

REPRODUCTIVE ASPECTS OF THE PRAWN *Macrobrachium amazonicum* IN A CONTINENTAL POPULATION LIVING DOWNSTREAM OF A HYDROELECTRIC DAM*

Lubia Maciel MIRANDA¹ 

Larissa Rosa RODRIGUES^{2*} 

João Alberto Farinelli PANTALEÃO³ 

Luciana Segura de ANDRADE¹ 

¹Universidade Federal do Triângulo Mineiro, *campus* Iturama - UFTM-CIT, Grupo de Ensino, Pesquisa e Extensão em Animais Aquáticos - GEPEAA. Av. Rio Paranaíba, 1229, CEP: 38280-000, Iturama, MG, Brazil.

²Universidade Estadual Paulista Júlio de Mesquita Filho - UNESP, Instituto de Biociências, Botucatu. Distrito de Rubião Júnior, s/n, CEP: 18618-000, Botucatu, SP, Brazil. larissa-r-rodrigues@hotmail.com (*corresponding author)

³Universidade de São Paulo - USP, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto - FFCLRP, Departamento de Biologia, Laboratório de Bioecologia e Sistemática de Crustáceos - LBSC. Av. Bandeirantes, 3900 - Vila Monte Alegre, CEP: 14040-900, Ribeirão Preto, SP, Brazil.

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ABSTRACT

The migratory behavior of females of the freshwater prawn *Macrobrachium amazonicum* (Heller, 1862) can indicate a strategy that optimizes the population establishment. With this idea in mind, we evaluated the reproductive biology of *M. amazonicum*, hypothesizing that females were evenly distributed downstream of Hydroelectric Dam. Specimens were collected monthly for one year, from six sites of Rio Grande river. The specimens were sexed and measured (carapace length; CL). A total of 14,697 adults were captured, 2,864 males (AM), 11,082 non-breeding females (AF) and 751 breeding females (BF). The smallest BF had 3.8 mm CL. The distribution of demographic groups was assessed by a Principal Component Analysis (PCA), which explained 95.16% of the distribution over the collection sites. Breeding females were more abundant in the sites closest to the dam. This result can be explained by rainfall, which varied significantly throughout the year. As the breeding females migrated upstream toward the dam and were more abundant there, our hypothesis of homogeneous distribution was rejected. This behavior probably optimizes larval dispersion. The reproduction was continuous with peaks in the period preceding the maximum rainfall.

Keywords: fishing resources; Amazon River Prawn; carcinology; anthropic impacts; management plan.

ASPECTOS REPRODUTIVOS DO CAMARÃO DULCÍCOLA *Macrobrachium amazonicum* EM UMA POPULAÇÃO VIVENDO A JUSANTE DA BARRAGEM DE UMA USINA HIDRELÉTRICA

RESUMO

O comportamento migratório das fêmeas de *Macrobrachium amazonicum* (Heller, 1862) pode revelar estratégias para otimizar o estabelecimento da população. Com essa ideia em mente, avaliamos a biologia reprodutiva de *M. amazonicum*, hipotetizando que as fêmeas estavam uniformemente distribuídas a jusante da Usina Hidrelétrica. Os espécimes foram coletados mensalmente durante um ano, em seis localidades do Rio Grande, identificados quanto ao sexo e tiveram mensurado o comprimento da carapaça (CL). Foram capturados 14.697 camarões adultos, sendo 2.864 machos (AM), 11.082 fêmeas não-ovígeras (AF) e 751 fêmeas embrionadas (BF). A menor fêmea BF possuía 3,8 mm CL. A distribuição dos grupos demográficos foi avaliada por uma Análise de Componentes Principais (PCA), a qual explicou 95,16% da distribuição ao longo dos pontos de coleta (BF mais próximas da barragem). Tal explicação provavelmente foi relacionada com a precipitação, a qual variou significativamente ao longo do ano. Nossa hipótese de distribuição homogênea foi rejeitada, uma vez que as fêmeas ovígeras sobem o rio até as proximidades da barragem, provavelmente para otimizar a dispersão das larvas. A reprodução foi contínua com picos em períodos que antecedem os valores máximos de precipitação.

Palavras-chave: recurso pesqueiro; camarão-da-amazônia; carcinologia; impacto antrópico; plano de manejo.

INTRODUCTION

The freshwater prawn *Macrobrachium amazonicum* (Heller, 1862) - also known in some Brazilian regions as “camarão-sossego”, “camarão-canela”, “camarão-regional” or “camarão-da-amazônia” (Maciel and Valenti, 2009) - is endemic of tropical and

subtropical regions of South America, where it is also widely distributed (Melo, 2003). In Brazil this species occurs in the states Acre, Roraima, Rondônia, Amapá, Amazonas, Pará, Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Bahia, Tocantins, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, São Paulo and Paraná (Melo, 2003).

The occurrence of *M. amazonicum* in reservoirs and rivers of the south, southeast, and northeast of Brazil is a consequence of unintentional and/or intentional anthropogenic actions (Magalhães et al., 2005; Vergamini et al., 2011). In the 1940s *M. amazonicum* was introduced in several dams of Brazil's northeast to support the fish farming and provide food to carnivorous fishes (Paiva and Campos, 1995). The same process probably also occurred in the southeast.

Such hydroelectric dams are necessary for water supply and energy production, but they modify the environment and create a lentic environment upstream (Agostinho et al., 2008). The environment upstream of a reservoir is controlled by climate, whereas downstream it is controlled by the opening and closing of the dam (Melo et al., 2016). Dams affect the species abundance and composition of freshwater communities (Agostinho et al., 2008). They are one of the main causes of fragmentation of aquatic environments (Dynesius and Nilsson, 1994; Roni et al., 2008), as they change the influx of organic matter in the trophic networks by changing the influx of water and nutrients in the reservoir (Agostinho et al., 2008). In turn, this affects the population dynamics of aquatic organisms living upstream and downstream (Odinetz-Collart, 1988).

The populations of *M. amazonicum* reproduce continuously and breeding females might be found year-round (Odinetz Collart, 1991; Bialecki et al., 1997; Sampaio et al., 2007), with a peak in the rainy period (Silva et al., 2005; Bentes et al., 2011). However, reproductive traits such as fecundity vary depending on temperature, rainfall, and hydrological properties (Pantaleão et al., 2018). Regarding the proportion of males and females, studies of Odinetz-Collart (1991); Sampaio et al. (2007) and Silva et al. (2017) reported female-biased sex ratios, where females represented 70% (Sampaio et al., 2007; Silva et al., 2017) to 85% of the population (Costa and Silva et al., 2017).

The knowledge of a species' reproductive biology is extremely important for the understanding of its life cycle. It also helps planning a more sustainable use of resources so that they can be a source of income for local communities without harming the populations (Andrade et al., 2015). In this way, aiming to support the economic and social development as well as the environmental protection of the region ("Triângulo Mineiro"), we investigated the reproductive cycle of *M. amazonicum*, focusing on the spatio-temporal abundance of breeding females. Our study sites were located along the Rio Grande river, downstream of the Água Vermelha Hydroelectric Dam, between the states of Minas Gerais and São Paulo. In these sites *M. amazonicum* is often captured and sold as bait for recreational fishing (LRR and LSA, personal observation).

Among the species of *Macrobrachium* Spence Bate, 1868 of different regions of the planet, besides *M. amazonicum*, just a few species have an extended larval development (nine stages;

Guest, 1979) that takes place entirely in freshwaters (Anger, 2013). The hypothesis of our study was that breeding females were evenly distributed in the sampling sites, since they do not migrate toward the sea ("freshwater amphidromy", *sensu* McDowall, 1992) to spawn in estuaries. They differ, in this respect, from congeners that have the same type of larval development and are amphidromous, like *Macrobrachium ohione* (Smith, 1874) (Olivier and Bauer, 2011).

MATERIAL AND METHODS

Characterization of the sampling sites

The Água Vermelha Hydroelectric Dam (also named "José Ermirio de Moraes") was built between 1973 and 1979 between the municipalities Ouroeste (SP) and Iturama (MG) (Figure 1). Previously, the area was known as "Cachoeira dos Índios" and had six waterfalls: "Tombo das Andorinhas", "Caldeirão do Inferno", "Tombo dos Dourados", "Tombo das Três Pedras", "Tombo da Fumaça" and "Véu de Noivas". Several affluents contribute to increase the volume upstream of the falls, including the creek "Água Vermelha", which brings eroded sediments that increase turbidity.

Downstream of the dam, six sites were chosen for this study (Figure 1):

- Site I: Contains many large boulders that were deposited there during the construction to avoid erosion. The riparian vegetation is absent. It is located 1,036 m from the dam, in the São Paulo margin (19°21'31"S; 50°21'19"W).
- Site II: The area has a mixture of unconsolidated and consolidated substrates, and grasses are present in the margins. Located 1,017 m away from the dam, in the Minas Gerais margin (19°21'25"S; 50°21'12"W).

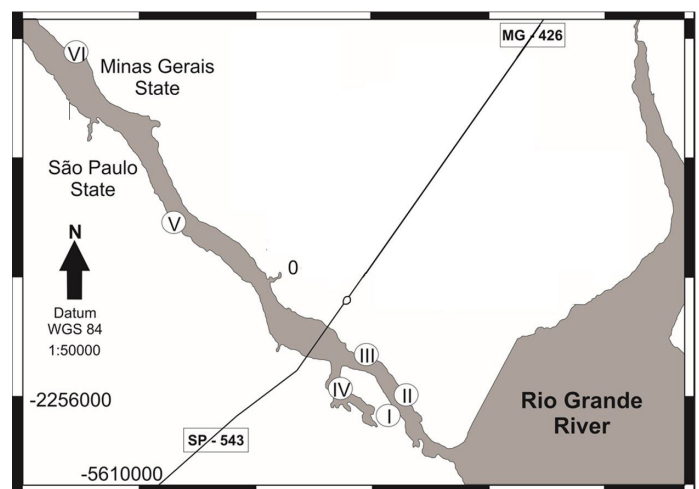


Figure 1. Map of the Rio Grande river, downstream of the Água Vermelha Hydroelectric Dam, between the states of Minas Gerais and São Paulo, Brazil. The numbers indicate the location of sampling sites I to VI.

- Site III: Boulders and grasses are present. The site is frequently visited by amateur fishermen. Located 1,245 m away from the dam, in the Minas Gerais margin (19°51'19"S; 50°21'17"W).
- Site IV: Located in a small island relatively well-preserved, with non-consolidated substrate. There are plenty riparian vegetation and abundant submerse and floating macrophytes. It is 2,792 m away from the dam (19°51'12"S; 50°21'51"W).
- Site V: Area of non-consolidated substrate, and relatively well-preserved margins, with abundant grasses and trees. Also has abundant submerse and floating macrophytes. It is 3,490 m away from the dam in the São Paulo margin (19°50'45"S 50°22'33"W).
- Site VI: Next to a spring, where the water is dark and oily. The site has well-preserved margins with abundant vegetation and non-consolidated substrate. Macrophytes are also present. It is 4,368 m away from the dam in the Minas Gerais margin (19°50'20"S; 50°23'30"W).

Precipitation data was obtained from AES Tietê, based on the database of Brazil's Nacional Water Agency ("Agência Nacional das Águas"; ANA, 2019).

Biological material

The collections were made once a month, from September 2017 to October 2018, over a day. The prawns were collected with a funnel-shaped sieve (55 cm diameter opening, 4 mm mesh). The sampling effort was of one person who dragged the sieve at 180°, three times, around 09:00 h am. In addition, "covo" traps (similar to a "Matapi", but made of plastic material - see Pantaleão et al., 2018 for details of the trap) were baited with grinded corn and placed in the river margin for 6 hours (09:00 – 15:00 h). The prawns were stored in glass containers, cooled, and preserved in 70% ethanol.

In the laboratory of "Universidade Federal do Triângulo Mineiro" (UFTM) *campus* Iturama, the animals were identified under microscope according with Melo (2003), sexed (identified by the presence or absence of the male appendix on the second pair of pleopods (Valenti, 1998), and measured (standard carapace length - CL: orbital angle to the posterior margin of the carapace, excluding the rostrum) with a digital caliper (0.01 mm precision).

Data analyses

The abundance data were tested for to normality (Shapiro and Wilk, 1965; $\alpha = 0.05$) and homoscedasticity (Levene's Test, $\alpha = 0.05$) prior choosing a statistical test (Sokal and Rohlf, 1995). When necessary, the data were log-transformed ($\log(x+1)$) to satisfy the test's assumptions.

A Principal Components Analysis (PCA) was used to investigate the relationship between abundance (AM = adult males; AF = non-breeding females; BF = breeding females), and the sampling sites and months. The PCA uses linearized data to show the most important components of the ordination of the original variables (McCune and Grace, 2002). The coordination scores were calculated by linear combination, and the relative contribution of each variable

to each component was calculated from intra-set operations (McCune and Grace, 2002). The significance of eigenvalues was accessed by randomization tests (Monte Carlo), using 9999 randomized runs per analysis. All multivariate analyses were done using PC-ORD 6.0 (McCune and Mefford, 2011), considering $\alpha = 0.05$ (Zar, 2010).

The monthly precipitation data were compared using an Analysis of Variance (one-way ANOVA). When the overall difference between months was significant, a post-hoc Tukey Test was used to identify the differences (Zar, 2010). These analyses were done using BioEstat 5.3 (Ayres et al., 2007).

RESULTS

In total we captured 14,697 *M. amazonicum* adults: 2,864 males (AM), 11,082 non-breeding females (AF) and 751 breeding females (BF) (Table 1). The size (CL) of the smallest BF was 3.8 mm. The size (CL) of the smallest breeding females was used as a threshold to avoid the inclusion of juveniles in the analyses. In the same way, a threshold of 4.26 mm was used for the males, which is the size at the onset of morphological maturity estimated by Pantaleão et al. (2012), for another continental population of *M. amazonicum*. All individuals below these thresholds were not used in this study and were excluded from the analyses (4,876 individuals).

The PCA indicated that 95.16% of the total variation of the distribution of the prawns was explained by the months (Table 2).

Table 1. *Macrobrachium amazonicum*. Temporal and spatial abundance of adult non-breeding females (AF), breeding females (BF) and adult males (AM) in the Rio Grande river, downstream of the Água Vermelha Hydroelectric Dam.

Sampling period	AF	BF	AM	Total
2017 October	1039	94	589	1722
November	829	107	139	1075
December	543	75	164	782
2018 January	451	50	151	652
February	295	41	96	432
March	406	68	162	636
April	1227	29	184	1440
2018 May	1984	70	298	2352
June	1368	54	316	1738
July	1043	35	289	1367
August	601	36	106	743
September	1296	92	370	1758
Sampling Site	FA	FE	MA	Total
I	1888	202	370	2460
II	3241	253	867	4361
III	1789	192	371	2352
IV	1239	71	456	1766
V	1354	2	287	1643
VI	1571	31	513	2115

Males and AF were negatively correlated with Axis 1 (PC1) ($p < 0.01$), whereas BF were more correlated with axis 2 (PC2), and less with PC1 (Table 2).

Since the PCs are orthogonal, it is possible to analyze the relationship between samples and variables, as well as to estimate the influence of each variable per sample (Table 2, Figure 2). In this way, the PCA shows that the abundance of AM and AF is more influenced by months and sampling sites. However, only

the spatial distribution of BF differed significantly (ANOVA, $F = 4.75$, $p < 0.001$) when the closest and farthest sites were compared (Figure 3). The abundance of AF and AM did not differ between sites (ANOVA, $p > 0.05$).

Rainfall differed significantly between months (ANOVA, $F = 4.78$, $p < 0.001$), and the period of March–October was the driest (Figure 4).

Table 2. *Macrobrachium amazonicum*. Statistical summary of the first two components of the Principal Components Analysis of the temporal and spatial distribution of adult non-breeding females (AF), breeding females (BF) and adult males (AM) in the Rio Grande river, downstream of the Água Vermelha Hydroelectric Dam. PC1 = Axis 1; PC2 = Axis 2.

Demographic groups (temporal distribution)	PC1	PC2
Eigenvalues	1,987	0,868
% of variance	66,235	28,924
AF	-0,9579	0,1625
BF	-0,4991	0,8656
AM	-0,9162	0,3034

DISCUSSION

During our study, BF were significantly more abundant in the sites closest to the dam. This pattern was not observed in the other demographic groups (AM and AF). These results contradict our hypothesis and suggest that *M. amazonicum* BF living downstream of the dam, in the river Rio Grande, undertake an upstream migration. This finding contrasts with the behavior of the other species of *Macrobrachium* that have an extended larval development, which migrate downstream toward estuaries (Bauer, 2004; Bauer and Delahoussaye, 2008; Brown et al., 2010; Olivier and Bauer, 2011).

The size of the smallest BF found was 3.8 mm CL, which is smaller than the sizes reported for other *M. amazonicum* populations

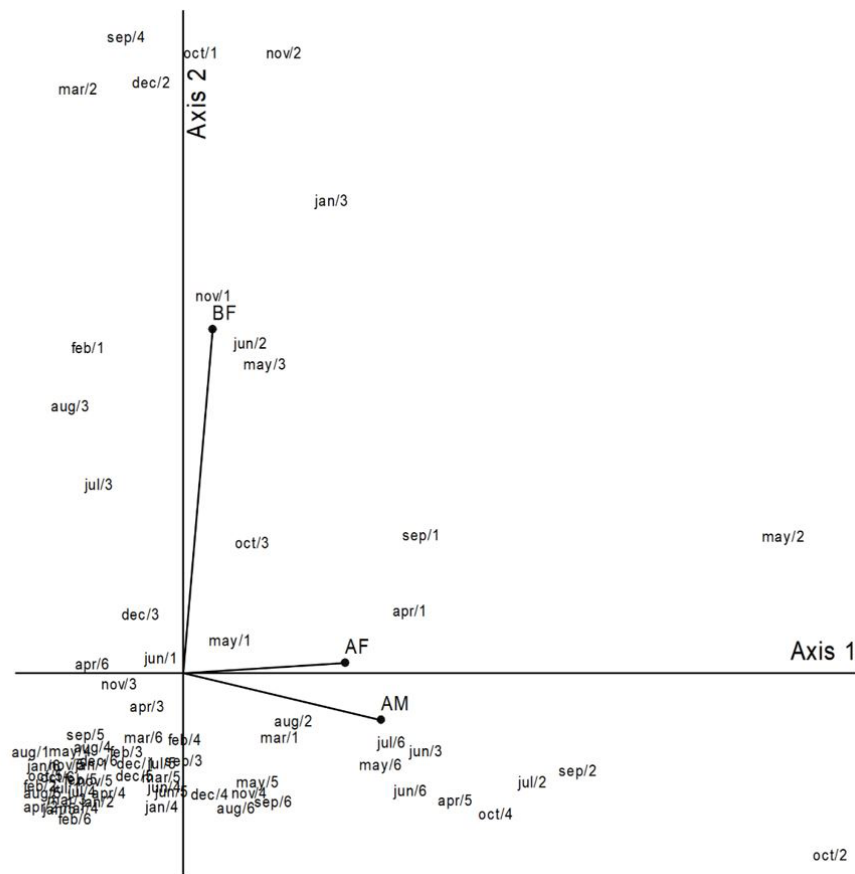


Figure 2. *Macrobrachium amazonicum*. Principal Component Analysis showing the correlation between demographic groups, months, and sampling sites. AF = adult non-breeding females, BF = breeding females, AM = adult males.

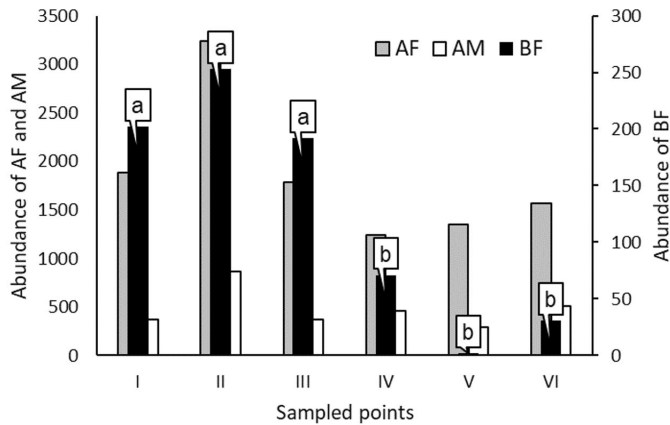


Figure 3. *Macrobrachium amazonicum*. Abundance of non-breeding adult females (AF), adult males (AM) and breeding females (BF) in six sampling sites along the Rio Grande river, downstream of the Água Vermelha Hydroelectric Dam. Site I was nearest to the dam, whereas site IV was the farthest. Different letters indicate significant differences in the abundance of breeding females between sampling sites (ANOVA, $p < 0.001$).

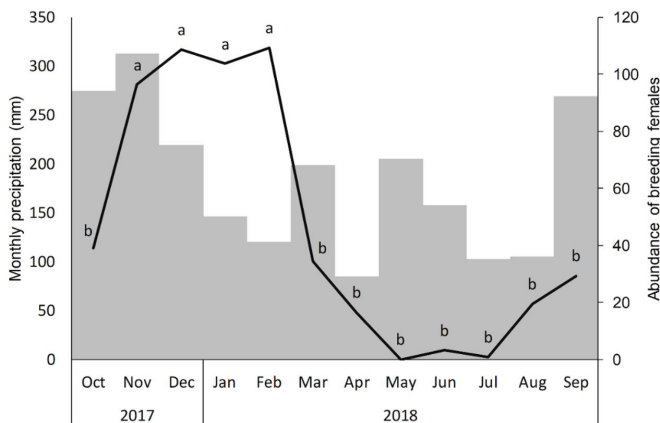


Figure 4. *Macrobrachium amazonicum*. The line indicates the monthly rainfall in the Rio Grande river, downstream of the Água Vermelha Hydroelectric Dam. The bars indicate the abundance of breeding females. Different letters indicate significant differences in rainfall between months (ANOVA, $p < 0.001$).

from reservoirs. For example, Pantaleão et al. (2012) reported 5.35 mm in the Tietê river, state of São Paulo, and Silva et al. (2017) reported 6.0 mm in the Araguari river, in the state of Minas Gerais. In a previous study by Paschoal et al. (2019), also in the Rio Grande river, the size of the smallest breeding female was 7.1 mm. This early female sexual maturity could be a response to a high fishing pressure, given that this species has a high phenotypic plasticity (Maciel e Valenti, 2009). The phenotypic plasticity in the size at the onset of morphological maturity can vary between populations and individuals. An early sexual maturity has been pointed as a response to a high fishing pressure in other decapods as well, such as in the swimming crabs *Arenaeus cribrarius*

(Lamarck, 1818) in Ubatuba (SP) (Andrade et al., 2013). In a study on the allometric growth of the crab *Uca thayeri* (Rathbun, 1900), Negreiros-Fransozo et al. (2003) highlighted that individuals inhabiting extreme environments can start reproducing earlier in life if resources are scarce or of low quality. Thus, an early sexual maturity seems to be a viable strategy to maintain the populations even under stressful situations.

During our study *M. amazonicum* individuals were captured every month, and the reproduction was continuous with a few peaks. Bond and Buckup (1982) suggested that a continuous reproduction is common in this genus and that peaks of reproductive activity are possible. The same pattern has been observed in other populations of *M. amazonicum* (Odinetz-Collart, 1991; Bialecki et al., 1997; Sampaio et al., 2007). Besides the continuous reproduction, *M. amazonicum* shows a fast development and colonization of a variety of environments, including the ones originated by the construction of dams. This is likely facilitated by its wide morphological and ecological plasticity (Vergamini et al., 2011). The reproductive period of freshwater decapods is usually associated with rainfall and variation in temperature and photoperiod (Pinheiro and Hebling, 1998), and/or with the hydrological properties of each environment (Pantaleão et al., 2018).

In this study it was possible to observe that, despite the presence of BF year-round, the highest peak preceded the months with more rainfall (Figure 4), suggesting that females synchronized the spawning with the period of highest rainfall. In an estuary in the northeast of Pará, Freire et al. (2012) also observed BF every month, but with a peak in January–February, i.e., the rainy season of that region. The rainy period can contribute positively to larval dispersion since with the increase in water volume, the larvae are carried downstream to sites farther away from the dam. Some authors pointed out that to optimize larval dispersion is a good reproductive strategy since it increases survival chances by decreasing the intraspecific competition (Welcomme, 1985; Odinetz-Collart and Enriconi, 1993).

Breeding females were more abundant in the sites near the dam. This fact was demonstrated in our multivariate analyses, where AM and AF were more homogeneously distributed among the sites (Figure 2). The sites closest to the dam were characterized by the presence of boulders arranged during the construction of the dam. These boulders formed microhabitats and increased the availability of shelters. Moreover, fisheries near the dam are forbidden, which may have also contributed to this result. The Rio Grande river species protection plan includes a closed season and a ban on fishing activities (including bait) up to 1,500 m downstream of the hydroelectric dam (Brasil, 1998; IBAMA, 2006, IBAMA, 2009). A plausible hypothesis is that BF migrate to shelter in this region of the river. This hypothesis is based on previous studies which also observed *M. amazonicum* migrating in certain periods and places. For instance, in the Amazon, Odinetz-Collart and Enriconi (1993) observed that, upon the increase current speed in periods of higher rainfall, the individuals migrated to flooded areas that provided a more protected environment. Intriguingly, the migration registered in this study differs from that of congeners whose larvae need brackish water to complete their development, as for example

Macrobrachium rosenbergii (De Man, 1879) (Brown et al., 2010). Thus, the migration of *M. amazonicum* BF in the Rio Grande river was upstream. We suggest that this type of migration might be characteristic of continental populations of this species, whose full life cycle is completed in freshwaters. Future studies should investigate this phenomenon aiming to understand the mechanisms involved in this type of migration.

According to Costa and Silva et al. (2019), females may represent up to 85% of the population. Similarly, our results showed a female-biased sex ratio (F:M = 4.13:1) and females were 80.51% of the population. When comparing the nearest and farthest sites, relative to the dam, we observed a higher abundance of BF near the dam, whereas AM and AF were more equally distributed along the river. According with Coelho and Santos (1993), the distribution of males and females may be related to the reproductive process and apparently aims to optimize the larval dispersion, so the larvae can find the most sites appropriate to undergo each stage of the life cycle.

CONCLUSION

We conclude that *M. amazonicum* breeding females from a lotic environment downstream of a reservoir undertake an upstream migration to take shelter in the areas adjacent to the dam. This conclusion is corroborated by the multivariate analyses we performed, which indicated a significant higher abundance of breeding females near the dam. Moreover, the abundance of other demographic groups (AM and AF) was not affected by the distance to the dam. Altogether, the migratory behavior and the synchrony between spawning and the rainy season probably optimizes the larvae transport and seem to favor the rapid establishment of this species in the region.

Considering that *M. amazonicum* presents continuous reproduction and migration to protected areas, we believe that protective measures are efficient for this species.

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