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# Seasonal variation in the population structure of the freshwater prawn *Macrobrachium brasiliense* (Decapoda: Palaemonidae) in a neotropical region

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# ABSTRACT

The present study aims to describe the population structure of the freshwater prawn Macrobrachium brasiliense and to analyze whether it varies seasonally, with emphasis on abundance variation by demographic category, sex ratio, size, and morphotypes, in addition to analyzing the recruitment period and its relationship with rainfall. The collections of M. brasiliense were carried out in a Cerrado region, in the southeastern region of Brazil. The population structure was analyzed according to the size, sex, and life stage. The density of morphotypes was calculated by the proportion of each morphotype in the population. Male and female prawns were more abundant in the largest and smallest size classes, respectively. The juvenile morphotype was the most abundant among males (45.9%), while the "Mirim" and "Açu" morphotypes occurred in a similar proportion (27.87 % and 26.23 %, respectively). The population structure varied significantly between seasons (dry and rainy). A relationship of juvenile abundance with rainfall was recorded. The recruitment period was observed between the end of the rainy season and the beginning of the dry season, while adults were more abundant at the end of the dry season and the beginning of the rainy season. The information in this study contributes to the knowledge of the influence of seasonality and

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rainfall on populations of aquatic organisms in the Cerrado region, such as the prawn *M. brasiliense*. Rainfall seasonality affects the population structure of these organisms between seasons, possibly due to the top-down and bottom-up effects caused by different rates of nutrient input in such aquatic systems.

### **Keywords**

Bottom-up, Caridea, recruitment, seasonality, top-down

#### INTRODUCTION

The American neotropical region is characterized by a wide area that stretches between Central and South America (Morrone, 2014). In this region, the Caatinga, Cerrado and Chaco biomes constitute an area known as the "dry diagonal", which extends from the northeast of Brazil to the northwest of Argentina (Ab'Sáber, 1977; Silva, 1995; Zanella, 2011). Such biomes share among their main characteristics a relevant seasonality in relation to rainfall (Pinheiro *et al.*, 2002; Monteiro *et al.*, 2006; González *et al.*, 2012).

For the aquatic systems present in these regions (e.g., rivers, streams and lakes), rains play an extremely important ecological role; for example, they transport into these systems important organic matter and nutrients, which play a fundamental role in the food chain (Chaves et al., 2013; Fong et al., 2020). These organic fragments and nutrients are ingested by invertebrates (i.e., mollusks, insects and crustaceans), and subsequently these animals can be preyed upon by larger organisms, such as fish, reptiles and birds (Suberkroop, 1992; Post et al., 2000; McHugh et al., 2010). Among these invertebrates that inhabit rivers, and are fundamental in the food chain, are the palaemonid prawns, which are widely abundant in these environments (Coelho and Ramos-Porto, 1984; Mantel and Dudgeon, 2004).

The family Palaemonidae is considered a primary taxon in the infraorder Caridea, and aggregates several genera of marine, estuarine and freshwater prawns, including those belonging to the genus *Macrobrachium* Spence Bate, 1868. Some representatives of this genus, such as *Macrobrachium amazonicum* (Heller, 1862), *Macrobrachium rosenbergii* (De Man, 1879), and *Macrobrachium jelskii* (Miers, 1877) have been extensively studied because of their extensive geographical distribution and/or economic importance in the Brazilian territory (Melo, 2003; Magalhães *et al.*, 2005; Pileggi and Mantelatto, 2012).

Studies show that the distribution and population structure of freshwater prawns can vary between different locations, with the main factor being the physical and chemical conditions of the environment, which can be influenced by seasonality (Brooks *et al.*, 2005; Barros-Alves *et al.*, 2012; Paschoal *et al.*, 2019; Silva *et al.*, 2020; Macedo *et al.*, 2021; Perroca *et al.*, 2021). Thus, it is essential that studies on the seasonal variation in population structure of different organisms are carried out, in order to understand the effects of climate on such populations, considering that we are living in a time of great climatic changes on a global scale (Jourdan *et al.*, 2018; Souza-Dias *et al.*, 2018).

Therefore, we will investigate a population of M. brasiliense located in the Cerrado region in southeastern Brazil, with marked seasonality in terms of rainfall. The hypothesis that rainfall seasonality should affect population structure and reproduction leading to peak recruitment in the dry season was tested. This hypothesis is supported by the theory of upward (bottom-up) and downward (top-down) regulatory processes of population and community dynamics (Collar et al., 2017; Benke, 2018) and by several empirical studies that found a relationship between the reproductive period/recruitment with periods of greatest rainfall (Mantelatto and Barbosa, 2005; Nogueira et al., 2019b; Oliveira et al., 2019). The hypothesis proposes that: [1] different population structures occur between seasons (dry and rainy), i.e., immature and small individuals predominating in the dry season and a predominance of adult individuals and larger size classes in the rainy season; and  $\left[2\right]$  a significant relationship will occur between juvenile abundance and rainfall.

# MATERIAL AND METHODS

#### Study area and sampling methods

The Água Limpa stream (19°05'38"S 48°22'47"W) is located in the municipality of Uberlândia, state of Minas Gerais, a Cerrado region in southeastern Brazil (Fig. 1). The stream where the sampling was carried out consists of a stretch with a maximum of 2.0 m in width between the margins and with sandy sediments. The marginal vegetation of this stream consists of plants (*i.e.*, grasses, shrubs, and trees) characteristic of the Cerrado biome. This region has a

large seasonal variation in rainfall levels (ANA, 2014), with two well-defined seasons: a rainy season during spring and summer in the southern hemisphere (from October to March), with monthly average rainfall of a minimum of 113 and a maximum of 301 mm<sup>3</sup> per month (mean  $\pm$  SD = 217.83  $\pm$  71.61 mm<sup>3</sup>); and a dry period during autumn and winter (from April to September), with much lower monthly accumulated precipitation averages, with a minimum of 11 and a maximum of 86 mm<sup>3</sup> per month (mean  $\pm$  SD = 36.33  $\pm$  28.53 mm<sup>3</sup>).



Figure 1. Area of the Macrobrachium brasiliense sampling point (Água Limpa stream, Uberlândia, state of Minas Gerais).

The specimens were sampled monthly by two collectors who used circular sieves (50.0 cm in diameter; 2.0 mm mesh), from July 2012 to June 2013. The sieves were deployed in the submerged marginal vegetation, between depths of 15 to 120 cm, for a period of 90 minutes. In the field, the collected animals were kept in ice boxes and then transported to the laboratory. The specimens were preserved in 70 % alcohol and kept for later species identification, sexing and measurements.

#### Laboratory procedure

Prawns were identified to species level according to Melo (2003). The sex of each individual was identified by the presence (males) or absence (females) of the appendix masculina on the second pair of pleopods (Bauer, 2004). Individuals smaller than the smallest

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identified male were considered as undifferentiated juveniles. After these procedures, the prawns were measured with a caliper (0.1 mm precision), for the length of the carapace (CL, mm) and the total length of the second pair of chelipeds (left and right). The CL comprises the distance between the anterior post-orbital margin and the posterior margin of the carapace. The total length of the second pair of chelipeds is equivalent to the sum of the individual size of the ischium, merus, carpus, and propodus. Only individuals who presented both chelipeds with all the articles were used in the analysis.

Individuals of both sexes were classified into adults and juveniles according to the size of morphological sexual maturity proposed by Nogueira *et al.* (2019a), 8.64 mm and 8.03 mm CL for males and females, respectively. The male morphotypes of *M. brasiliense*  were identified according to Nogueira *et al.* (2020), using the major cheliped length (MCL), which was defined by comparing the length between the left and the right chelipeds. Male morphotypes are constituted by dominant and submissive individuals of the same population, in the case of *M. brasiliense* there are two types of morphotypes, one submissive ("Mirim" morphotype) and one dominant ("Açu" morphotype) (for more details on male morphotypes in *Macrobrachium* species, see Karplus and Barki, 2019; Nogueira *et al.*, 2020). Monthly rainfall data were obtained from the digital platform "HidroWeb" of the National System on Water Resources (SNIRH).

#### Population structure and dynamics

For the characterization of the population structure, the prawns were distributed in nine size classes established by the method proposed by Sturges (1926). The size frequency distribution of undifferentiated juveniles, males and females, adults and juveniles, was assessed according to the standard of normality by the Shapiro-Wilk test (a = 0.05). The overall sex ratio in all size classes was assessed using a binomial test (a = 0.05) (Wilson and Hardy, 2002). After identifying the morphotypes present in the population, the proportion of each group was calculated. The comparison between the size (CL) of males and females was assessed using the Mann-Whitney test (a = 0.05).

Considering the difference in rainfall patterns, the seasonal changes in population were tested, *i.e.*, if the abundance of prawns in each demographic category varied over the two seasons. For this, a multidimensional scaling (nMDS) was carried out considering two seasons (rainy vs. dry), based on Bray-Curtis similarity matrices (Clarke, 1993; Clarke and Warwick, 2001). This separation enables testing the hypothesis that the population structure of *M*. brasiliense is modified seasonally. One-way crossanalyses of similarity (ANOSIM R) were later used to test for significant differences in population structure between seasons ( $\alpha < 0.05$ ) (Clarke, 1993). In addition, correspondence analysis (CA) was used to evaluate the relationship between the sampling month and the number of prawns by demographic classes and/or by size classes (Lepš and Šmilauer, 2003). In this analysis,

absolute abundance values were used, considering the number of prawns in each month, demographic classes and size class. The analyzes mentioned in this paragraph were used because they are adequate to analyze a dataset with a low number of samples or absent data, not influencing the final results (Forcino *et al.*, 2015). Finally, we tested the relationship between undifferentiated juvenile abundance and rainfall using linear regression (a = 0.05).

# RESULTS

#### Population structure and density of morphotypes

A total of 253 individuals were collected during the sampling period, with 54 undifferentiated juveniles (UJ), 44 adult males, 53 juvenile males, 27 adult females and 75 juvenile females. The mean CL of UJ was 3.87 ± 0.70 mm (2.3–4.7 mm), 13.36 ± 3.46 mm (8.7–20.5 mm) in adult males, 6.57 ± 0.95 mm (4.8–8.5 mm) in juvenile males, 12.59 ± 3.05 mm (8.2–20.1 mm) in adult females, and  $5.95 \pm 0.77$  mm (4.8–7.9 mm) in juvenile females. The distribution of data from all demographic categories differed significantly from a normality pattern (undifferentiated juveniles: W =0.93, p = 0.02; adult and juvenile males: W = 0.87, p < 0.001; adult and juvenile females: W = 0.75, p < 0.0010.001), and the mean CL was significantly different between males and females (Mann-Whitney, U =3,176, *p* < 0.05).

The individuals were distributed in nine size classes with an interval of 2 mm. In general, females were more abundant in the smaller size classes, while a greater number of male individuals was observed in the larger classes (Fig. 2).

Juvenile males were observed only in classes 4.3 - | 6.3, 6.3 - | 8.3 and 8.3 - | 10.4, with greatest abundance in the second class mentioned, while adult males were more abundant in classes 8.3 - | 10.4, 10.4 - | 12.4, 16.5 - | 18.5 and 18.5 - | 20.5 mm CL (Fig. 2). Juvenile females are distributed in classes 4.3 - | 6.3 and 6.3 -| 8.3, with the greatest abundance in the first class mentioned, while adult females were more abundant in class 12.4 - | 14.4 mm CL (Fig. 2). UJ were only categorized into the two smallest size classes between 2.3 to 6.3 mm CL (Fig. 2). Despite the deviation in the general sex ratio in favor of females (1:1.25), there was no significant difference in relation to the proportion of males (Binomial test, p > 0.05). Among the eight largest size classes, the sex ratio was inclined towards females in three classes (4.3 –| 6.3, 6.3 –| 8.3 and 12.4 –| 14.4 mm; Fig. 3), while for males it was inclined towards

them in four classes (8.3 – | 10.4, 10.4 – | 12.4, 16.5 – | 18.5 and 18.5 – | 20.5 mm; Fig. 3), and, in class 14.4 – | 16.5 mm, the sex ratio was 1:1. However, significant differences in sex ratio were observed in only three classes, 4.3 – | 6.3 for females and 8.3 – | 10.4 and 16.5 – | 18.5 mm for males (Binomial test, p < 0.05).



**Figure 2**. Frequency of size of the carapace length (CL, mm) of the individuals of *Macrobrachium brasiliense* captured in the Água Limpa stream, Uberlândia, state of Minas Gerais. AM: adult males, AF: adult females, JM: juvenile males, JF: juvenile females, and UJ: undifferentiated juveniles.



Size classes (CL, mm)

**Figure 3**. Sex ratio by size classes (CL, mm) of individuals collected between July 2012 and June 2013 in Uberlândia, state of Minas Gerais. Black circles indicate a significant difference from a 1:1 ratio (Binomial Test, p < 0.05), white circles indicate that there was no significant difference.

Among the 97 males collected, only 61 individuals were identified as to their morphotype. Among the three existing morphotypes (Juveniles, "Mirim" and "Açu"), individuals were classified into 28 juveniles, 17 "Mirim" and 16 "Açu". The average CL among the juvenile morphotypes, "Mirim" and "Açu" was 7.01  $\pm$  1.03 mm, 10.45  $\pm$  1.37 mm and 16.46  $\pm$  2.56 mm, respectively (Tab. 1). The average major cheliped length (MCL) among juveniles, "Mirim" and "Açu" morphotypes was 13.97  $\pm$  2.06 mm, 22.55  $\pm$  2.73 mm and 41.19  $\pm$  9.44 mm, respectively (Tab. 1). The proportion of male morphotypes in the population was juveniles (45.9 %), "Mirim" (27.87 %) and "Açu" (26.23 %) (Tab. 1).

#### Seasonal variation in population structure and recruitment

During the sampling period, the highest rainfall was recorded in January (363.3 mm) and November (201.1 mm), while the lowest rainfall was observed in June (4.5 mm), July (13.9 mm), and August, when no rainfall was recorded (Fig. 4).

The nMDS ordination derived from the abundance of prawns in each demographic category recorded two groups for population structure (Fig. 5A). ANOSIM indicated a significant difference in the composition of the population in each season (rainy vs. dry) (ANOSIM; R = 0.320; p = 0.007; Fig. 5A). Composition varied across seasons (rainy vs. dry), and this variation was observed in CA (Fig. 5B, C). UJ (representatives of the first size class; SC 1) were more frequent in the months at the end of the rainy season and the beginning of the dry season (March, April, and May) (Fig. 5B, C). There was a correlation between the occurrence of UJ and rainfall (Linear regression, t = -3.63; p = 0.001). The recruitment period was verified by the occurrence of UJ between the months of March and May, with a prominent peak in March and April. On the other hand, adults (AF and AM) and representatives of the last size classes (SC 8) were more frequent at the end of the dry season and the beginning of the rainy season (August, September, and October) (Fig. 5B, C).

**Table 1.** Data on the proportion (%), average, minimum and maximum values of carapace length (CL) and major cheliped length (MCL) of male morphotypes of *Macrobrachium brasiliense*.

Morphotypes	N (%)	CL (Min–Max) mm	MCL (Min–Max) mm
Juveniles	28 (45.9)	7.01±1.03 (5.1–8.9)	13.97±2.06 (9-17.6)
"Mirim"	17 (27.87)	10.45±1.37 (8.5–13.6)	22.55±2.73 (18.7–27.7)
"Açu"	16 (26.23)	16.46±2.56 (11.9–20.5)	41.19±9.44 (28.5–56.8)



**Figure 4**. Monthly distribution of rainfall (bars) and undifferentiated juveniles (line) of *Macrobrachium brasiliense*, captured from July 2012 to June 2013 in Uberlândia, state of Minas Gerais. UJ: undifferentiated juveniles.





Figure 5. Non-metric multi-dimensional scaling (nMDS; A) plots and correspondence analysis (CA; B and C) evaluating the seasonal variation in the structure of the population of the prawn *Macrobrachium brasiliense* in a cerrado region of Brazil. AM: adult males, AF: adult females, JM: juvenile males, JF: juvenile females, and UJ: undifferentiated juveniles.

#### DISCUSSION

Our results show differences in the composition of the population structure between the dry and rainy seasons. The proposed predictions were confirmed, considering that the population structure differed between the dry and rainy seasons, and the abundance of juveniles was affected by rainfall; as recruits were observed at the end of the rainy season and the beginning of the dry season (predominant in the latter). The general characteristics of the population biology observed were similar in comparison with other populations of *M. brasiliense* investigated in the states of São Paulo and Mato Grosso do Sul (Mantelatto and Barbosa, 2005; Pereira and Chacur, 2009), mainly in relation to the population structure and the period of recruitment. In addition, this is the first population study that provides information on the occurrence and density of morphotypes within an *M. brasiliense* population.

Throughout the sampling period, individuals of both sexes were registered, except for the category of undifferentiated juveniles (UJ) that were collected at specific times. The frequency distribution of males and females of *M. brasiliense* between the size classes followed a pattern, with a greater number of females in the smallest size classes and a greater number of males in the largest classes, which may be a reflection of the reproductive strategy called "temporary female guarding" (Bauer, 2004), with dominant males that court and protect females during copulation. This model of population structure seems to be a pattern in M. brasiliense, considering all the populations studied so far (Mantelatto and Barbosa, 2005; Pereira and Chacur, 2009; Oliveira et al., 2019), as well as for other Macrobrachium species (Mattos and Oshiro, 2009; Gualberto et al., 2012; Nogueira et al., 2019b; Perroca et al., 2021). Therefore, this type of sexual system appears to be common within the genus, since most populations are characterized by males being larger than females, with males showing aggressive behavior during social interactions (Fielder and Lee, 1983; Karplus et al., 1992; Karplus and Barki, 2019).

In the studies by Mantelatto and Barbosa (2005), Pereira and Chacur (2009), and Oliveira *et al.* (2019) there is no information on morphotypes. In this sense, considering the density observed in the present study and the density of morphotypes in populations of similar species, it is important to note that the density of morphotypes in *M. brasiliense* males did not follow the patterns observed in *M. amazonicum* and *M. rosenbergii* (Cohen *et al.*, 1981; Santos *et al.*, 2006), since the density of the morphotypes "Açu" (dominant) and "Mirim" (submissive) were similar within the population.

It was observed that the juvenile morphotype (group with the smallest males) was the most abundant, similar to the "Small Male" morphotype in M. rosenbergii (Cohen et al., 1981). However, the morphotypes "Mirim" and "Açu" showed a similar proportion within the population, while the morphotypes of M. rosenbergii (Orange claw and Blue claw) and M. amazonicum (Cinnamon claw and Green claw) differ in proportion within their populations, with the dominant morphotype (Blue claw and Green claw, respectively) always being less abundant (Cohen et al., 1981; Santos et al., 2006). Many factors can influence the morphotype density of a population, such as habitat, availability, and competition for food, early sexual maturation, social hierarchy, and aggression (Karplus et al., 1986). Possibly, M. brasiliense may present lower levels of aggressiveness in relation to M. rosenbergii and M. amazonicum, with less agonistic confrontations between males, and therefore maintaining similar levels of abundance in the population. However, further studies addressing this theme are essential for understanding this behavior and its influence on the population dynamics of *M. brasiliense*.

In general, the sex ratio was inclined towards females in the population. This trend occurs frequently within the genus Macrobrachium (Garcia-Davila et al., 2000; Montoya, 2003; Mantelatto and Barbosa, 2005; Mattos and Oshiro, 2009; Tamburus et al., 2012; Pescinelli et al., 2016; Nogueira et al., 2019b), mainly in species in which males reach larger sizes compared to females. Many factors can influence sex ratio within the population, such as aggressiveness, migration, reproductive strategies, differential selection of microhabitats, and longevity (Karplus et al., 1991; Bauer, 2004; Karplus and Barki, 2019). Possibly, for M. brasiliense, the greater abundance of females in the population may be related to the reproductive strategy characterized by a series of agonistic behaviors, including aggression among males, which certainly can increase the mortality rates of this demographic category, influencing the sex ratio of the population.

The seasonal variation in the population structure is the result, at least in part, of the relationship between rainfall and the recruitment of UJ. Recruitment increases at the end of the rainy season, with the period with the highest recruitment intensity observed from March to July, a period similar to that recorded for populations in the states of São Paulo and Mato Grosso do Sul (Mantelatto and Barbosa, 2005; Pereira and Chacur, 2009), but different from the populations of the Amazon regions of Brazil and Peru (García-Davila et al., 2000; Oliveira et al., 2019). This difference between the recruitment periods may be related to local environmental factors, such as seasonal rainfall, food resources and predators (Mantelatto and Barbosa, 2005; Bittencourt and Armadio, 2007; Oliveira et al., 2019). Comparing previous studies, the rainy season and the hydrological cycle are the main factors that modulate these differences in population aspects between the southeast/central-west regions and the Amazon region.

The low abundance, or absence, of ovigerous females is common in populations of *M. brasiliense*, mainly in the populations of the central-west and southeast of Brazil (Mantelatto and Barbosa, 2005; Pereira and Chacur, 2009). In the present study, no ovigerous female was found; despite this fact, it is possible to estimate in which months the reproductive period of M. brasiliense occurs according to the delimitation of the recruitment period. It is known that M. brasiliense has abbreviated larval development (Pantaleão et al., 2011); therefore, the embryo incubation period can take an average of 39 days (Lavarias et al., 2002). In addition, the period between larval development into juveniles for Macrobrachium species with abbreviated development occurs on average from 5 to 11 days (Magalhães, 1989; 2016; Rodrigues and Bueno, 1995; Mejía et al., 2003). In this way, the entire embryonic and larval development process would occur in approximately 50 days; therefore, the peak of the reproductive period of this M. brasiliense population possibly occurs between January and February; a similar period to species that have the same type of embryonic development, such as Macrobrachium iheringi (Ortmann, 1897) and M. potiuna (Müller, 1880) (Mantelatto and Barbosa, 2005; Mattos and Oshiro, 2009; Nogueira et al., 2019b).

Our results show that there was a (negative) correlation between the occurrence of undifferentiated juveniles and rainfall, and also that there was a differential composition of the population structure between the dry and rainy season; following the

Population structure of Macrobrachium brasiliense

pattern observed in species with abbreviated larval development (Mantelatto and Barbosa, 2005; Pereira and Chacur, 2009; Nogueira *et al.*, 2019b). Such results are extremely relevant, as they reinforce the influence of environmental factors on these prawn populations, showing that rain and the entire regulation of population dynamics (bottom-up and top-down) plays a fundamental role in the development cycle of these animals.

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