Francisco), including isolated inland populations from the upper Paraná and Paraguay River Systems (Maciel and Valenti 2009, Pantaleão et al. 2012, 2014). In general, *M. amazonicum* breeds throughout the year, with reproductive peaks during the rainy season (Maciel and Valenti 2009).

Macrobrachium amazonicum can be classified into two distinct groups (Moraes-Valenti and Valenti 2010): coastal populations, which inhabit rivers close to estuarine waters; and continental populations, which live in rivers, lakes and other water bodies in inland areas of South America. Coastal populations are large (100–160 mm of total length), exhibit high fecundity (thousands of eggs), need brackish water for larval development and males can develop into four morphotypes; continental populations are smaller (~50 mm of total length), exhibit low fecundity (hundreds of eggs) and complete metamorphosis in freshwater (Moraes-Valenti and Valenti 2010).

Global temperature and precipitation patterns have changed and are predicted to change even more due to anthropogenically driven climate change (Meehl et al. 2007, Jeppesen et al. 2015). Climate change may influence reproductive performance in crustaceans because their patterns of life history are influenced by environmental conditions (Costa and Negreiros-Fransozo 1998). Environmental factors can have an effect on the reproductive parameters of *M. amazonicum*, and the variation previously observed seems to be related to the species' wide geographical distribution (e.g. Maciel and Valenti 2009, Meireles et al. 2013). For instance, the egg size in each brood varies according to the distance of the breeding site from the sea, and a progressive divergence of the continental and coastal populations had been suggested (Odinetz-Collart and Rabelo 1996, Maciel and Valenti 2009). These conclusions were made by comparing the results obtained for different regions and different populations (coastal and continental). However, no study has yet investigated the effects of the variation of environmental factors on the same population.

Macrobrachium amazonicum is the freshwater decapod of greatest economic importance in the Eastern South American subcontinent (Maciel and Valenti 2009). To date, the studied population represents the only exception for continental populations in which all four male morphotypes were found (Pantaleão et al. 2014), indicating that continental specimens can reach body sizes similar to those of coastal populations. In this context, the knowledge on the intraspecific variations that allow this species to complete its life cycle both in estuarine and continental waters is of great importance for their cultivation. The objective of this study was to investigate how environmental factors influence fecundity, egg size and volume, and reproductive output in females of *M. amazonicum* during a two-year period. We also compared our results with those obtained for other continental and coastal populations.

MATERIALS AND METHODS

ENVIRONMENTAL FACTORS

The water temperature (ºC) and O_2 concentration ($\mu g.L^{-1}$) were obtained monthly with a digital multimeter (Politerm RS-232, São Paulo, Brazil) at the sampling location. Subsurface water samples (approximately 20 cm) were collected in order to measure pH (pH meter) and Chlorophyll-a concentration ($\mu g.L^{-1}$). The proceedings to estimate the Chlorophyll-a concentration followed Golterman et al. (1978). Data on monthly rainfall were obtained from www.climate-data.org.

SAMPLING SITE

The samples were conducted in the lower of the Ibitinga Reservoir on the Tietê River. The dam is located in the municipality of Cambaratiba (24° 44’ 29” S; 49° 01’ 27”W), in the central-western region of the State of São Paulo, Brazil, in the basin of the Paraná River. The collection site was located downstream of the reservoir of Ibitinga Hydroelectric Power Plant, in a lotic environment with a sandy bottom and marginal vegetation consisting of grasses and aquatic macrophytes. The collection site was in a stretch of the Tietê River with great sports fishing activity.

SAMPLING

Females with embryos were sampled monthly from December 2011 to September 2013, during the day, from marginal vegetation and from the river bottom. We used a combination of a 60 x 60 cm^2 sieve (2 mm knot-to-knot mesh size) and a trap similar to a “Matapi” (made of natural fiber), commonly used in the Amazon region in Brazil (see Odinetz-Collart 1993), but made of plastic material (Fig. 1). This trap was chosen in order to avoid a selective sampling, and it was placed near the macrophytes at 1-2 meter deep. The bait used for this sample was crushed corn and fish viscera. The time of each sampling method was 15 minutes for sieve and 30 for the trap. Immediately after sampling, individuals were stored in individual plastic bags with ice to preserve the eggs, and then transported to the Laboratory of Biology of Marine and Freshwater Shrimp (LABCAM) of UNESP, Bauru, São Paulo, where prawns were kept frozen until the analyses.

REPRODUCTIVE PARAMETERS

For each month, 20 females with embryos were haphazardly selected for analyses. When there were fewer than 20 individuals, all of them were measured. Females with embryos had their carapace length (CL) measured as the distance between the orbital angle and the posterior margin of the carapace, with a digital caliper (0.01 mm). Embryos were classified according to the development stage as follows: Stage I, homogeneous color within the egg, no eye pigments visible; Stage II, eye pigments barely visible; Stage III, eyes fully developed (Wehrtmann 1990, García-Guerrero and Hendrickx 2009). Subsequently, ten eggs of each female were cautiously removed from the parental pleon and measured as length (longest axis) and width (shortest axis) under a microscope (Leica ICC50 HD, Wetzlar, Germany), with 100x magnification. The software LAS – Leica Application Suite, version 4.1.0, was used for image acquisition. Afterward, females were immersed in a sodium hypochlorite solution (0.05%) and then the total number of embryos in each female was cautiously extracted with a fine forceps and then counted. Fecundity of each female was calculated (= number of embryos per female). We employed here the concept of realized fecundity (number of eggs attached under the abdomen) according to Anger and Moreira (1998).

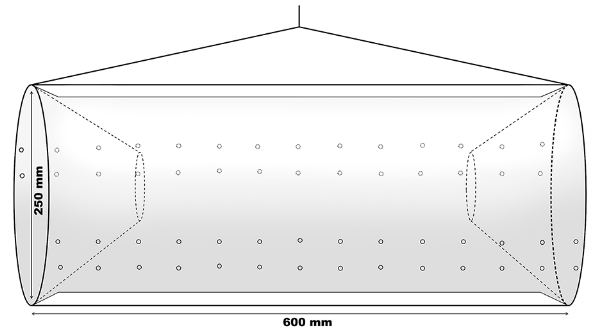

Figure 1 - Representation of the plastic trap used for collections of *Macrobrachium amazonicum* (Heller, 1862) at the studied region.

Egg volume (EV) was calculated as: EV = π * l * h * $(h)^2$; where “l” is length; “h” width in mm and π = 3.14 (Wehrtmann 1990). For estimation of reproductive output (RO), the entire egg mass and females’ bodies were dried in an oven at 60 ºC for 48 hours. RO was calculated by dividing the total dry egg mass by the female dry mass without the eggs, which was determined by an analytic balance (0.0001g precision) (Clarke et al. 1991). Following the recommendations of Zimmermann et al. (2015), RO was estimated only for females carrying early egg developmental stage (ES I), because the weight gain of females during egg incubation might lead to a subestimation of RO when calculating the regression of the egg mass weight on female body weight.

STATISTICAL ANALYSES

Assumptions of normality of distributions and homogeneity of variances were verified through Shapiro–Wilk and Levene's tests, respectively. The significance level for all statistical tests was set at $\alpha = 0.05$.

The seasons (rainy and dry) adopted for the studied location were based on Franchito et al. (2008), where the rainy season is set from October to March, and the dry season from April to September.

Differences in the environmental variables values, CL, EV in each ES and RO for each sampled season (rainy 1, dry 1, rainy 2, dry 2) were compared using ANOVA or the non-parametric equivalent Kruskal-Wallis, followed by the post-hoc Tukey or Dunn (non-parametric) tests (Zar 1999). We ran all the analyses using linearized data (ln) to achieve normality and to the parametric test (ANOVA) be performable. When it was not possible, the equivalent non-parametric test (Kruskal-Wallis) was used. The applied test is indicated for each analyzed feature. The relationships fecundity/CL, EV (in each stage)/CL and RO/CL were assessed with Linear Regressions (Zar 1999). We used the adjusted mean fecundity for correlations (Spearman) with the environmental factors to neutralize the effect of female size on fecundity. This methodology was based on the study of Nicola and Almodóvar (2002).

Linear regressions of log-transformed data (ln) were plotted for the number of eggs and CL. Subsequently, the Analysis of Covariance (ANCOVA; Zar 1999) was applied to determine the relationship between CL (independent variable) and fecundity (dependent variable), using the egg developmental stage (ES) and year seasons as co-variables, to detect possible differences among fecundities in each ES or season.

RESULTS

ENVIRONMENTAL FACTORS

The water temperature ranged from 19.7 to 30 °C (24.38 ± 3.29 °C). Higher values were observed in rainy seasons and there were statistically significant differences between rainy and dry seasons (ANOVA, $p < 0.05$) (Fig. 2).

Monthly rainfall of the studied region ranged from 0 to 332 mm^3 (88.7 ± 88.9 mm^3). There were statistically significant differences among all the sampled seasons (ANOVA, $p < 0.01$) (Fig. 2).

The chlorophyll-a concentration ranged from 0.26 to 51.8 µg/l (8.05 ± 11.82 µg/l). Values increased from the first rainy season compared to the other seasons. There were statistically significant differences among seasons (ANOVA, $p < 0.05$) (Fig. 2).

The O_2 concentration ranged from 3.1 to 8.8 mg/l (6.24 ± 1.96 mg/l). These values increased along the studied period, with statistically significant differences observed among seasons (Kruskal-Wallis, $p < 0.05$) (Fig. 2).

The pH ranged from 6.53 to 8.93 (7.51 ± 0.57) with a significant decrease in the mean values by seasons from the rainy season 1 to rainy season 2 (Kruskal-Wallis, $p < 0.05$) (Fig. 2).

FEMALES WITH EMBRYOS AND FECUNDITY

A total of 248 females with embryos was collected: 138 at egg stage I, 55 at stage II and 55 at stage III. The rainy season 2 was the period with the

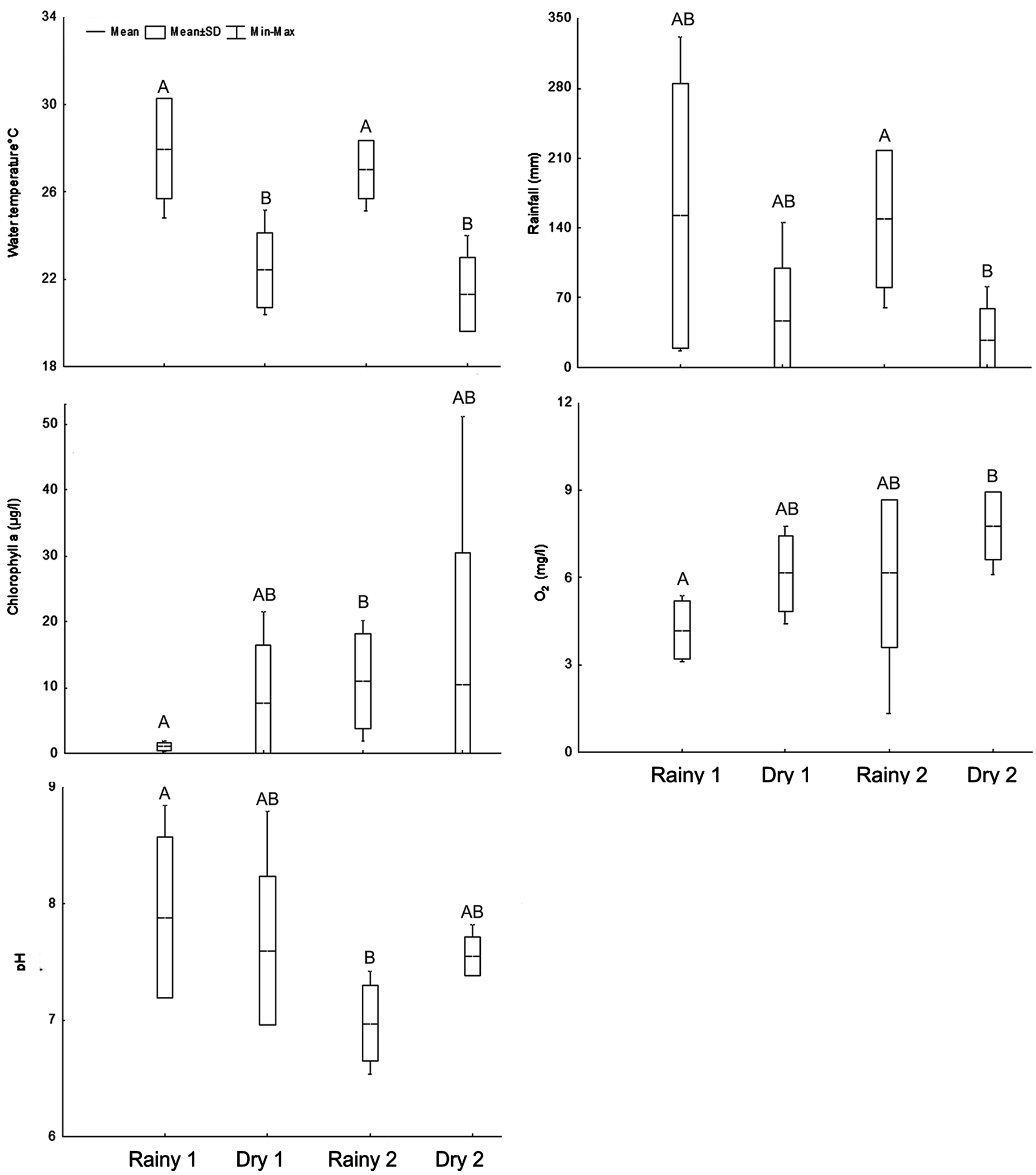

Figure 2 - Mean ± standart deviation, minimum and maximum values of each environmental factor: water temperature, rainfall, chlorophyll-a and O_2 concentration and pH.

highest capture of females (105), while dry season 2 had the lowest capture (31). Complete data about number of females at each ES and season is shown in Table I.

Mean CL was 13.41 ± 2.13 mm and ranged from 8.99 to 22.30 mm. There were no statistically significant differences in the CL of females collected among each sampled season (ANOVA, $p > 0.05$). Fecundity varied from 104 to 4264 eggs (mean 921.21 ± 621.51) (Table I). There was a positive correlation between fecundity and CL (Linear Regression, $p < 0.01$).

The ANCOVA showed no statistically significant differences between the ES for the correlation fecundity/female size (CL) (Table II), so we used data from the pulled three egg stages to compare the fecundity among seasons. Statistically

TABLE I
Fecundity and variation in percentage of females per egg stage (ES) of *Macrobrachium amazonicum* (Heller, 1862), according to size classes of females with embryos analyzed and sampled season. Results expressed by mean ± standard deviation.

Season	Size Class	N	Mean fecundity	Minimum fecundity	Maximum fecundity	ES		
rainy 1	8.9 - | 11.2	14	317 ± 298	104	502	I: 57%	II: 7%	III: 36%
	11.2 - | 13.5	38	503 ± 279	125	1020	I: 53%	II: 34%	III: 13%
	13.5 - | 15.8	14	908 ± 300	275	1350	I: 57%	II: 29%	III: 14%
(n=67)	15.8 - | 18.1	1	1746	-	-	I: 100%	-	-
	18.1 - | 20.4	0	-	-	-	-	-	-
	20.4 - | 22.7	0	-	-	-	-	-	-
dry 1	8.9 - | 11.2	14	343 ± 227	147	521	I: 71%	II: 7%	III: 22%
	11.2 - | 13.5	10	480 ± 275	231	994	I: 50%	II: 10%	III: 40%
	13.5 - | 15.8	3	690 ± 209	584	853	I: 67%	II: 33%	-
(n=31)	15.8 - | 18.1	4	931 ± 367	666	1383	I: 100%	-	-
	18.1 - | 20.4	0	-	-	-	-	-	-
	20.4 - | 22.7	0	-	-	-	-	-	-
rainy 2	8.9 - | 11.2	5	503 ± 384	296	692	I: 60%	II:20%	III:20%
	11.2 - | 13.5	39	914 ± 633	481	2520	I: 56%	II: 28%	III: 15%
	13.5 - | 15.8	46	1435 ± 618	378	2328	I: 46%	II: 24%	III: 30%
(n=105)	15.8 - | 18.1	13	1851 ± 537	571	3136	I: 62%	II: 15%	III: 23%
	18.1 - | 20.4	1	1394	-	-	-	-	III: 100%
	20.4 - | 22.7	1	4264	-	-	-	II: 100%	-
dry 2	8.9 - | 11.2	1	367	-	-	-	-	III: 100%
	11.2 - | 13.5	16	534 ± 687	132	860	I: 50%	II: 31%	III: 19%
	13.5 - | 15.8	13	776 ± 702	421	1248	I: 62%	II: 7%	III: 31%
(n=45)	15.8 - | 18.1	10	1471 ± 691	499	2216	I: 50%	II: 20%	III: 30%
	18.1 - | 20.4	5	2268 ± 753	1370	2894	-	-	-
	20.4 - | 22.7	0	-	-	-	-	-	-

significant differences were found among rainy and dry seasons (Fig. 3).

The fecundity of *M. amazonicum* was negatively correlated with pH (Spearman, $p < 0.05$), i.e., the highest adjusted mean fecundity values were correlated with a decrease in the pH (Table III). There were statistically positive correlations among adjusted mean fecundity and values of water temperature, rainfall and chlorophyll-a concentration (Spearman, $p < 0.05$). There was no statistically significant correlation between O_2 concentration and the adjusted mean fecundity (Spearman, $p > 0.05$) (Table III).

EGG VOLUME (EV) AND REPRODUCTIVE OUTPUT (RO)

A significant increase (Kruskal-Wallis, $p < 0.05$) in the mean EV was observed among ES (ES1 = 0.1604 ± 0.03 mm³; ES2 = 0.1773 ± 0.03; ES3 = 0.2024 ± 0.04) (Table IV), and there was no significant correlation between EV (in each stage) and CL (Linear Regression, $p > 0.05$). There were no statistically significant differences in the EV in each ES among the sampled seasons (ANOVA, $p > 0.05$).

Mean RO was 7.4%, with no significant correlation with CL (Linear Regression, $p > 0.05$).

TABLE II
Results of the Covariance analysis (ANCOVA) of the relationship between female size (CL) and fecundity for *Macrobrachium amazonicum* (Heller, 1862).

Relationship	Factor (Group)	Par. (log)	*F*	*p*
Egg stage	I vs. II	*a*	1.464	0.227
		b	3.244	0.073
	I vs. III	*a*	2.956	0.087
		b	2.560	0.111
	II vs. III	*a*	0.593	0.442
		b	0.032	0.858
Season	Rainy 1 vs. Dry 1	*a*	---	---
		b	6.648	0.011*
	Rainy 1 vs. Rainy 2	*a*	86.675	0.000*
		b	0.196	0.658
	Rainy 1 vs. Dry 2	*a*	0.802	0.372
		b	0.169	0.681
	Rainy 2 vs. Dry 1	*a*	---	---
		b	6.764	0.010*
	Rainy 2 vs. Dry 2	*a*	84.851	0.000*
		b	0.896	0.345
	Dry 1 vs. Dry 2	*a*	---	---
		b	7.500	0.007*

* = statistically significant values.

TABLE III
Test results of Spearman correlations between the adjusted mean fecundity values of *Macrobrachium amazonicum* (Heller, 1862) and the studied environmental factors in Tietê River, State of São Paulo, Brazil.

	Water temperature	Rainfall	Chlorophyll-a	O_2	pH
Correlation coefficient	0.25	0.165	0.406	-0.046	-0.493
p	< 0.001*	0.01*	< 0.001*	0.48	< 0.001*
Number of samples	256	256	256	256	256

* = statistically significant values.

Mean RO in the rainy season 2 was statistically higher than in other seasons (Kruskal-Wallis, $p < 0.05$) (Table IV).

DISCUSSION

The studied population showed statistically significant variation in reproductive performance when exposed to a range of environmental conditions during the studied period. *Macrobrachium amazonicum* showed to be a flexible species, able to handle not only different environments (for review, see Maciel and Valenti 2009), but also fluctuations in environmental parameters into the same river.

The absence of embryo loss during embryo development is not typical in caridean shrimps (Anger and Moreira 1998), although observed in the specimens captured in the present study. Similarly, such absence was also noted for *M. acanthurus* (Wiegmann, 1836) (Tamburus et al. 2012), which was explained as a possible mechanism of parental

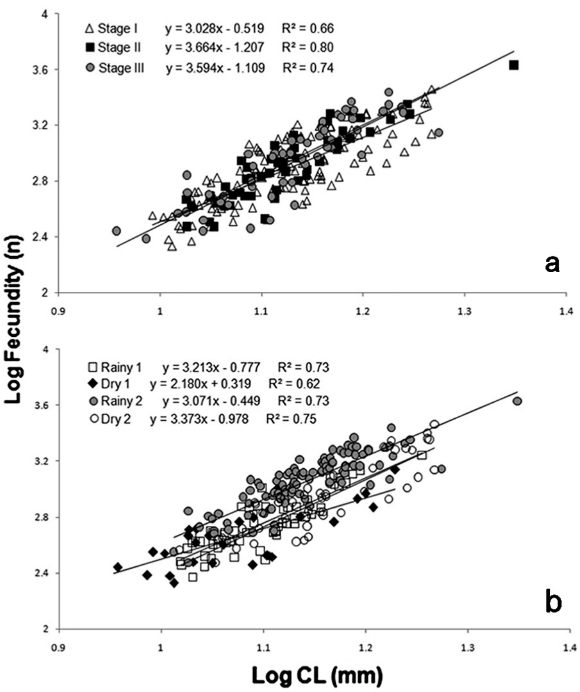

Figure 3 - Correlation between female size (CL) and fecundity of *Macrobrachium amazonicum* (Heller, 1862) from Tietê River, using as covariable: **a**) egg stage; **b**) year season.

care against the most common causes of egg loss (e.g. parasites). Such mechanism is probably part of the grooming behavior. The cleaning of brooded embryos by females is an important type of grooming behavior in many decapod species, which usually use the posterior pereopods with propodal setal brushes to clean the eggs and remove foul particles and parasites (Martin and Felgenhauer 1986). Under experimental conditions, brooded embryos of caridean shrimps not cleaned by females suffered significant mortality (Bauer 1979). Another alternative to avoid embryo loss might be the burrowing behavior, commonly found in many decapod species (Bauer 1979, 1981), including representatives of *Macrobrachium* Spence Bate, 1868 (Santos et al. 2015).

Our results demonstrated a positive correlation between fecundity and female size in *M. amazonicum*, which corroborated other studies focusing this species (Lobão et al. 1986, Scaico 1992, Da Silva et al. 2004). Fecundity usually increases with female size in caridean shrimps, decapods, and crustaceans in general (e.g. Reid and Corey 1991, Anger and Moreira 1998, Correa and Thiel 2003, Lara and Wehrtmann 2009, Tamburus et al. 2012, Herrera-Correal et al. 2013).

The observed variations in fecundity, with significantly higher values in the rainy seasons, are probably related to the fluctuations in environmental variables. Water temperature, rainfall and chlorophyll-a values were significantly higher in those periods and were positively correlated with fecundity. Previous studies performed with other crustacean groups - and even with other taxa (e.g. ctenophores, insects and fishes) - have demonstrated that variations in environmental conditions can influence fecundity (Nicola and Almodovar 2002, Leone and Mantelatto 2015, McNamara and Londsdale 2014, Clissold and Simpson 2015, Bourdeau et al. 2016, Wafer et al. 2016).

The Tietê River, along its course, suffers various impacts such as pollution, loss of riparian vegetation, and presence of dams, built mainly for electrical energy generation (Smith et al. 2014). These numerous consecutive dams create a group of reservoirs that receive and accumulate organic and inorganic matter from adjacent systems, with pulses of nutrients concentration in rainy seasons, probably due to runoff (Rodgher et al. 2005, Smith et al. 2014, Esteves et al. 2015). The clutch size of *Macrobrachium* species is influenced by temporary environmental factors (Mashiko 1990). Therefore, during rainy seasons, the increased temperature and improved feeding conditions due to rainfall, probably stimulated females to invest more energy towards reproduction, increasing fecundity and RO.

When comparing distinct populations of *M. amazonicum* from different locations, an increase in fecundity is usually accompanied by a decrease in egg volume (Maciel and Valenti 2009, Meireles et al. 2013). When studying a population for two years singly, however, we noted a distinct pattern:

TABLE IV
Variation in the mean egg volume (EV) by egg stage (ES) and reproductive output (RO) of *Macrobrachium amazonicum* (Heller, 1862), according to year seasons analyzed. Results expressed by Mean ± Standard deviation. Different letters represent significant differences.

Season	Mean CL	ES	Mean EV	% (females)	Mean RO (ES I)
rainy 1 (n=67)	12.60 ± 1.59	1	0.15 ± 0.04	55	5.98 ± 1.37^{A}
		2	0.18 ± 0.04	27	
		3	0.23 ± 0.04	18	
dry 1 (n=31)	11.95 ± 2.14	1	0.16 ± 0.04	68	5.88 ± 6.20^{A}
		2	0.19 ± 0.04	10	
		3	0.21 ± 0.04	22	
rainy 2 (n=105)	14.03 ± 1.86	1	0.17 ± 0.03	51	9.82 ± 3.95^{B}
		2	0.18 ± 0.03	25	
		3	0.19 ± 0.03	24	
dry 2 (n=45)	14.90 ± 2.24	1	0.16 ± 0.03	58	6.24 ± 2.82^{A}
		2	0.17 ± 0.03	18	
		3	0.20 ± 0.03	24	

the increase in fecundity was not followed by increase in egg volume during the studied seasons. This was already proposed for caridean shrimps, in which female overall investment (reproductive output) and investment per offspring (egg size) are not linked, because overall investment is set by conditions experienced by the female, while investment per offspring is related to conditions awaiting newly hatched larvae (Mashiko 1990, Clarke 1993, Hancock 1998). The Ibitinga reservoir is considered a eutrophic system, so high chlorophyll-a concentrations are expected independently of bloom events (Londe et al. 2016). This could explain the absence of increment in egg volume during seasons in the present study, because feeding conditions (plankton) awaiting newly hatched larvae were abundant throughout the year in the studied site.

The CL of females did not correlate statistically with RO. This absence of significant relationship between size and RO seems to be common for Palaemonidae (Zimmermann et al. 2015). The observed values of RO (ranging from 5.98 ± 1.37 to 9.82 ± 3.95; mean = 7.4%) were closer (but still lower) to those found for coastal populations of the species [11.74% and 10%, Lima et al. (2014) and Meireles et al. (2013), respectively].

Zimmermann et al. (2015) compiled the data of RO of various Palaemonidae representatives, and the values found for all the other species were also higher than values observed in the present study. These results include other *Macrobrachium* species: *M. hainanense* (Parisi, 1919) 10.5 ± 3.8%, studied by Mantel and Dudgeon (2005); *M. carcinus* (Linnaeus, 1758) 12.0 ± 4.0%, studied by Lara and Wehrtmann (2009); *M. acanthurus* 19.1 ± 4.5% and *M. olfersii* (Wiegmann, 1836) 21.7 ± 6.6%, studied by Anger and Moreira (1998) [see Table II of Zimmermann et al. (2015), for details]. Continental specimens of *M. amazonicum* usually produce larger eggs because their larvae probably do not have an adequate nutritional source, so they are endowed with food (yolk) to help them subsist during larval development, while coastal females compensate the low energy invested in reproduction by producing a higher number of eggs in each spawn (Meireles et al. 2013). The RO observed in the present study, however, was lower than that found for a coastal population by Meireles et al. (2013). It is possible that the great primary production of Ibitinga reservoir, together with a continuous reproduction, allowed females to invest less energy in each brood at Tietê River.

The mean EV significantly increased during developmental stages, although it did not significantly correlated with CL in. This fact was already recorded for the studied species and for other representatives of *Macrobrachium* (e.g. Odinetz-Collart and Rabelo 1996, Lara and Wehrtmann 2009, Tamburus et al. 2012, Lima et al. 2014), suggesting that increase in egg volume during development in this genus is independent of the female size. The increase in size and volume during egg development seems to be a common feature among crustaceans (Zimmermann et al. 2015, Moraes et al. 2017) and is a result of gradual water uptake during embryogenesis (Pandian 1970, Lardies and Wehrtmann 1997, Lara and Wehrtmann 2009).

Some shrimp populations from Paraná-Paraguay basin (those from Pantanal region) were recently described as a separate endemic species, *Macrobrachium pantanalense* Dos Santos, Hayd and Anger, 2013. Considering that some previously studied populations are now *M. pantanalense*, we decided here to use *M. amazonicum* sensu stricto in Table V to compare the various populations studied to the date.

A general pattern for females in relation to body size, fecundity and egg volume can be identified (Table V). Continental populations are generally smaller, exhibit lower fecundities and higher egg volumes, when compared to coastal females. The population studied here, however, did not follow this pattern for some studied reproductive traits. Concerning size and fecundity, females from Tietê River showed the highest values ever recorded for a continental population, and they can be considered intermediate or similar to those of coastal populations. Regarding egg volume, once more specimens from the present study showed values closer to coastal populations. These differences in reproductive traits of Tietê River specimens compared to other continental populations are probably related to the high availability of nutrients in the studied site, as demonstrated by the analysis of photosynthetic pigments (chlorophyll-a concentrations up to 51.8 µg/l). Differences in reproductive parameters between coastal and continental populations were already attributed primarily to the hydrological and geographical particularities of each location. Such differences can directly influence the life history of each population, more than latitudinal differences (Meireles et al. 2013).

In a previous study at the same sampling site, Pantaleão et al. (2014) reported a strong human disturbance in this stretch of Tietê River. Such disturbance is caused by an excessive external supply of nutrients, as fish food (pellets), viscera of caught fish and corn, to attract fish for sport fishing. The occurrence of the four male morphotypes described for *M. amazonicum* (Moraes-Riodades and Valenti 2004) was recorded for the first time in a continental population (Pantaleão et al. 2014) in the same sampling location, and the authors attributed this occurrence to the great availability of nutrients in Tietê River. Considering the characteristics of the studied locality (high concentrations of solid nutrients and chlorophyll-a), we can affirm that our results support the hypothesis of Pantaleão et al. (2014), in which the differences in reproductive parameters between coastal and continental populations were mainly related to the availability of nutrients.

As illustrated here, reproductive parameters of *M. amazonicum* differed markedly between continental and coastal populations. These differences are sometimes interpreted as evidence of speciation process between these groups. When studying seven populations of the species in the Amazon Basin, Odinetz-Collart and Rabelo

TABLE V
Maximum carapace length (CL), maximum fecundity, and mean egg volume (EV, at stage 1, when data was available) of *Macrobrachium amazonicum* (Heller, 1862) females of distinct populations living at different types of environment.

Type of environment		Maximum CL (mm)	Maximum fecundity	Egg volume (mm^3)	Locality	Longitude	Reference
Coastal / Estuarine	Lotic	16.2	2,200	0.14	Ceará, Brazil	38º 51´	Guest 1979
		19.4	1,277	0.11	Amazon River, Brazil	-	Kensley and Walker 1982
		-	1,344	-	Pará, Brazil	48º 30´	Lobão et al. 1986
		26.0	5,706	-	Tocantins River, Pará, Brazil	49º 29´	Odinetz-Collart and Magalhães 1994
		-	3,375	-	Pará, Brazil	48º 45´	Lucena-Frédou et al. 2010
		29.6	7,417	0.12	Amazon River, Amapá, Brazil	51º 08´	Lima et al. 2014
	Lentic	-	2,673	0.11	Pernambuco, Brazil	37º 97´	L.A. Vega-Pérez, unpublished data
		-	2,193	-	Ceará, Brazil	37º 49´	Da Silva et al. 2004
		19.4*	2,956	0.13	Pará, Brazil	48º 32´	Meireles et al. 2013
Continental	Lotic	22.3	4,264	0.16	Tietê River, São Paulo, Brazil	49º 01´	***Present study***
	Lentic	-	2,259	0.39	Lakes of Amazon River, Brazil	60º 01´	Magalhães 1985
		18.0	2,165	-	Lakes of Amazon River, Brazil	59º 48´	Odinetz-Collart 1991
		18.0	617	-	Dam of Tocantins River, Pará, Brazil	49º 38´	Odinetz-Collart and Magalhães 1994
		18.0	2,850	-	Lakes of Amazon River, Brazil	59º 48´	Odinetz-Collart and Magalhães 1994

* = mean values. Egg volume estimated by egg size data, when necessary.

(1996) noted differences in reproductive features between these groups, and suggested a progressive divergence of this species from a typical littoral population to an inland form in a still active adaptive process. The continental population studied here, however, exhibits reproductive characteristics that can be considered closer to those of coastal populations.

A possible explanation for the differences in reproductive traits found in the present study, when compared with other continental populations, is that *M. amazonicum* is not native of Tietê River. The species was probably introduced between 1966 and 1973, together with *M. jelskii* (Miers, 1877) at the CESP (Companhia Energética de São Paulo) fish-farming stations, as part of the process of transplanting of the Sciaenidae fish *Plagioscion squamosissimus* (Heckel, 1840) from reservoirs of northeastern Brazil (Torloni et al. 1993, Magalhães et al. 2005). Thus, shrimp from Tietê River were relatively recently introduced, and are originate from a coastal population, which was confirmed by genetic data (Vergamini et al. 2011). Regardless of the fact some continental populations are under speciation process, our results confirm a great plasticity of the species, since even completing the entire life cycle in freshwater, females exhibit reproductive features similar to those of coastal populations, and males develop into four morphotypes (Pantaleão et al. 2014).

The correlation found in the present study between reproductive parameters and environmental variables corroborates the affirmation in which the wide variation in population and reproductive parameters observed among the geographical distribution of *M. amazonicum* are related to the environmental characteristics that each population is inserted (Pantaleão et al. 2012, 2014, Meireles et al. 2013). Thus, we suggest that further studies investigate the potential of continental populations of *M. amazonicum* for aquaculture, because continental populations can show fecundity values and reach body sizes similar to those of coastal populations, which are generally used for commercial cultivation. The cultivation of populations with an entirely freshwater life cycle would significantly reduce the costs of production.

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