Population dynamics and reproductive features of the Amazon River prawn *Macrobrachium amazonicum* (Heller, 1862) in Neotropical reservoirs under drought events

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Abstract. Here, we describe population and reproductive dynamics of four populations of *Macrobrachium amazonicum* in reservoirs during drought events. Additionally, we analyze possible phenotypic changes in this species promoted by fish predation. Two populations had a large-size phenotype (with large body proportions and morphotypes in males) while a small-size phenotype (with reduced sizes and no morphotypes) was found in the two other populations. Overall, females were larger than males and there were varying sex ratios among the four studied populations. All populations had bimodal or polymodal patterns in their monthly size-class frequency, suggesting a seasonal influence and a potentially great capacity of these populations to adapt to adverse environmental conditions. No major changes were found in the patterns of sex ratio, recruitment, frequency of (larger) male morphotypes and female ovarian development stages during drought events. *Macrobrachium amazonicum* is a resilient species and undergoes continuous reproduction. Females with immature ovaries were predominant in all populations, performing multiple spawns and exhibiting rapid ovarian development cycles. In males, the initial morphotype (TC - translucent claw) was predominant in populations with a social hierarchy. Males of dominant morphotypes (GC1 and GC2 - green claw 1 and 2) use more energy to carry out and maintain metabolic processes, which could probably one of the explanations why their number in populations are limited. We did not find any clear evidence that fish predation affected phenotypes, suggesting that phenotypic plasticity could be more related to intrinsic factors, which would have to be further investigated.

Keywords. Caridea, drought, phenotypes, reproduction, synergistic events.

Introduction

Reservoirs are man-made artificial environments intended for specific purposes, such as water supply, recreation and energy production. They are considered intermediate environments due to the storage and release of water masses. They have lentic features upstream, being similar to lakes, and lotic features downstream, resembling features of rivers. In these environments, the water cycle is dependent on water retention time, with fluctuations in water levels and variations in rainfall over time (Henry 1999; Wang *et al.* 2012). In recent years, severe droughts have drastically altered these environments in Brazil, especially those located in the Paraná River Basin (Melo *et al.* 2016; Nobre *et al.* 2016; Paschoal *et al.* 2015, 2019a, 2020). Melo *et al.* (2016) and Paschoal *et al.* (2020) found that the water supply was significantly compromised in reservoirs in the southeast region of Brazil due to a prolonged drought, i.e., a situation of water scarcity.

The main cause of low water stands in reservoirs is reduced rainfall which can be caused by climate events (e.g., 'El Niño') resulting in a decrease and change in water levels. This event added to anthropogenic changes (e.g., opening of the floodgates, water retention, pollution and others) promotes significant changes in reservoir waters. The combination of both was responsible for altering the physicochemical characteristics of aquatic environments (e.g., changing the chemical composition of sediments and water) and for promoting major changes in this ecosystem, such as a significant reduction of feeding and nursery areas and high-quality habitats, in addition to altering biotic and abiotic patterns of coastal zones (Henry 1999; Bouvy *et al.* 2003; Keitel *et al.* 2015; Paschoal *et al.* 2015, 2020; Sousa *et al.* 2021). Thus, the entire benthic community in these environments can be affected by this water instability. Patterns of spatio-temporal distribution and reproduction of these benthic organisms are altered by the environmental changes, which can even modify the life cycles of animals (Paschoal *et al.* 2015, 2019a, 2020; Sousa *et al.* 2021). Among the animals possibly being affected by such changes are prawns of the genus *Macrobrachium* Spence Bate, 1868. The distribution, population and reproductive features of these animals in Neotropical reservoirs may be changed on a spatio-temporal scale due to droughts (De Grave & Mantelatto 2013; Paschoal *et al.* 2019a).

The Amazon River prawn *Macrobrachium amazonicum* (Heller, 1862) is the most widespread species of its genus in reservoirs of the Paraná River Basin. This species is used in aquariums and as bait in fishing, and it is believed that individuals were introduced accidentally and/or on purpose in these areas (Magalhães *et al.* 2005; Vergamini *et al.* 2011). This species showcases great reproductive flexibility and high intraspecific variability among populations (Odinetz-Collart 1991a; Maciel & Valenti 2009; Vergamini *et al.* 2011; Paschoal *et al.* 2019a). Paschoal & Zara (2020, 2022, 2023) and Paschoal *et al.* (2019a, 2019b) verified three phenotypes for this species, based on the evaluation of its life history, and morphological and reproductive characteristics: i) large-size amphidromous prawns - prawns have large body proportions (both sexes), males show four morphotypes, ovigerous females carry thousands of small-size eggs and their larvae depend on estuarine environments for their development; (ii) large-size hololimnetic prawns - both sexes have large body proportions, four well-defined male morphotypes, ovigerous females carry thousands of intermediate-size eggs and their larvae complete their development in freshwater; and (iii) small-size hololimnetic prawns - prawns have small body proportions, absence of male morphotypes, ovigerous females carry hundreds of large-size eggs and their larvae complete their development in freshwater. The presence of morphotypes in males is not known in the small-size phenotype, while populations with the large-size phenotype have a social hierarchy with four different male morphotypes: translucent claw (TC), cinnamon claw (CC), green claw 1 (GC1) and green claw 2 (GC2). The morphotype development is sequential (TC → CC → GC1 → GC2), with TC being the initial morphotype and CC the intermediary morphotype, both are submissive, agile (high active), have small body dimensions (reach up 73 mm in TC and 74 mm in CC) and small chelipeds (reach up 55 mm in both morphotypes). The GC1 morphotype is subdominant, showing large body dimension (reach up 105 mm) and robust green chelipeds (reach up 99 mm), which never exceed the body size. The GC2

morphotype is dominant, sedentary, had a large body dimension (reach up 105 mm) and robust green or brownish green chelipeds (reach up 176 mm), always exceeding the body size. The latter morphotype plays a major role in this social hierarchy (Pantaleão *et al.* 2012, 2014; Paschoal & Zara 2019, 2022).

The great phenotypic plasticity of *M. amazonicum* populations is not yet fully understood (Paschoal & Zara 2020, 2022). Some authors suggest that the phenotypic differences in the species are caused by intrinsic factors of the animals (i.e., physiological and behavioral differences) (Moraes-Riodades & Valenti 2004; Augusto & Valenti 2016), the viability of nutritional resources in the sampling areas (Pantaleão *et al.* 2012, 2014) or the type of mating system in a given population (Paschoal & Zara 2020, 2022). In addition, it has been found that predation by fishes can also induce phenotypic changes (i.e., life history and/or morphology) in caridean shrimps due to physiological responses to chemical signals from the predators (i.e., kairomones) (Ocasio-Torres *et al.* 2014, 2015a, 2015b), but such association has never been investigated in *M. amazonicum*. Within this context, the present study evaluated population dynamics and reproductive aspects in four populations of *M. amazonicum* with two distinct phenotypes in Neotropical reservoirs during drought events and tested whether the presence of different phenotypes was caused by fish predation. Here, we hypothesize that the situation of water scarcity in Neotropical reservoirs acted as a stressing factor, also modifying the population biology and reproductive patterns of the Amazon River prawn in a space-temporal scale. If this is the case, it is possible that the populations will not recover their usual patterns when water levels are restored.

Material and methods

Sampling

Sampling was carried out between October 2014 and December 2015, during the 2014–2016 El Niño climate event. This El Niño event was as intense as the one recorded in 1997–1998 and was responsible for causing severe droughts in the southeastern region of Brazil (NWS/NOAA 2017). The sampling period was divided according to the influence of El Niño, following the Niño 3.4 index. The months of October 2014 to January 2015 were regarded as a neutral period, February 2015 to March 2015 were considered as showing an alternation in neutrality related to the onset of El Niño, and April 2015 to December 2015 were regarded as months in El Niño (NWS/NOAA 2017).

Monthly collections were carried out in the Grande River (Paraná River Basin) at four sampling sites (Fig. 1). Two points were located at the Furnas hydroelectric power station, in the municipalities of Carmo do Rio Claro (CRC, 20°57′20″ S, 46°09′14″ W) and São José da Barra (SJB, 20°43′10.6″ S, 46°11′26.4″ W), and two others at the Marechal Mascarenhas de Morais hydroelectric power station, in the municipalities of Cássia (CAS, 20°30′53.6″ S, 46°50′16.4″ W) and São João Batista do Glória (SBG, 20°39′43.5″ S, 46°32′5.8″ W), in the Minas Gerais state, southeastern Brazil (Fig. 1). The Furnas hydroelectric power station megareservoir is formed by the Grande and Sapucaí Rivers and has a flooded area of 1440 km^2. The Marechal Mascarenhas de Morais hydroelectric power station reservoir is located between the Furnas (upstream) and Luiz Carlos Barreto de Carvalho (downstream) power stations and has a flooded area of 250 km^2 (Paschoal *et al.* 2019a). The monthly values of accumulated precipitation and water column levels at the hydroelectric power stations were obtained from the databases of the National Water Agency (ANA 2017) and the National Electric System Operator (ONS 2017), respectively.

The prawns were captured by active sampling using a sieve with a diameter of 60 cm and a mesh of 1.25 mm, which was moved along the marginal vegetation and macrophyte banks for 30 minutes by a collector. Also, passive sampling occurred using six traps (85 cm length × 35 cm width and height, mesh size 2 mm), baited with beef liver, which were removed after four hours. Immediately after capture, the animals were anesthetized by chilling (ten minutes on ice) and then preserved in 70% ethanol. Subsequently, they were placed in labeled flasks and transported to the laboratory, where they were identified according to Pileggi (2009).
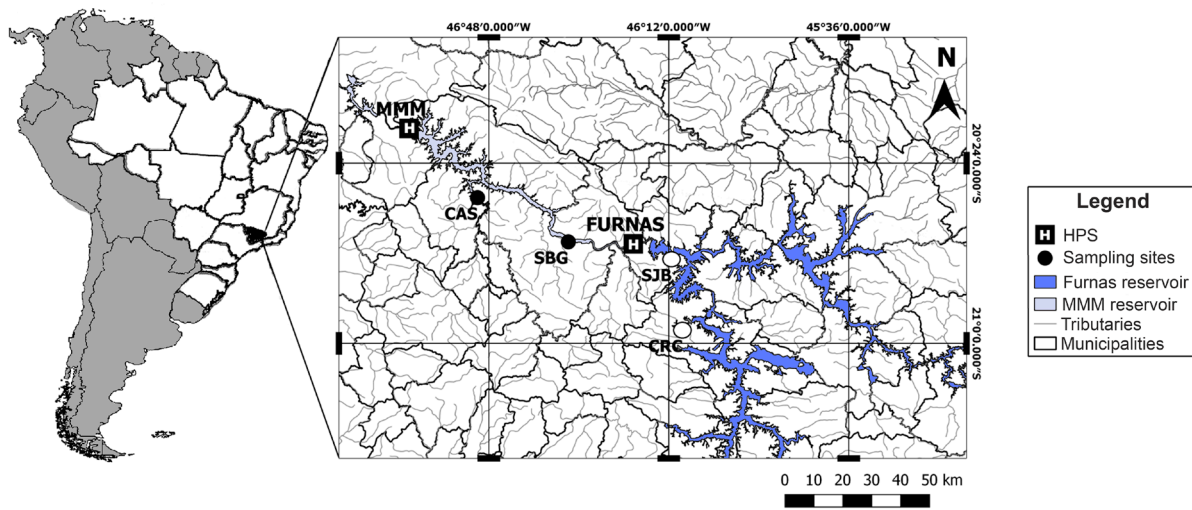
Figure 1 – Sampling sites at reservoirs of Furnas (black circles) and Marechal Mascarenhas de Morais - MMM (white circles) hydroelectric power stations (HPS), Minas Gerais state, southeastern Brazil. Abbreviations: CAS = Cássia; CRC = Carmo do Rio Claro; SBG = São João Batista do Glória; SJB = São José da Barra. The map was adapted from Paschoal *et al.* (2019a).

Biometry and reproductive aspects

The prawns obtained during the monthly collections were counted and divided into subsamples following the criteria proposed by Wenner *et al.* (1991). All animals were measured and sexed in samples containing n ≤ 80 individuals. In cases where the samples had 80 < n < 160 individuals, 80 individuals were randomly selected to be analyzed. Finally, 50% of the captured specimens were verified if the number of individuals collected was 160 < n < 320 and 25% were verified if n ≥ 321.

Sex determination in *M. amazonicum* was carried out through three steps: (a) observation of secondary sexual characters; (b) verification of gonopore positions; and (c) dissection of the reproductive system (Paschoal & Zara 2020, 2022, 2023). Individuals in which sexual characters could not be observed were considered as indeterminate and removed from statistical analyses (n = 272, 5.22% of the subsamples analyzed). Subsequently, carapace length (CL: distance between the posterior margin of the eye orbit and the median point of the posterior margin of the carapace) and total length (TL: distance between the posterior margin of the eye orbit and the distal portion of the spine of the telson) of all prawns were measured.

The ovarian stages of non-ovigerous and ovigerous females in different populations were determined by the macroscopic morphology of these organs. Reproductive systems of preserved females were carefully removed. The ovaries were classified into five stages of development according to Paschoal & Zara (2023): initial (immature ovaries) - stages I and II; intermediate (ovary in maturation) - stage III; and final (mature ovaries) - stages IV and V. Additionally, the egg masses of ovigerous females were classified according to the amount of yolk in the eggs into three stages: initial (1), intermediate (2) or final (3) (Anger & Moreira 1998).

In males, the presence of morphotypes in populations was verified by inspecting the size and color of chelipeds, the angulation of spines on the carpus and propodus, and the pubescence on dactyls (Moraes-Riodades & Valenti 2004; Pantaleão *et al.* 2014); these data were compared to the results of previous

morphometric analyzes carried out by Paschoal & Zara (2020) to identify different morphological groups. Males were separated into: translucent claw (TC), cinnamon claw (CC), green claw 1 (GC1) and green claw 2 (GC2). It is worth noting that TC and CC morphotypes show submissive behavior in the presence of GC1 and GC2 morphotypes, which are dominant (Paschoal & Zara 2020, 2022).

Predation by fishes

The association between the ichthyofauna and the absence/presence of morphotypes in the Amazon River prawn was investigated in the populations of the Furnas and Marechal Mascarenhas de Morais hydroelectric power stations. In November 2015, fishes were captured using gillnets with mesh sizes 80/60/40/20 mm between consecutive nodes (30 m × 1.70 m) arranged in descending order of mesh size in aquatic environments. For seven days, the nets were kept submerged for 24 hours near the shore at the CAS and SJB sampling sites. The captured specimens were identified according to Ota *et al.* (2018) and dissected to remove their stomachs. The stomachs were fixed in 10% formaldehyde and subsequently analyzed under a stereomicroscope to morphologically identify food items.

Data analysis

The monthly and total sex ratios were compared among the four investigated populations using the Chi-square test (χ^2 - α: 0.05) with an expected ratio of 1 ♀:1 ♂. Differences between the average sizes of females and males in the analyzed populations were evaluated with *t*-tests (α: 0.05) (Gotelli & Ellison 2004).

The population structure of *M. amazonicum* was analyzed by determining the distribution frequency of carapace length (CL) of male and female individuals using classes with 1 mm intervals for the SJB and CRC populations and 2 mm for the CAS and SGB populations. The intervals were determined according to the Sturges (1926) equation. The normality of length-frequency distributions for each sex was assessed using the Shapiro-Wilk test (α: 0.05) (Gotelli & Ellison 2004). Individuals with CL equal or smaller to the values established for physiological maturity by Paschoal & Zara (2020) in the four populations were considered as immature (i.e., recruits) and verified monthly in the subsamples.

The relative frequencies of females showing different stages of ovarian development were estimated monthly in each population. The pattern of the reproductive cycle (i.e., continuous or not) in *M. amazonicum* was determined by observing ovarian maturation peaks over time (Sampaio *et al.* 2007). Pearson's correlation coefficient was used to evaluate the association between accumulated precipitation and water level with the frequency of females with ovaries in the initial, intermediate and final stages of maturation. For ovigerous females with ovaries at different stages, data from monthly collections were grouped and the cumulative relative frequency for each population was analyzed to verify whether *M. amazonicum* females restart their ovarian cycle and are capable of reproducing after spawning. The relative frequency of different male morphotypes was estimated monthly for those populations with different morphotypes. The Pearson's correlation coefficient was used to test for an association between accumulated precipitation, water level and female abundance with the frequency of male morphotypes in populations.

For the analysis of the ichthyofauna diet, food items were grouped according to absence (0) or presence (1) in the stomachs. This allowed the data to be subjected to a multiple correspondence analysis, which could assess possible relationships between several dependent categorical variables (Abdi & Valentin 2007). All calculations and statistical analyzes were performed with R 3.3.1 software (R Development Core Team 2017).

Results

A total of 13 203 individuals were collected during the 15 months of sampling. Individuals from the two populations in the Marechal Mascarenhas de Morais hydroelectric power station had large body proportions ($\overline{CL}$ = ♂ - ♀: 9.02 and 10.59 mm in SGB; ♂ - ♀: 13.05 and 14.80 mm in CAS) and four different morphotypes in males, while the populations from the Furnas hydroelectric power station had individuals of smaller sizes $\overline{CL}$ = ♂ - ♀: 6.90 and 8.15 mm in SJB; ♂ - ♀: 7.31 and 8.65 mm in CRC) and no different male morphotypes. Due to the presence of two phenotypes, the populations from the Marechal Mascarenhas de Morais hydroelectric power station, are considered herein as large-size populations and those from the Furnas hydroelectric power station, as small-size populations (*sensu* Paschoal & Zara 2020; Paschoal *et al.* 2019a).

In subsamples containing 5206 individuals (39.43% of the total sample) (see Appendix 1, Tables S1 and S2, for further details on raw data), the normality in length-frequency distributions was only observed in females in the populations of SJB (♂ = W: 0.82 - *p*: 0.02; ♀ = W: 0.87 - *p*: 0.08), CRC (♂ = W: 0.82 -
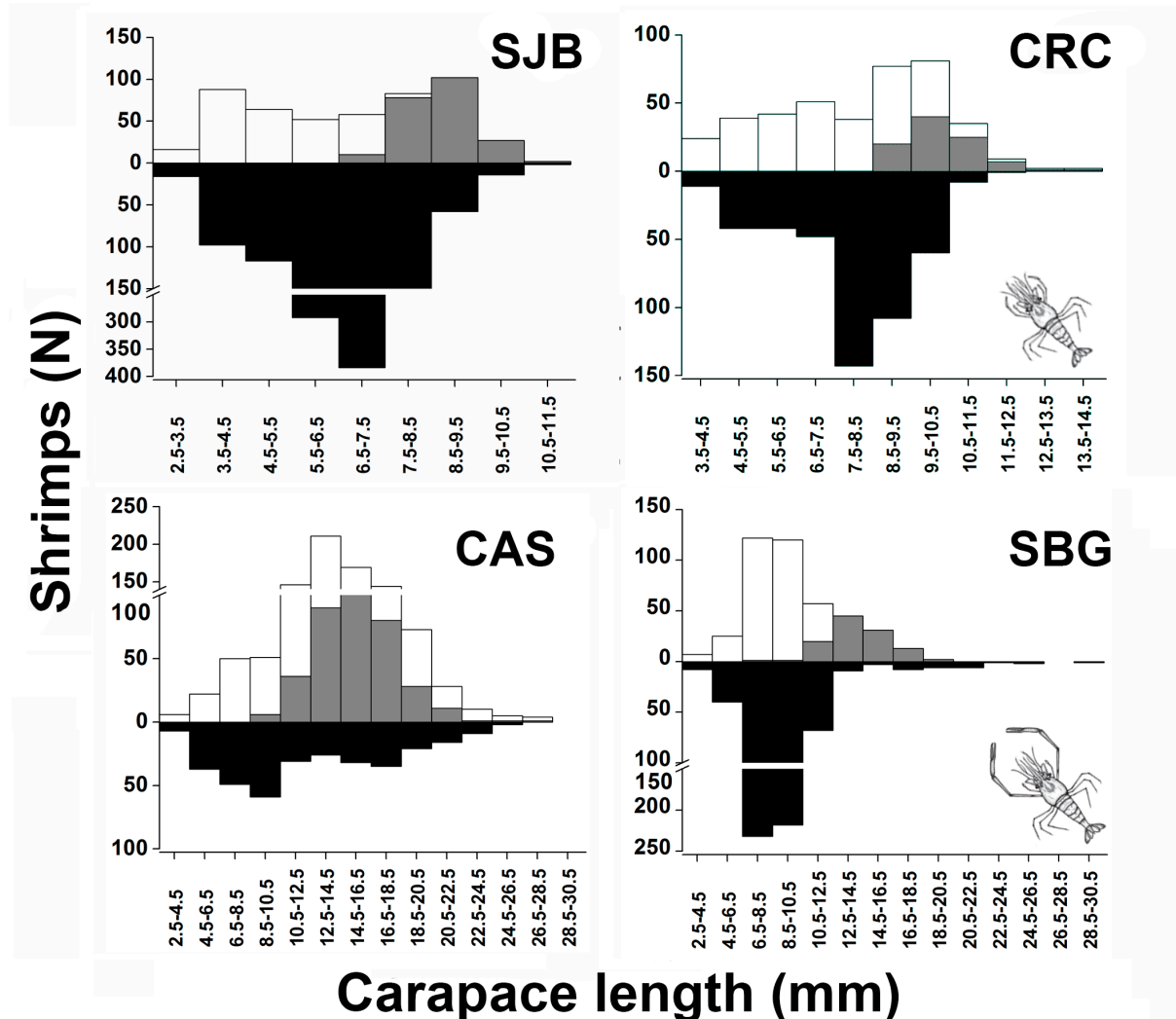

Figure 2 – Length-frequency distributions (carapace length in mm) for non-ovigerous females (white), ovigerous females (gray) and males (black) of *M. amazonicum* in small-size (SJB and CRC) and large-size (CAS and SBG) populations collected from October 2014 to December 2015. Abbreviations: CAS = Cássia; CRC = Carmo do Rio Claro; SBG = São João Batista do Glória; SJB = São José da Barra. Prawn illustrations were adapted from Pantaleão *et al.* (2014).

p: 0.02; ♀ = W: 0.90 - *p*: 0.17) and SBG (♂ = W: 0.66 - *p* < 0.001; ♀ = W: 0.70 - *p*: 0.09), while males only exhibited a normal distribution in the CAS population (♂ = W: 0.94 - *p*: 0.47; ♀ = W: 0.80 - *p* < 0.01) (Fig. 2). In all studied populations, females reached significantly larger body sizes than males (SJB - *t*: -21.50, CRC - *t*: 13.68, CAS - *t*: -6.69 and SBG - *t*: 9.59; *p* < 0.0001) (Fig. 3).

In CRC, the total sex ratio was close to 1♀:1♂, without predominance of either sex (1♀:1.11♂ - χ²: 1.13, *p*: 0.05). Males predominated in SJB (1♀:1.69♂ - χ²: 51.70, *p* < 0.001) and SBG (1♀:1.21♂ - χ²: 4.93, *p* < 0.001). In CAS, there was a predominance of females (4.22♀:1♂ - χ²: 293.02, *p* < 0.001). The sex ratio did not change over the months in CRC. The number of males in the SJB population was almost always greater than the number of females, varying from 1♀:1.08♂ (January 2015 - χ²: 0.08, *p*: 0.05) to 1♀:8.20♂ (November 2014 - χ²: 14.09, *p* < 0.001), with the exception of August 2015, when females predominated (1.82♀:1♂ - χ²: 7.10, *p* < 0.001). Differences in sex ratios over the months were recorded for the CAS population with a female bias. In CAS, the sex ratio ranged from 1.51♀:1♂ (November 2015 - χ²: 1.54, *p*: 0.05) to 19♀:1♂ (September 2015 - χ²: 32.40, *p* < 0.001). In the SBG population, the sex ratio did not change throughout the study, with the exception of April 2015, when males predominated (1♀:4♂ - χ²:10.75, *p* < 0.001) (Fig. 4).
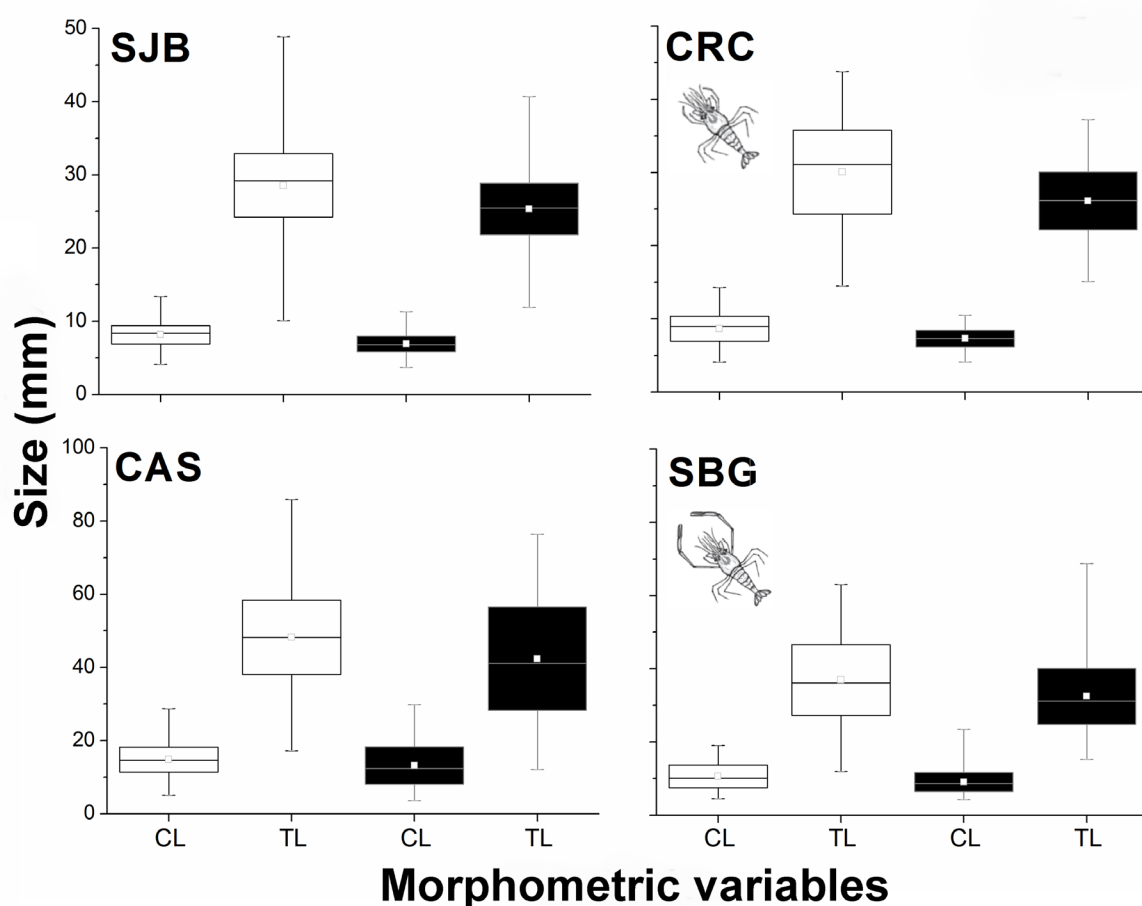

Figure 3 – Minimum, maximum (whiskers), and mean values (squares), and standard deviations (boxes) of carapace length (CL) and total length (TL) for females (white) and males (black) of *M. amazonicum* in small-size (SJB and CRC) and large-size (CAS and SBG) populations collected from October 2014 to December 2015. Abbreviations: CAS = Cássia; CRC = Carmo do Rio Claro; SBG = São João Batista do Glória; SJB = São José da Barra. Prawn illustrations were adapted from Pantaleão *et al.* (2014).
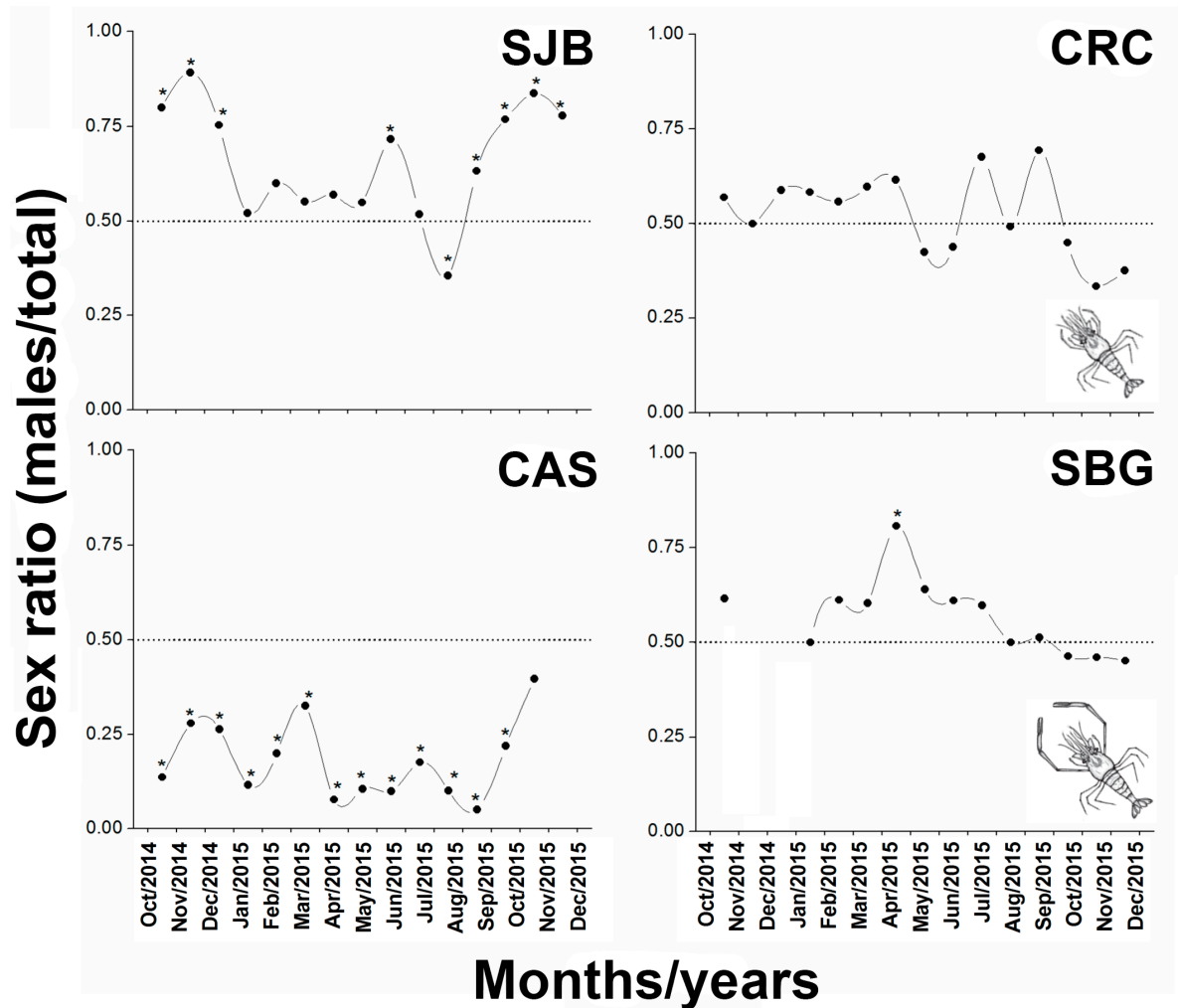
Figure 4 – Sex ratio (males/total) in small-size (SJB and CRC) and large-size (CAS and SBG) populations of *M. amazonicum* collected from October 2014 to December 2015. Abbreviations: CAS = Cássia; CRC = Carmo do Rio Claro; SBG = São João Batista do Glória; SJB = São José da Barra. * Statistically significant at $p < 0.05$. Prawn illustrations were adapted from Pantaleão *et al.* (2014).

All populations exhibited bimodal or polymodal patterns in their monthly length-frequency distributions. The population structure did not change between the periods of climate neutrality, onset of El Niño and in El Niño during the analyzed period (Figs 5–6). Except for the CAS population, which had its highest abundance in December 2014 (Fig. 6), all other populations had their highest abundances during the peak of the El Niño event (Figs 5–6). Due to the severe regional drought, the SBG population was not sampled in the months of November 2014 and December 2014, as all water masses in this location had disappeared. After the recovery of water levels in this sampling area, there was a rapid recovery of the structural patterns in this population. The sampling point of the CAS population was inaccessible due to a regional flood in December 2015, preventing sampling (Fig. 6).

In small-size populations, the percentages of immature individuals among the samples were approximately 15% (N: 282) in SJB and 11% (N: 92) in CRC, with recruitment peaks during spring and summer (Fig. 5). In the large-size population of CAS, 8% (N: 122) of the collected prawns were recruits, without a clear recruitment pattern during the study period. The SBG population, with 18% (N: 203) of immature individuals, was the only population showing an almost continuous recruitment pattern during the sampling months (Fig. 6).
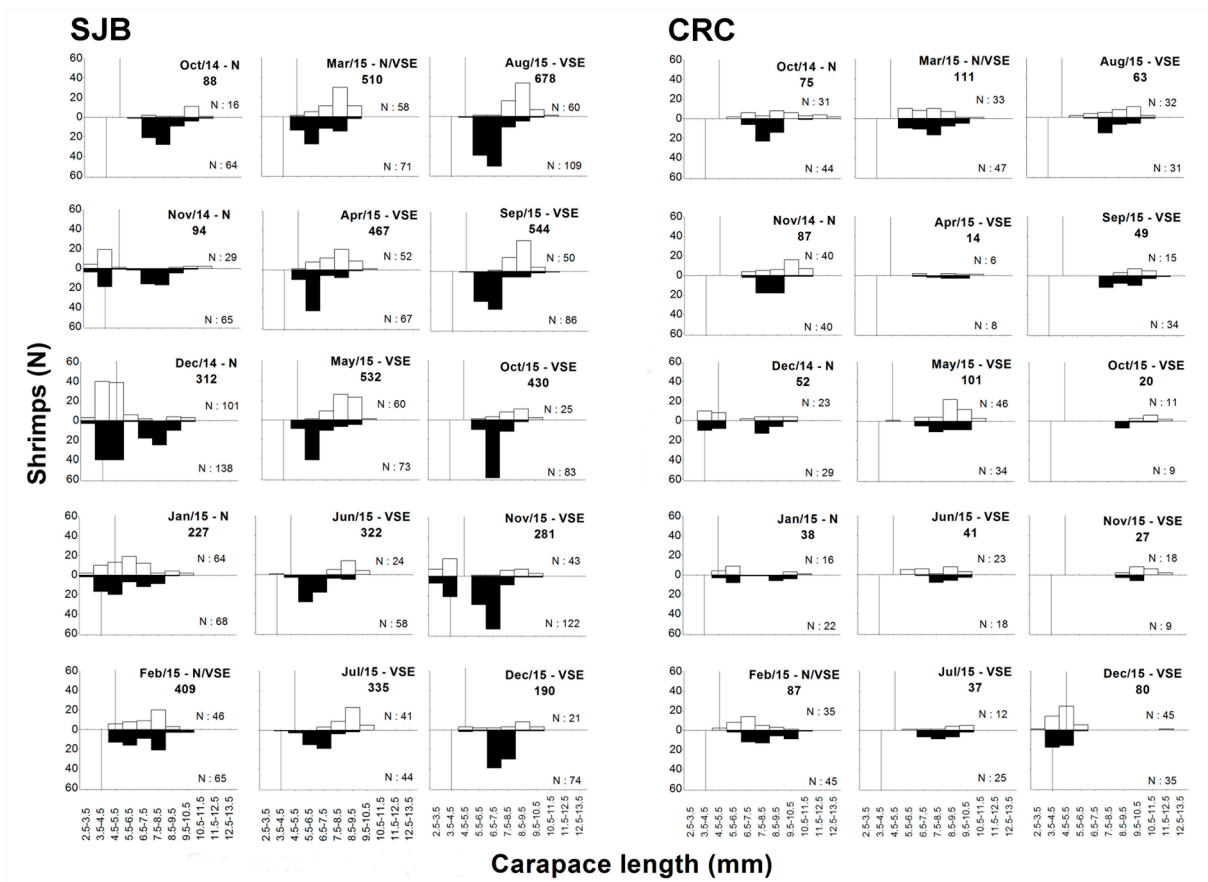
Figure 5 – Distribution of monthly length frequency estimated as carapace length (mm) in females (white) and males (black) of *M. amazonicum* sampled from October 2014 to January 2015 in the small-size populations of SJB and CRC (Minas Gerais, southeastern Brazil). Values in bold correspond to the total number of captured individuals. The lines indicate the beginning of recruitment in the population. Abbreviations: CRC = Carmo do Rio Claro; SJB = São José da Barra; N = neutral period; N/VSE = onset of El Niño; VSE = El Niño event.

Females with different stages of ovarian development were observed monthly in all populations, illustrating an absence of ovarian maturation peaks in *M. amazonicum*. In all populations, females in initial (I and II) and intermediate (III) stages of ovarian maturation were more abundant (Fig. 7). In small-size populations, the number of females in initial stages increased as water levels in the reservoirs rose (r = 0.68, *p* < 0.01) and tended to decrease with increasing rainfall (r = -0.15, *p*: 0.25). In large-size populations, females in initial stages followed an inverse pattern, with a tendency to increase their relative frequency with increasing rainfall (r = 0.44, *p*: 0.09) and decrease their frequency with increasing reservoir levels (r = -0.05, *p*: 0.86) (Fig. 7). In all populations, the majority of ovigerous females carrying egg masses in initial stage (1) had immature or intermediate stage ovaries, while the majority of females carrying eyed eggs (stages 2 and 3) had ovaries in final stages of development (Fig. 8).

In males from large-size populations, dominant morphotypes were less frequent than others. Commonly, the initial morphotype TC was the most abundant, especially in the SBG population (Fig. 9). In CAS, 42.67% of males were TC, 27.04% were CC, 18.57% were GC1 and 11.73% were GC2, with a ratio of 4 TC: 3 CC: 2 GC1: 1 GC2. In this population, the presence of morphotypes tended to decrease with increasing rainfall (r = -0.34, *p*: 0.23) and did not correlate with water levels (r = 0.03, *p*: 0.93). On
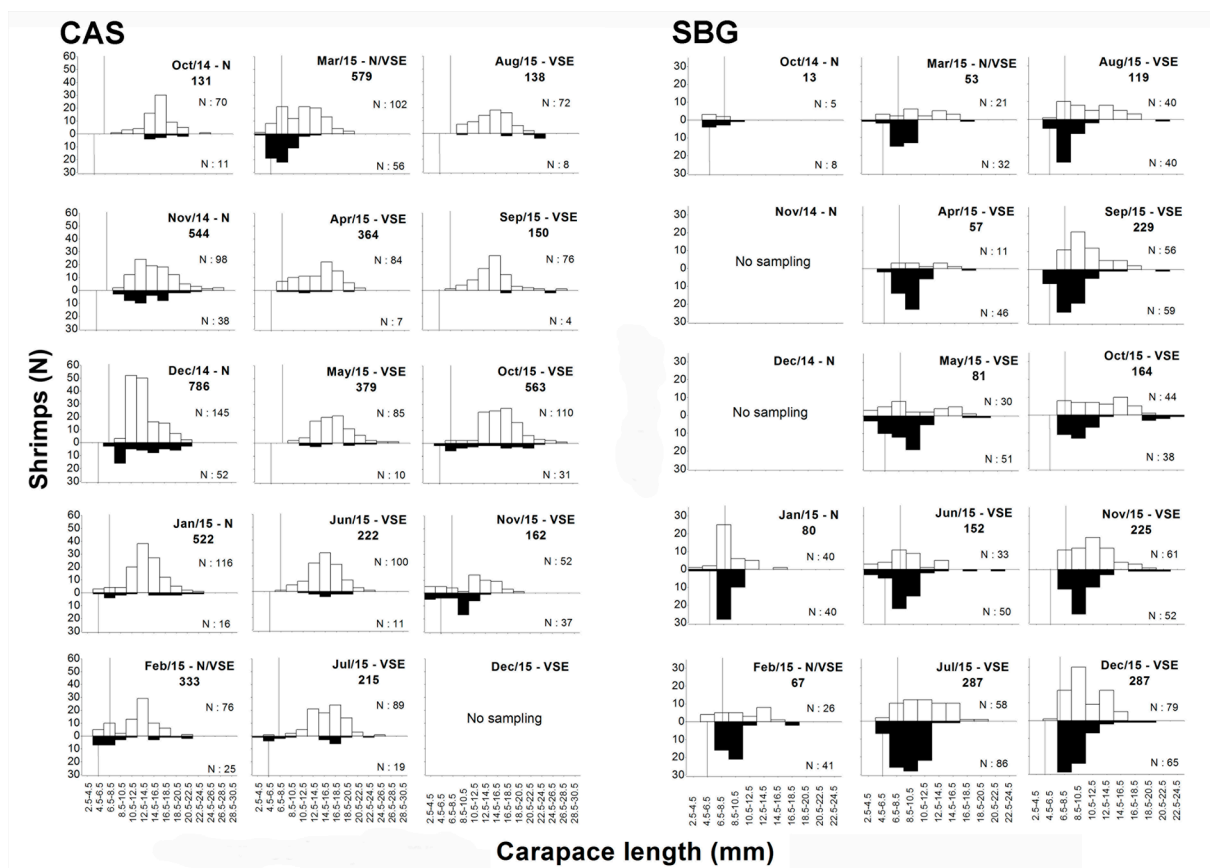
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Figure 6 – Distribution of monthly length frequency estimated as carapace length (mm) in females (white) and males (black) of *M. amazonicum* sampled from October 2014 to January 2015 in the large-size population of CAS and SBG (Minas Gerais, southeastern Brazil). Values in bold correspond to the total number of captured individuals. The lines indicate the beginning of recruitment into the population. Abbreviations: CAS = Cássia; N = neutral period; N/VSE = onset of El Niño; SBG = São João Batista do Glória; VSE = El Niño event.

the other hand, the presence of dominant morphotypes was related to the abundance of females in the population (r = 0.61, *p*: 0.02). In months with a lower occurrence of females, such as February 2015 and November 2015 (67 and 60%, respectively, Fig. 6), no males with GC1 and GC2 morphotypes were found. In the SBG population, 79.22% of males were TC, while 17.62% were CC and only 1.35 and 1.81% were GC1 and GC2, respectively. The proportion of morphotypes in this population was 7.9 TC: 1.8 CC: 0.1 GC1: 0.2 GC2. The abundance of dominant morphotypes in this population had a little connection with occurrence of females (r = 0.23, *p*: 0.48) and was not directly related with water levels (r = -0.09, *p*: 0.74) or accumulated precipitation (r = -0.14, *p*: 0.62) in this area.

Six species of predatory fish were recorded in both reservoirs: the characiforms *Astyanax fasciatus* (Cuvier, 1819), *A. lacustris* (Lütken, 1875) and *Hoplias malabaricus* (Bloch, 1794), the siluriform *Pimelodus maculatus* (Lacèpéde, 1803), and the cichlids *Oreochromis niloticus* Linnaeus, 1758) and *Cichla kelberi* (Kullander & Ferreira, 2006) (Table 1). Due to the similarity of the ichthyofauna in the reservoirs, the raw data regarding fish sampling were grouped and the food items found in the stomachs of fishes were separated into the following categories: *M. amazonicum*, fishes, egg masses, debris, insects, plant fragments and bait. It can be seen that *H. malabaricus* and *C. kelberi* both had *M. amazonicum* as one of the main components of their diets, while the other fish species were more generalist (Fig. 10, Table 1). Typically, the exoskeletons of preyed prawns were intact, but lacking appendages.
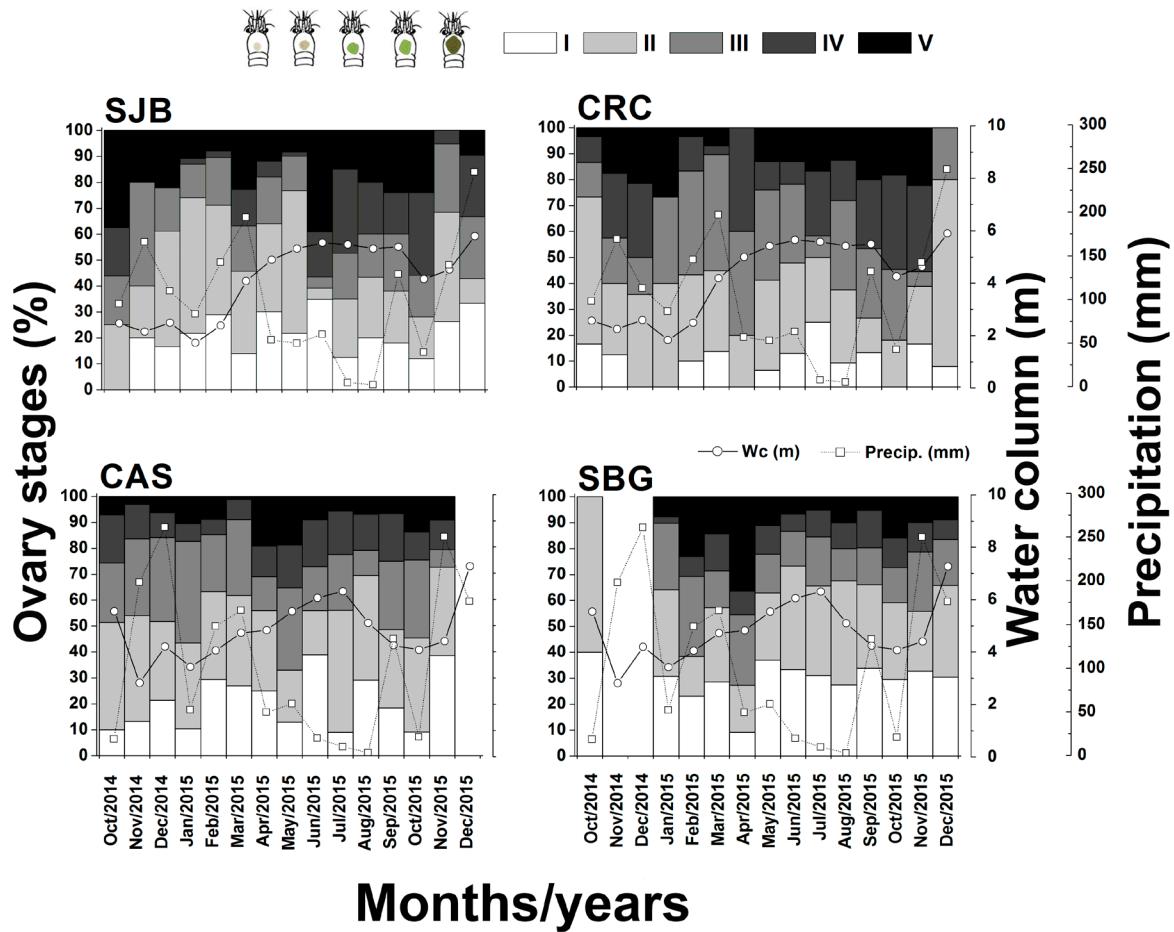
Figure 7 – Variations in the relative frequency of ovarian development stages (I to V) in females of *M. amazonicum* in small-size (SJB and CRC) and large-size (CAS and SBG) populations and values of accumulated precipitation and water levels sampled from October 2014 to December 2015. Abbreviations: CAS = Cássia; CRC = Carmo do Rio Claro; SBG = São João Batista do Glória; SJB = São José da Barra.

Discussion

The populations of *M. amazonicum* from both Neotropical reservoirs had different population and reproductive patterns, despite occurring in distinct parts of the same water system. Furthermore, these aquatic environments are structurally homogeneous and have similar physicochemical characteristics, as verified by Paschoal *et al.* (2019a). Therefore, the differences found between populations may be more related to intrinsic characteristics (i.e., genetic characters and physiological differences) than to environmental variations but this needs to be further studied. This pattern differs from the one found by Freire *et al.* (2017) in populations of *M. amazonicum* in the Tucuruí reservoir (state of Pará, northern Brazil) who described distinct morphological groups in populations from the same river basin. However, they associated such phenotypic changes with variations in salinity and water flow, environmental parameters to which the animals were exposed.

In all populations of the current study, females were significantly larger than males and also dominated the CAS population. On the other hand, males were more frequent in the SJB population while there was no predominance of any of the two sexes in the other two populations. The differences in size
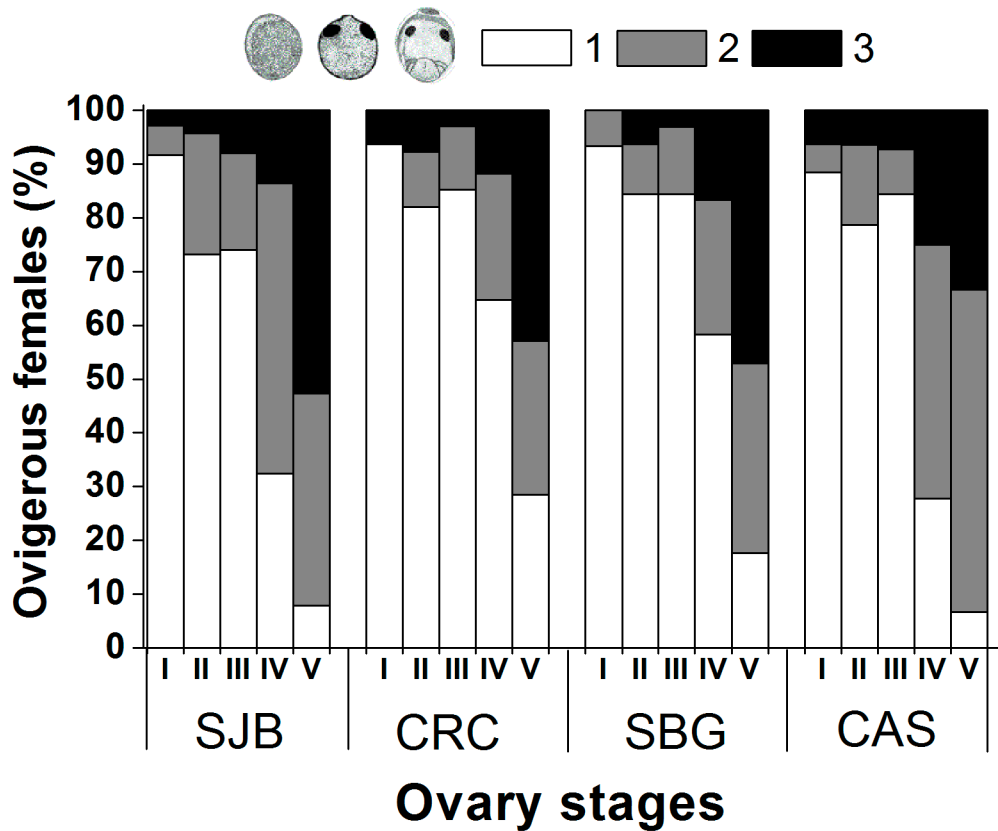
Figure 8 – Variations in the cumulative relative frequency of ovarian development stages (I to V) in ovigerous females of *M. amazonicum* with eggs at different embryonic stages (1 to 3) in small-size (SJB and CRC) and large-size (CAS and SBG) populations sampled from October 2014 to December 2015. Abbreviations: CAS = Cássia; CRC = Carmo do Rio Claro; SBG = São João Batista do Glória; SJB = São José da Barra. Egg illustrations were adapted from Habashy *et al.* (2012).

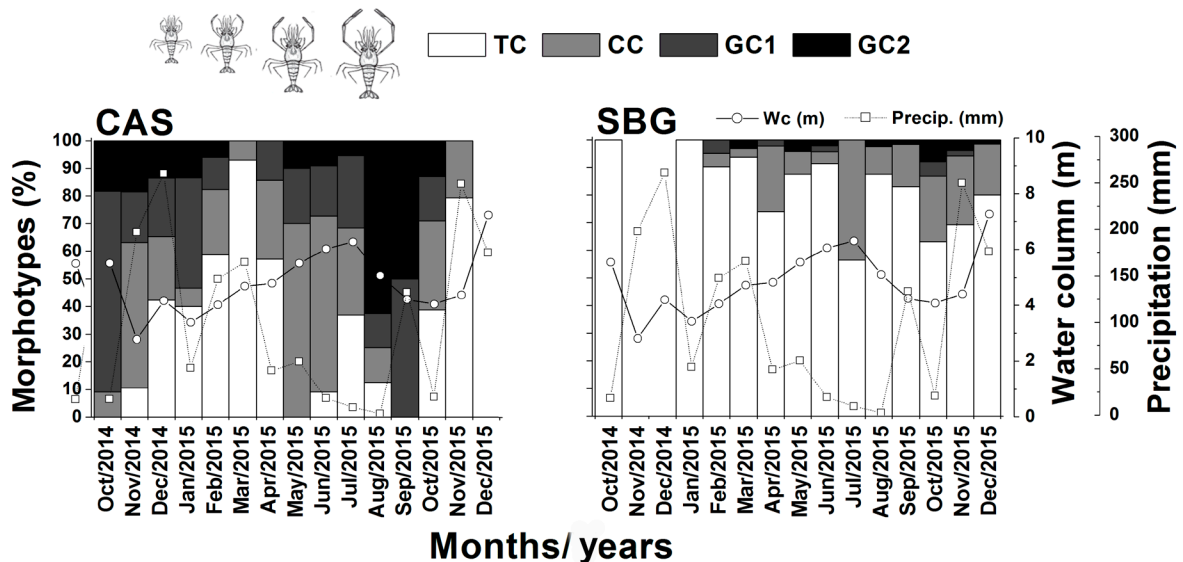Figure 9 – Variations in the relative frequency of male morphotypes of *M. amazonicum* in large-size populations (CAS and SBG) and in the values of accumulated precipitation and water levels from October 2014 to December 2015. Abbreviations: CAS = Cássia; CC = cinnamon claw; GC1 = green claw 1; GC2 = green claw 2; SBG = São João Batista do Glória; TC = translucent claw. Prawn illustrations were adapted from Pantaleão *et al.* (2014).

TABLE 1

Food items identified in the stomachs of fishes caught at the Furnas and Marechal Mascarenhas de Morais (MMM) hydroeletric power stations (HPS). To carry out the multiple correspondence analysis, the items were grouped into absence (0) and presence (1) categories. Abbreviation: M.a. = *Macrobrachium amazonicum*.

Species	Furnas HPS	MMM HPS	Stomach contents						
	N	N	*M.a.*	Fish	Eggs	Debris	Insects	Plants	Bait
Astyanax fasciatus	332	500	1	1	1	1	0	1	1
Astyanax lacustris	216	300	1	1	1	1	0	1	1
Pimelodus maculatus	5	15	1	1	1	1	1	0	0
Oreochromis niloticus	3	3	1	1	0	1	0	0	1
Hoplias malabaricus	3	4	1	1	0	0	0	0	0
Cichla kelberi	3	4	1	1	0	0	0	0	0

between the sexes of *M. amazonicum* can be explained by the precocity of sexual maturity observed in males and by the investment in either robust chelipeds (i.e., sexual weapons) in the large-size male phenotype or sperm production in the small-size phenotype reducing the body growth of these animals (Paschoal & Zara 2020, 2022). Larger body size in females could be directly related to the optimization of reproductive success, as larger spawns are associated with larger body sizes (Paschoal *et al.* 2019b, Paschoal & Zara 2023). According to Fisher (1930), natural selection favors the production of offspring in a 1♀:1♂ ratio, with equal costs for the production of each sex. However, Wilson & Pianka (1963)
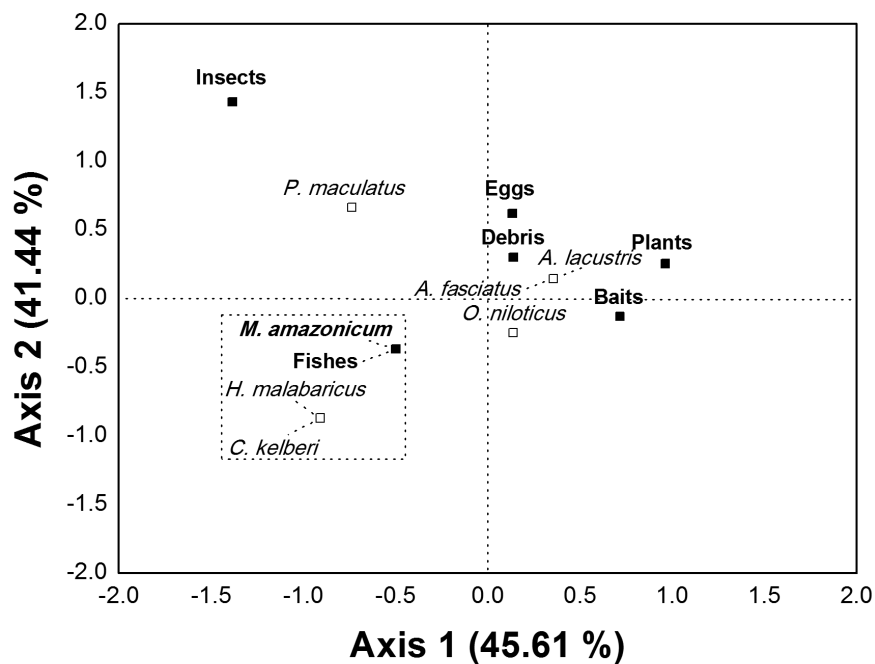

Figure 10 – Dimensional plot of food resources (black squares) used by the ichthyofauna (white squares) of the Furnas and Marechal Mascarenhas de Morais hydroelectric power stations using multiple correspondence analysis.

pointed out that the sex ratio might be biased by several factors (e.g., available nutrients, habitat type, mortality and different growth rates). Commonly, populations of *M. amazonicum* are dominated by females with larger body proportions and this pattern has been associated with differences in mortality rates, differential recruitment, migration and specific predation (Odinetz-Collart 1991b; Hayd & Anger 2013; Lima *et al.* 2014; Rocha *et al.* 2015; Costa *et al.* 2016). Odinetz-Collart (1991b) suggested that such a sex ratio pattern is typical for populations from lentic environments, although in the current study, only the CAS population fits this pattern. Paschoal *et al.* (2013) suggested that caridean shrimps perform circadian migrations to search for food, copulate and regulate physiological processes, and that males and females may use different niches, which would explain the predominance of a certain sex in a location over time. Such niche differentiation is expected to occur also in the populations of *M. amazonicum* analyzed here since dominant males (morphotypes GC1 and GC2) had nocturnal and cryptic habits (they usually live hidden during daylight in shelters) and ovigerous females sought refuge in macrophytes or shallow areas near the shore (Paschoal & Zara 2020; Paschoal *et al.* 2019a).

The population structure of *M. amazonicum* in the analyzed Neotropical reservoirs was not significantly affected by drought events. In crustaceans, the distribution of size-class frequencies varies throughout the year due to recruitment, mortality, behavioral patterns and the ability to adapt to the environment (Tsuchida & Watanabe 1997). Unimodality in distribution is common in tropical crustaceans and is related to reproductive events and continuous recruitment over time (Goodbody 1965; Diáz & Conde 1989). On the other hand, bimodality or polymodality would mainly indicate the seasonality of events and/or high peaks of recruitment and mortality in a given population (Ragonese & Bianchini 1996). The latter distribution pattern was observed in all *M. amazonicum* populations from the two sampled reservoirs. These reservoirs are environments altered by anthropogenic impacts and being characterized by intense fluctuations in the level of the water column, which cause instability in some benthic communities and alter aspects of the population and reproductive biology of certain species (Andrade *et al.* 2012; Paschoal *et al.* 2015, 2020; Sousa *et al.* 2021). However, *M. amazonicum* showed a high adaptive capacity in the current study to environmental variations and resilience to adverse weather conditions, with the continuous presence of viably reproductive animals and recruitment of juveniles over time, even during drought events. Similar to the present study, Odinetz-Collart (1991b), described a rapid response to environmental changes by the Amazon River prawn after the construction of the Tucuruí hydroelectric power station. The author analyzed the negative impacts of the project on populations of *M. amazonicum*, noting changes in the population structure of the shrimp species at the start of the construction, which stabilized shortly afterwards with this species quickly recovering its normal patterns.

Females of *M. amazonicum* showed continuous reproduction in the current study, with no peaks in ovarian maturation over time and a higher frequency of females with immature ovaries in the populations. Many ovigerous females with immature ovaries carried eggs at the initial stage while females with mature ovaries carried fertilized eggs (stages 2 and 3), indicating that females of *M. amazonicum* can restart their reproductive cycle and reproduce again immediately after spawning. These patterns were also observed in populations of this species in lotic environments (Sampaio *et al.* 2007; Bentes *et al.* 2011), as well as in other species of the genus *Macrobrachium* (Valenti *et al.* 1986; Mossolin & Bueno 2002). In small-size populations, females with immature and intermediate ovaries were more frequent in months with higher water levels, while they were more abundant in rainy months in large-size populations. Odinetz-Collart (1991a, 1991b) pointed out that females of *M. amazonicum* undergo multiple spawnings and that gonadal maturation may be associated with an increase in the volume or flow of rivers. The author noted that this strategy could have a double adaptive value, as it can facilitate larval dispersal due to the increase in flooded areas promoted by rain or increase the food availability for larvae during the rise up of water column levels.

The initial male morphotype TC was most frequent in populations with social hierarchy, followed by the intermediate morphotype CC, while the dominant morphotypes GC1 and GC2 were much less frequent. This pattern of sequential decrease in morphotypes was also recorded by Pantaleão *et al.* (2014) in *M. amazonicum* males (2 TC: 1 CC: 1 GC1: 1 GC2) and by Cohen *et al.* (1981) in *M. rosenbergii* (De Man, 1879) (5 small male - SM: 4 orange claw - OC: 1 blue claw - BC). However, it differs from the results obtained by Santos *et al.* (2006) (3 TC: 6 CC: 1 GC in *M. amazonicum*) and Iketani *et al.* (2016) (2 SM: 5 OC: 3 BC in *M. rosenbergii*), in which the authors obtained a greater number of individuals with the intermediate morphotype. When analyzing the physiological differences between male morphotypes in *M. amazonicum*, Augusto & Valenti (2016) found that dominant morphotypes required higher rates of daily food intake and had greater oxygen consumption than submissive animals. Additionally, the authors observed that these individuals were sedentary and had reduced swimming capacity due to their robust chelipeds. Thus, it is possible that the lower number of dominant morphotypes in the analyzed populations can be attributed to a higher energy cost for maintaining metabolic processes and difficulties in obtaining the resources required to carry out such processes.

No evidence was found for the induction of different male morphotypes in *M. amazonicum* by predation by fishes in the analyzed populations, as both phenotypes (with or without different male morphotypes) were recorded in both hydroelectric power stations despite coexisting alongside predatory fishes. In the caridean shrimp *Xiphocaris elongata* (Guérin-Méneville, 1855), exposure to predatory fishes was causing body changes in this species, leading to two different phenotypes with a long rostrum (LR) and short rostrum (SR), respectively. In addition to having a longer rostrum, LR shrimps had larger and heavier abdomens when compared to SR shrimps (Ocasio-Torres *et al.* 2014, 2015a, 2015b). These authors attributed the phenotypic changes in these shrimps to physiological responses to chemical signals from predators (i.e., kairomones). However, such a response was not observed for the *M. amazonicum* populations studied here, since the captured ichthyofauna was identical in both reservoirs and predation was greater on females (Paschoal, personal observation). Thus, the absence or presence of morphotypes in these *M. amazonicum* populations appears to be associated to intrinsic factors and the abundance of males with dominant morphotypes is better correlated to the number of females in the populations.

Conclusions

Macrobrachium amazonicum proved to be a resilient species, as the population and reproductive dynamics of this species in the analyzed Neotropical reservoirs were not significantly altered by drought events, thus rejecting the initial hypothesis, water scarcity acting as a stressing factor by modifying the population biology and reproductive patterns of the Amazon River prawn. In this species, females are larger than males, as they tend to allocate more energy to body growth, which is directly correlated to spawn size. Males tend to invest energy in acquiring robust chelipeds or in sperm production, reducing their body size. In *M. amazonicum*, there was no clear pattern of sex ratios illustrating the great reproductive flexibility of this species. The Amazon River prawn shows continuous reproduction, with females having a rapid ovarian maturation cycle and the ability to perform multiple spawnings. Populations with different male morphotypes include a larger number of males with submissive morphotypes; dominant male morphotypes require a large amount of energy to maintain metabolic processes, which can limit their proportion in populations. Predation by fish does not seem to influence the presence of different male morphotypes in *M. amazonicum* populations.

Acknowledgements

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Appendix

TABLE S1

Quantity of non-ovigerous and ovigerous females, males and indetermined prawns of *M. amazonicum* analyzed in subsamples of small-size (SJB and CRC) and large-size (CAS and SBG) populations collected from October 2014 to December 2015. Abbreviations: CAS = Cássia; CRC = Carmo do Rio Claro; SBG = São João Batista do Glória; SJB = São José da Barra.

Sampling site	Non ovigerous females analysed	Ovigerous females analysed	Males analysed	Indetermined analysed	Prawns analysed
SJB	309	219	1027	160	1715
CRC	256	94	391	75	816
CAS	890	355	295	30	1570
SBG	384	113	601	7	1105

TABLE S2

The total number of collected prawns (N), prawns analyzed in subsamples (n) and females and males analyzed in these subsamples in small-size (SJB and CRC) and large-size (CAS and SBG) populations collected on a monthly basis from October 2014 to December 2015. Abbreviations: CAS = Cássia; CRC = Carmo do Rio Claro; SBG = São João Batista do Glória; SJB = São José da Barra.

Sampling site	Month/year	Prawns collected (N)	Subsample analysed (n) according to Wenner *et al.* (1991)	Females analysed	Males analysed
SJB	Oct/14	88	80	16	64
CRC	Oct/14	75	75	31	44
CAS	Oct/14	131	81	70	11
SBG	Oct/14	13	13	5	8
SJB	Nov/14	94	94	29	65
CRC	Nov/14	87	80	40	40
CAS	Nov/14	544	136	98	38

Sampling site	Month/year	Prawns collected (N)	Subsample analysed (n) according to Wenner *et al.* (1991)	Females analysed	Males analysed
SBG	Nov/14	–	–	–	–
SJB	Dec/14	312	239	101	138
CRC	Dec/14	52	52	23	29
CAS	Dec/14	786	197	145	52
SBG	Dec/14	–	–	–	–
SJB	Jan/15	227	132	64	68
CRC	Jan/15	38	38	16	22
CAS	Jan/15	522	132	116	16
SBG	Jan/15	80	80	40	40
SJB	Feb/15	409	111	46	65
CRC	Feb/15	87	80	35	45
CAS	Feb/15	333	101	76	25
SBG	Feb/15	67	67	26	41
SJB	Mar/15	510	129	58	71
CRC	Mar/15	111	80	33	47
CAS	Mar/15	579	158	102	56
SBG	Mar/15	53	53	21	32
SJB	Apr/15	467	119	52	67
CRC	Apr/15	14	14	6	8
CAS	Apr/15	364	91	84	7
SBG	Apr/15	57	57	11	46
SJB	May/15	532	133	60	73
CRC	May/15	101	80	46	34
CAS	May/15	379	95	85	10
SBG	May/15	81	81	30	51
SJB	Jun/15	322	82	24	58
CRC	Jun/15	41	41	23	18
CAS	Jun/15	222	111	100	11
SBG	Jun/15	152	80	33	47
SJB	Jul/15	335	85	41	44
CRC	Jul/15	37	37	12	25
CAS	Jul/15	215	108	89	19
SBG	Jul/15	287	144	58	86
SJB	Aug/15	678	169	60	109
CRC	Aug/15	63	63	32	31
CAS	Aug/15	138	80	72	8
SBG	Aug/15	119	80	40	40
SJB	Sep/15	544	136	50	86
CRC	Sep/15	49	49	15	34

Sampling site	Month/year	Prawns collected (N)	Subsample analysed (n) according to Wenner *et al.* (1991)	Females analysed	Males analysed
CAS	Sep/15	150	80	76	4
SBG	Sep/15	229	115	56	59
SJB	Oct/15	430	108	25	83
CRC	Oct/15	20	20	11	9
CAS	Oct/15	563	141	110	31
SBG	Oct/15	164	82	44	38
SJB	Nov/15	281	165	43	122
CRC	Nov/15	27	27	18	9
CAS	Nov/15	162	89	52	37
SBG	Nov/15	225	113	61	52
SJB	Dec/15	190	95	21	74
CRC	Dec/15	80	80	45	35
CAS	Dec/15	–	–	–	–
SBG	Dec/15	287	144	79	65