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ORIGINAL ARTICLE

Filling gaps in the biology of the endemic and threatened freshwater shrimp *Macrobrachium candango* (Caridea: Palaemonidae) through basic morphometric and reproductive approaches

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ABSTRACT

Macrobrachium candango Mantelatto, Pileggi, Pantaleão, Magalhães, Villalobos and Álvarez, 2021 is an endemic shrimp species to the Brazilian Central-West region (Brasília, Federal District). The present study aims to analyze the relative growth, morphometry, morphological sexual maturity, and fecundity of this species. Specimens were collected from tributaries of the Paranoá Lake hydrographic basin, Brasília, during sporadic periods between 1983 and 2012. Relative growth was analyzed for different structures (carapace, abdomen, second abdominal pleura, merus, carpus, and propodus). The laterality and heterochely patterns were evaluated based on the dimensions of the propodus length. Fecundity was calculated as the average total number of eggs per female and egg size was measured to obtain the volume. There were differences in relative growth ($p < 0.05$) of the structures analyzed between juveniles and adults, and distinct allometric patterns were observed between the life stages, which could reflect the habit of these animals at each developmental stage. No pattern of laterality and heterochely was observed between the chelipeds of the animals analyzed ($p > 0.05$). The lack of laterality may indicate that this species directs energy to the smallest propodus when the largest propodus is injured. Egg volume ranged from 4.41 to 7.71 mm^3, and fecundity ranged from 38 to 61 eggs, indicating a life cycle with abbreviated larval development. The characteristics presented herein are unprecedented for *M. candango* and present relevant information needed to assess the conservation status of this species, which is currently threatened.

KEYWORDS

Conservation, fecundity, heterochely, laterality, relative growth

INTRODUCTION

Freshwater shrimps present great examples of adaptation to environments that constantly change or fluctuate, as they present a complex set of characters regarding reproduction, behavior, growth and morphology throughout their lifecycles, that are closely linked to habitat and life history (Holthuis, 1952; Pereira, 1997; Bauer, 2004; Anger, 2013). Among the most complex aspects of the evolutionary process of this taxon is the embryonic development that can be abbreviated or extended, which directly affects the number and size of eggs that will be incubated (Magalhães and Walker, 1988; Sankoli *et al.*, 1993; Odinetz-Collart and Magalhães, 1994; Pereira and Garcia, 1995), and represents a phylogenetic premise in some groups (Pileggi and Mantelatto, 2010).

In Brazil, the family Palaemonidae is widely diverse, with species occupying different environments from the coastal region to inland waters in different watersheds (Coelho and Ramos-Porto, 1984; Pileggi and Mantelatto, 2010; Mantelatto *et al.*, 2016). Among the genera of this diverse family, the Brazilian species of *Macrobrachium* Spence Bate, 1868 received special attention during the last decade with regard to updated taxonomy (Pileggi and Mantelatto, 2012; Dos Santos *et al.*, 2013; Mantelatto *et al.*, 2016; Rossi *et al.*, 2020), and most recently a taxonomic revision proposed a new nomenclatural and phylogenetic rearrangement in which all the six American species of the genus *Cryphiops* Dana, 1852 were accommodated in the genus *Macrobrachium* (see Mantelatto *et al.*, 2021). Regarding this latter group, the only known species from Brazilian territory is *Macrobrachium candango* Mantelatto, Pileggi, Pantaleão, Magalhães, Villalobos and Álvarez, 2021 (originally described as *Cryphiops brasiliensis* Gomes Corrêa, 1973), which is endemic to the Paranoá Lake hydrographic basin in Brasília, Federal District (Gomes Corrêa, 1973; Mantelatto *et al.*, 2021).

The only information available on this species was registered in its description (Gomes Corrêa, 1973), which addressed its morphological characters and compared them with those of *Macrobrachium caementarius* (Molina, 1782) (as *Cryphiops caementarius*) occurring in coastal areas of Chile. In the same study, some observations about its fecundity were also reported (three ovigerous females incubated between 42 and 63 eggs). Reports from local collections and observations indicate that the abundance of *M. candango* is naturally low, with a high degree of endemism (Mantelatto *et al.*, 2016), causing the species to be categorized as threatened according to IUCN criteria. Additionally, their habitats have been affected by anthropogenic actions such as pollution and deforestation (Mantelatto *et al.*, 2016; 2021). Shrimps have an important ecological role within aquatic ecosystems (March *et al.*, 2002), and in the case of *M. candango*, which is an endemic species in a region of Brazil, its disappearance from the environment can cause irreversible problems to these ecosystems, influencing the local food chain (March *et al.*, 2002; De Souza and Moulton, 2005). Therefore, due to this degree of endemism, it is necessary to carry out constant monitoring studies addressing *M. candango*, in order to properly understand its ecological role in the Paranoá Lake ecosystem.

Faced with this scenario we searched for more information by visiting its type locality (ECM and FLM) to collect new specimens. During these field activities, we were positively surprised to find a considerable collection of lots of this species deposited at the Aquatic Crustaceans Collection of the Reserva Ecológica do IBGE (Instituto Brasileiro de Geografia e Estatística), Brasília - Federal District, which serve as the basis for the preparation of this article.

Thus, considering that knowledge about biological characteristics is fundamental for understanding the life cycle, and necessary for defining conservation strategies, particularly for species with low abundance and endemism, the present study aims to investigate basic aspects (relative growth, morphometry, morphological sexual maturity and fecundity) about the biology of *M. candango*. In the future this information can be used to assess the conservation status of this species.

Material and Methods

Scientific and field collections

The field collection resulted from surveys carried out in 122 lotic stretches of tributaries forming the Paranoá Lake hydrographic basin, collected from 28 sampling points distributed along the four main tributaries of the Paranoá Lake (Fig. 1): Riacho Fundo (three sites, including the type locality), Ribeirão do Torto (three sites), Ribeirão Bananal (five sites), and Ribeirão Gama (17 sites, 11 in the Taquara stream and six in the Roncador stream), which recorded the species in only 23 % of the sampled locations. The previous collection of *M. candango* deposited at the IBGE's Aquatic Crustaceans Collection consists of 345 lots containing 932 specimens. Samplings occurred sporadically between 1983 and 2012, specifically in November/1983; February, April and August/1985; November/1986; February and March/1987; May/1988 to April/1989; July/1989; May/1990; October/1992; September/1998; October/2005; September/2009; and May and July/2012. All collections were performed using trawls (mesh size 3 mm).

All locations where specimens were present in the streams of Torto and Bananal (Brasilia National Park), Roncador (IBGE Ecological Reserve) and Taquara (IBGE Ecological Reserve, Area of Relevant Ecological Interest Capetinga - Taquara and Ecological Station of the Botanical Garden of Brasilia) are within conservation units. Only the locations in Riacho Fundo, which includes the type locality, are not within an environmental protection area. Only one lot, with one specimen, was collected in a transition zone between the Milho Cozido stream and the Santa Maria Reservoir (Ribeirão do Torto), while all other specimens were captured in lotic environments of the Paranoá Lake tributaries.

The third author (MCLBR) and his team were responsible for all expeditions. Two permanent licenses issued by SUDEPE (Superintendência do Desenvolvimento Pesca; 1983 to 1989) and IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis) in the Federal District (1990 – 2009) allowed the collection of fish and aquatic crustaceans in these respective periods. Those responsible for the Conservation Units also authorized the collections. The surveys carried out in the Brasilia National Park, in 2012, were done in collaboration with CAESB (Companhia de Saneamento Ambiental do Distrito Federal) to prepare the environmental impact study about the Santa Maria Dam construction to renew the environmental license for that enterprise. Therefore, the authorization for scientific activity was issued directly by the ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade), with consent of the Brasilia National Park.

After sampling, the material was screened in the field and shrimps were placed in a solution of clove oil and water for five minutes for euthanasia, and later placed in containers with 70 % alcohol and deposited in the scientific collection of the Reserva Ecológica do IBGE.

Laboratory analysis

The sex of shrimps was checked under a stereomicroscope, following a protocol suggested by Valenti *et al.* (1989) for the genus *Macrobrachium*, which requires observing the presence (male) or absence (female) of the male appendage on the second

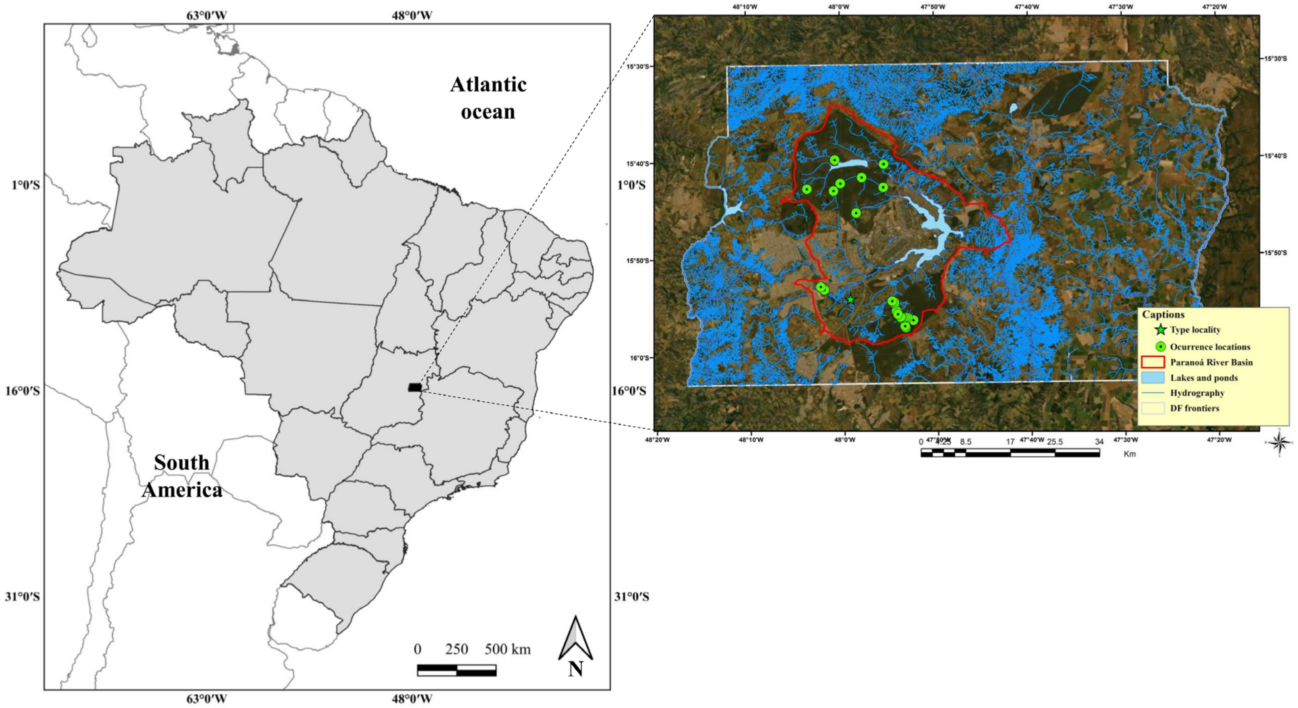

Figure 1. Brazilian territory and location of the study area in black, amplification of the study area showing streams from the Paranoá Lake basin in Brasília, Federal District, Brazil.

pair of pleopods. Subsequently, they were identified to species level according to Melo (2003) and the length of the following structures were measured with a caliper (0.01 mm): carapace (CL), abdomen (AL), merus (ML), carpus (CaL), and propodus (PrL), along with the width of the second abdominal pleura (PW) (Fig. 2). The merus, carpus, and propodus selected for analysis constitute the cheliped of the second largest pair of pereopods (independent of the side). All animals used in the analyses presented intact structures.

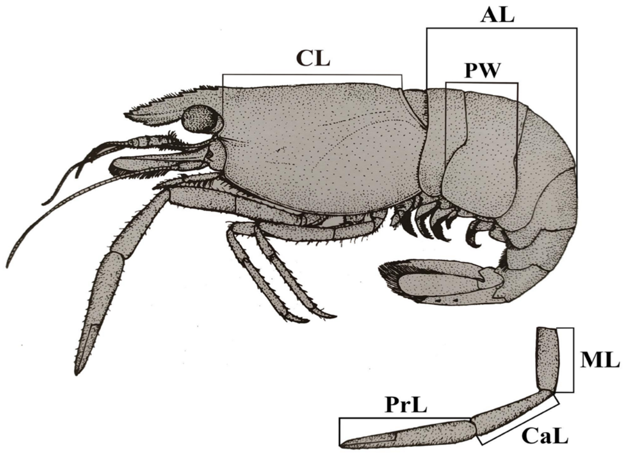

Figure 2. *Macrobrachium candango* Mantelatto, Pileggi, Pantaleão, Magalhães, Villalobos and Álvarez, 2021. Structures used in morphometric analyses: (CL) carapace length; (AL) abdomen length; (PW) pleura width; (ML) merus length; (CaL) carpus length; (PrL) propodus length. Adapted from Melo (2003).

Relative growth

The comparative analysis of body dimensions was based on the measurements described above. Data normality was verified with the Shapiro-Wilk test ($\alpha = 0.05$). The non-hierarchical analysis of K-means clustering (Sokal *et al.*, 1979) was used considering the morphometric relationships measured between the groups of males and females (juveniles and adults). This analysis distributes the data set into groups that are previously established by an interactive process, which minimizes the variance between groups. After determining K-means, a discriminant analysis was performed to refine the data for categorization (Sampedro *et al.*, 1999). Afterwards, the data was submitted to a covariance analysis (ANCOVA) to test the angular and linear coefficients between the groups defined by the analyzes. This showed whether the data for each relationship fit better to a single equation or whether morphometric relationships should be represented by different linear equations.

In the relative growth analysis, changes in the allometric coefficient were verified in the development of body structures related to the independent variable (CL). Scatter plots were constructed from the data set obtained by measuring body structures and adjusted to the allometric equation $y = ax^b$ (Hartnoll, 1974, 1978; Hawkins and Hartnoll, 1982). Subsequently, the data was linearized ($\log y = \log a + b \times \log x$) in which "y" is the structure dimension studied, "x" the carapace length, "a" the intersection of the axis "y" and "b" the allometric coefficient (angular) that represents the slope and angle of the line. The allometric constant "b" was calculated for each morphometric relationship and the null hypothesis (H_0: $b = 1$) was tested with the Student test ($\alpha = 95$ %). The values of the allometric constant correspond to isometric growth ($b = 1$), positive allometry ($b > 1$) or negative allometry ($b < 1$) (Zar, 2010).

Morphological sexual maturity was estimated from the inflection break of the points resulting from the lines drawn based on the equations of adults and juveniles in the CL x PrL and CL x PW relationships for males and females, respectively. These relationships were chosen because they best reflect the variations that occur during the reproductive phases (juveniles and adults) (Mantelatto and Barbosa, 2005; Pescinelli *et al.*, 2018).

Laterality and heterochely

The laterality pattern of males and females was investigated using the chi-square test ($\alpha = 0.05$) (Pearson, 1900), based on the propodus length of both chelipeds (right and left) of the second pair of pereopods.

The heterochely analysis was performed based on the final result of the laterality test, using the Kruskal-Wallis test and its Dunn's post-hoc test (Daniel, 1990). In the heterochely test, the largest propodus x smallest propodus (independent of the side) was compared due to the lack of laterality pattern.

Fecundity

Fecundity was obtained from the total number of eggs adhered to pleopods. Therefore, 15 eggs were removed from the pleopods of each ovigerous female (OF) and the length and width of eggs were measured under a stereomicroscope to calculate egg volume (Anger and Moreira, 1998). The egg volume (EV) was calculated as: $EV = \pi * l * h * (h)^2$; where "l" is the length; "h" is width in mm and $\pi = 3.14$ (Wehrtmann, 1990). The developmental stage of the embryos was classified into two stages, being early (eggs with homogeneous color and lacking visible eye pigmentation) and late (embryos with fully developed eyes) (Anger and Moreira, 1998). The relationships between CL/PW and CL/number of eggs were investigated using a linear regression. Monthly rainfall data for the years that ovigerous females occurred were obtained from the digital platform HidroWeb of the SNIRH (Sistema Nacional de Informações sobre Recursos Hídricos).

RESULTS

A total of 262 individuals were analyzed, including 157 males (59.9 %) and 105 females (40.1 %). The mean CL for males was 16.44 ± 4.34 mm, ranging from 6.8 to 25.2 mm, and for females was 11.5 ± 2.86 mm, ranging from 4.8 to 17.4 mm, with a significant difference in mean CL between sexes (Mann-Whitney, $p < 0.001$). To analyze the relative growth of the largest cheliped articles, a total of 166 individuals (102 males and 64 females) with intact appendages were examined.

Relative growth

The ANCOVA analysis (Tab. 1) showed that adult male individuals differed statistically ($p < 0.01$) from juvenile males in the morphometric relationships related to pleura and chelipeds (CL × PW, CL × PrL, CL × CaL, and CL × ML), however, in the CL × AL morphometric relationship there was no difference between these groups ($p > 0.05$). The same pattern occurred in females, with statistical difference ($p < 0.01$) between adult and juvenile females in almost all relationships investigated herein (CL × PW, CL × PrL, CL × CaL, and CL × ML), except for CL × AL ($p > 0.05$, Tab. 1).

Significant correlations were observed in all morphometric relationships ($p < 0.01$) (Tab. 2). Since the CL × AL relationship did not differ significantly (ANCOVA, $p > 0.05$) between the demographic categories (adults and juveniles) of both sexes, these were represented by a single equation obtained through linear regression analysis. For males, a negative allometric growth was observed for the CL × PW and CL × AL relationships. Regarding chelipeds (CL × PrL, CL × CaL, and CL × ML), a positive allometric pattern was observed for adult males. For juvenile males, isometry was observed for CL × PrL and negative allometry was observed for the other relationships (CL × CaL and CL × ML).

For females (adult and juvenile), negative allometry was observed in the relationship CL × AL, while a negative allometry and an isometry were observed for adults and juveniles, respectively, in the CL × PW relationship. Regarding chelipeds (CL × PrL, CL × CaL, and CL x ML), an allometric pattern was observed between adults and juveniles in all relationships, with negative allometric growth (Tab. 2).

Based on CL × PrL and CL × PW morphometric relationships, the size of morphological sexual maturity was estimated at 17.6 and 10.9 mm CL for males and females, respectively (Fig. 3).

Table 1. *Macrobrachium candango* Mantelatto, Pileggi, Pantaleão, Magalhães, Villalobos and Álvarez, 2021. Results of covariance analyses (ANCOVA) with morphometric data. AM: adult males; JM: juvenile males, AF: adult females; JF: juvenile females; CL: carapace length; AL: abdomen length; PW: pleura width; ML: merus length; CaL: carpus length; PrL: propodus length.

Relationship	Group	Par. (log)	F	*p*
CL × AL	AM × JM	*a*	2.44	0.12
		b	0.47	0.49
	AF × JF	*a*	2.90	0.09
		b	0.75	0.39
CL × PW	AM × JM	*a*	-	-
		b	4.12	<0.05
	AF × JF	*a*	10.50	<0.05
		b	1.67	0.20
CL × ML	AM × JM	*a*	-	-
		b	12.64	<0.05
	AF × JF	*a*	7.29	<0.05
		b	2.32	0.13
CL × CaL	AM × JM	*a*	-	-
		b	25.05	<0.05
	AF × JF	*a*	18.16	<0.05
		b	0.70	0.41
CL × PrL	AM × JM	*a*	-	-
		b	28.94	<0.05
	AF × JF	*a*	19.93	<0.05
		b	0.15	0.70

Table 2. *Macrobrachium candango* Mantelatto, Pileggi, Pantaleão, Magalhães, Villalobos and Álvarez, 2021. Regression analysis of morphometric data. The carapace length (CL) was used as an independent variable. CL: carapace length; AL: abdomen length; PW: pleura width; ML: merus length; CaL: carpus length; PrL: propodus length.

Relationship	Group	N	*a*	*b*	r^2	Regression *p*-values	*T* (b=1)	Allometry
CL × AL	Males	157	0.5501	0.7625	0.71	<0.01	6.11	-
	Females	105	0.5334	0.7898	0.67	<0.01	3.92	-
CL × PW	AM	96	0.0292	0.5956	0.59	<0.01	7.92	-
	JM	61	-0.1710	0.7446	0.77	<0.01	4.84	-
	AF	57	0.0754	0.6460	0.15	<0.01	1.75	-
	JF	48	-0.3218	0.9425	0.63	<0.01	0.54	=
CL × ML	AM	55	-1.3104	1.6975	0.59	<0.01	3.64	+
	JM	47	-0.3053	0.8780	0.60	<0.01	1.75	-
	AF	31	0.2650	0.4027	0.19	<0.01	3.87	-
	JF	33	-0.1359	0.7288	0.49	<0.01	2.03	-
CL × CaL	AM	56	-1.0809	1.5808	0.63	<0.01	3.59	+
	JM	46	-0.1919	0.8396	0.72	<0.01	2.07	-
	AF	34	0.3088	0.4324	0.21	<0.01	3.89	-
	JF	30	0.0619	0.5993	0.41	<0.01	2.98	-
CL × PrL	AM	52	-1.6405	2.2371	0.61	<0.01	4.98	+
	JM	50	-0.1363	0.9913	0.78	<0.01	0.11	=
	AF	35	0.1384	0.7780	0.52	<0.01	1.72	-
	JF	29	0.1481	0.7100	0.55	<0.01	2.36	-

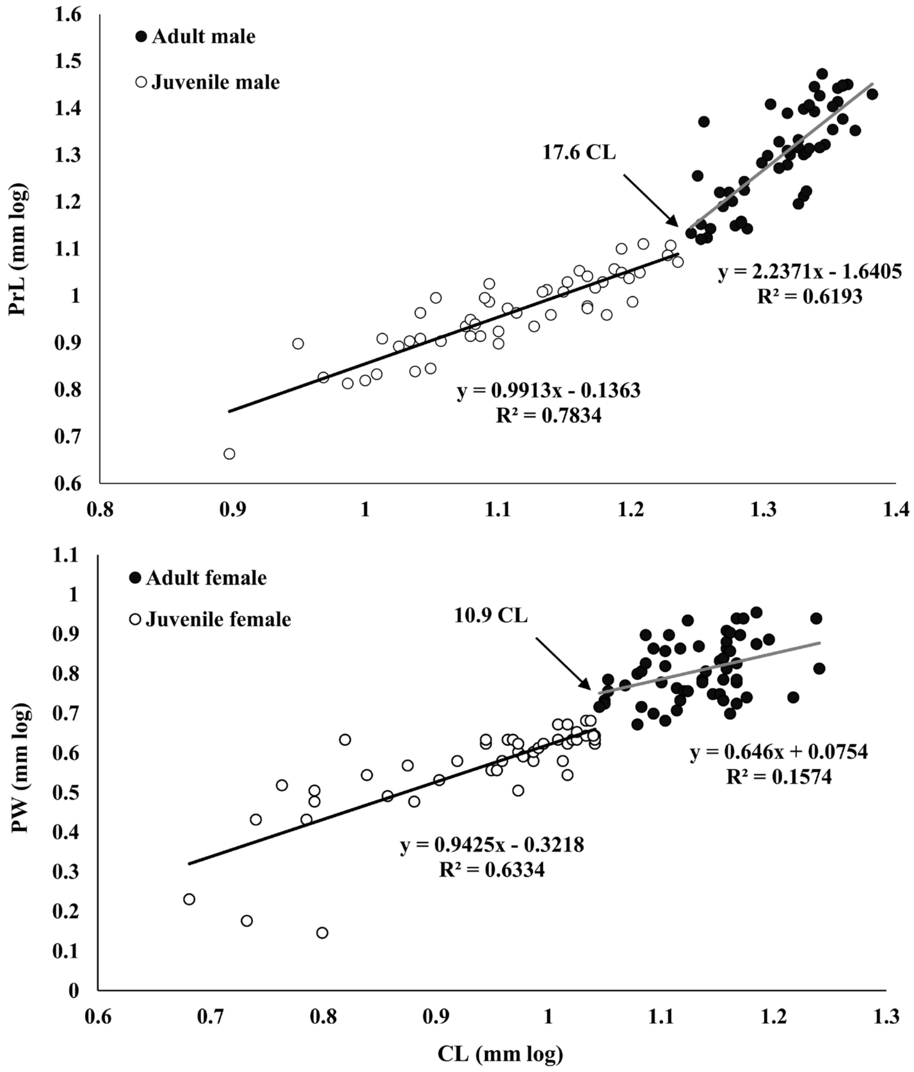

Figure 3. *Macrobrachium candango* Mantelatto, Pileggi, Pantaleão, Magalhães, Villalobos and Álvarez, 2021. Scatter plots of the selected morphometric relationships in males and females, highlighting the separation of groups (adults and juveniles). The arrows indicate the inflection break and the respective size estimated at the beginning of morphological sexual maturity, which corresponds to the CL of the smallest individual in the interruption of juvenile and adult equations, in relation to CL × PrL (males) and CL × PW (females). (CL) carapace length; (PrL) propodus length; (PW) pleura width.

Laterality and heterochely

There was no defined laterality pattern in males and females (males: $\chi^2 = 0.35$ and $p = 0.84$; females: $\chi^2 = 0.07$ and $p = 0.96$) and, therefore, individuals may present either right or left propodus as most developed. In males, the right and left propodus were more robust in 52.9 % and 47.1 % cases, respectively. In females this proportion was 48.3 % and 51.7 %, respectively.

Due to the lack of laterality pattern, the heterochely analyses compared the largest propodus × smallest propodus. The average length of the largest and smallest propodus of adult males was 20.03 ± 5.1 mm and 16.64 ± 3.86 mm, while in juvenile males it was 9.71 ± 2.25 mm and 8.73 ± 2.1 mm, respectively. The average length of the largest and smallest propodus of adult females was 9.9 ± 1.48 mm and 9.2 ± 1.52 mm, while in juvenile females it was 7.07 ± 0.92 mm and 6.42 ± 0.9 mm, respectively.

Heterochely was not found within the demographic categories (adult and juvenile males; adult and juvenile females), *i.e.*, the length of the largest propodus was not significantly different from the smallest propodus ($p > 0.05$). However, significant differences in the propodus length were observed between all demographic categories, and sexual dimorphism based on propodus length can be characterized in both life stages. The length of the largest and smallest propodus of adult males differed significantly from all other demographic categories ($p < 0.01$). The length of the largest propodus of juvenile males and adult females was only significantly different from the propodus (largest and smallest) of juvenile females ($p < 0.01$), as well as adult males (see Tab. 3).

Reproductive aspects

Fifty OF were used with a mean CL of 13.9 ± 1.08 mm, ranging from 12.2 to 15.3 mm. The average egg volume (EV) was 5.68 ± 0.93 mm^3, ranging from 4.41 to 7.71 mm^3. The average fecundity was 49 ± 11, ranging from 38 to 61 eggs. Among the 15 OF analyzed, only two females incubated embryos in the late stage of development. The average volume of eggs in the early and late stages was 5.63 ± 0.94 mm^3 and 6.03 ± 1.13 mm^3, respectively. There was no correlation between CL and number of eggs ($p > 0.05$), however, there was a positive correlation between PW and number of eggs ($p < 0.05$). Based on all individuals sampled, a higher abundance of OF was observed in October/2005, followed by September/2009, January/1989, August/1988 and November/1988 (Fig. 4a). In most cases, OF were found in months with a high volume of rainfall, except for August/1988 (Fig. 4b).

DISCUSSION

Forty-nine years after the species was described, detailed information about the morphometry and reproduction of *M. candango* was gathered from data collected for a 30-year time period and analyzed for the first time herein, revealing information about aspects of its life history.

Morphometric aspects

The development pattern of PW in males and females was similar, except for juvenile females that presented isometric development. This group of juvenile females has this difference possibly due to the need for the pleura to be well developed until its adult phase, which is when this structure will have the function of expanding the size of the hatchery chamber, allowing these females to hatch more eggs (Nagamine and Knight, 1980; Mantelatto and Barbosa, 2005; Pralon and Negreiros-Fransozo, 2006; Pantaleão *et al.*, 2012; Pescinelli *et al.*, 2018). Therefore, this structure develops at the same rate as the carapace during the juvenile phase, but modifies its growth pattern when reaching sexual maturity, which is when the adult female starts to invest more energy in gonadal development (Sampaio *et al.*, 2007).

In the morphometric relationships related to the chelipeds of adult and juvenile males, a distinct pattern was found among these groups, where adult males

Table 3. *Macrobrachium candango* Mantelatto, Pileggi, Pantaleão, Magalhães, Villalobos and Álvarez, 2021. Dunn's test results comparing the propodus length (largest × smallest) between adult and juvenile males and females. LPAM: largest propodus of adult males; SPAM: smallest propodus of adult males; LPJM: largest propodus of juvenile males; SPJM: smallest propodus of juvenile males; LPFM: largest propodus of adult females; SPJF: smallest propodus of adult females; LPJF: largest propodus of juvenile females; SPJF: smallest propodus of juvenile females. ns = non-significant.

Structures	LPAM	SPAM	LPJM	SPJM	LPAF	SPAF	LPJF	SPJF
LPAM	-	ns	$p<0.01$	$p<0.01$	$p<0.01$	$p<0.01$	$p<0.01$	$p<0.01$
SPAM	ns	-	$p<0.01$	$p<0.01$	$p<0.01$	$p<0.01$	$p<0.01$	$p<0.01$
LPJM	$p<0.01$	$p<0.01$	-	ns	ns	ns	$p<0.01$	$p<0.01$
SPJM	$p<0.01$	$p<0.01$	ns	-	ns	ns	ns	$p<0.05$
LPAF	$p<0.01$	$p<0.01$	ns	ns	-	ns	$p<0.01$	$p<0.01$
SPAF	$p<0.01$	$p<0.01$	ns	ns	ns	-	ns	$p<0.01$
LPJF	$p<0.01$	$p<0.01$	$p<0.01$	ns	$p<0.01$	ns	-	ns
SPJF	$p<0.01$	$p<0.01$	$p<0.01$	$p<0.05$	$p<0.01$	$p<0.01$	ns	-

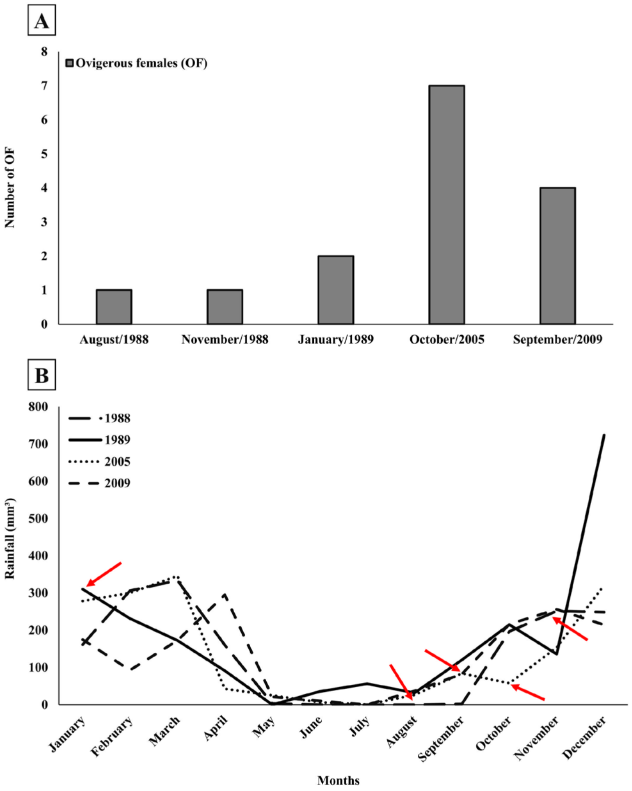

Figure 4. *Macrobrachium candango* Mantelatto, Pileggi, Pantaleão, Magalhães, Villalobos and Álvarez, 2021. **A**. Number of ovigerous females obtained during the collection period. **B**. Monthly rainfall variation in the years when ovigerous females were found (1988, 1989, 2005, and 2009). Red arrows indicate in which months the ovigerous females occurred.

invest more energy than juveniles in the development of the articles of the largest cheliped. During the life stages of shrimps, chelipeds play important roles in feeding and agonistic behaviors (Nagamine and Knight, 1980; Valenti *et al*., 1989); thus, the unequal development of this structure between life stages may be related to its different functions (Nagamine and Knight, 1980). Adult individuals require highly developed chelipeds for disputes over females or mating behaviors, on the other hand, juveniles do not dispute sexual partners, possibly this group uses this structure for more general functions such as foraging and for body cleaning (Hartnoll, 1978, 1982; Mariappan *et al*., 2000; Correa and Thiel, 2003).

For females, the morphometric relationships of the chelipeds showed the same type of development between adults and juveniles (allometrically negative). Again, this result refers to the functional role of these appendages in these categories (Nagamine and Knight, 1980; Mariappan *et al*., 2000), because females might use chelipeds differently than males and may not require these appendages to be robust. Therefore, they use less energy to develop this structure, justifying the allometric pattern found, in addition, these results reinforce the sexual dimorphism found in the propodus length between males and females.

Analyzing the average length of the largest and smallest propodus between the demographic categories, significant differences were observed between these groups, with sexual dimorphism between adult and juvenile males and females. Sexual dimorphism based on the length of the chelipeds or propodus is a characteristic that has been widely observed in other shrimp species (Koshy, 1973; Nagamine and Knight, 1980; Mariappan and Balasundaram, 1997; Mossolin and Bueno, 2003; Karplus and Barki, 2019), and this unique trait mainly refers to the sexual behavior of these animals, where males use chelipeds to dispute and guard females before and after copulation (Bauer, 2004; Karplus and Barki, 2019).

The size of the morphological sexual maturity observed in this study was similar to that observed for *Macrobrachium iheringi* (Ortmann, 1897) (Nogueira *et al*., 2019), a species that presents a similar body size variation to that of *M. candango*. Furthermore, in both species males reach morphological sexual maturity at larger sizes than females, indicating that possibly *M. candango* has the reproductive strategy called "mate guarding" (Bauer, 2004), as was suggested for *M. iheringi* (see Nogueira *et al*., 2019); a result that is correlated with the occurrence of sexual dimorphism in body size and chelipeds, and with different patterns of allometric development between males and females.

The lack of a laterality pattern seems to be a common feature in *Macrobrachium* species that have heterochely, this was also observed in *Macrobrachium olfersii* (Wiegmann, 1836) by Mossolin and Bueno (2003), and in *Macrobrachium brasiliense* (Heller, 1862) by Nogueira *et al*. (2020), where the males and females analyzed did not have a constant between which propodus (left or right) would be the most developed. Therefore, it has been suggested that this characteristic (*i.e*., laterality) may not be genetically predetermined (Mossolin and Bueno, 2003). In some decapod crustaceans, such as brachyuran crabs, the lack of a laterality pattern is common (Smith and Palmer, 1994; Santos *et al*., 2018). These crabs usually use the largest cheliped as a weapon in agonistic contests. If these individuals lose this appendage during these disputes, the other cheliped (the smallest) will become the largest (Smith and Palmer, 1994). Possibly this also occurs in *M. candango*, since these individuals have a major cheliped, this structure can be used as the main weapon during disputes over resources, therefore, this appendage is more likely to be injured or amputated.

Reproductive features

Based on the low fecundity and large volume of *M. candango* eggs, it can be inferred that this species has abbreviated larval development, where the embryos develop for a longer time within the egg. After hatching, larvae originate in the final stage of development, leaving few morphological characteristics to be considered juveniles, these characteristics will be developed in two or three larval stages, which precede the juvenile phase (Sankoli *et al*., 1993; Anger, 2013). Some species of freshwater shrimps exhibit this characteristic, in which low fecundity along with large eggs is correlated to the type of larval development, as recorded, for instance, for *M. brasiliense*, *M. iheringi*, *Macrobrachium nattereri* (Heller, 1862), and *Macrobrachium totonacum* Mejía, Alves and Hartnoll, 2003 (Pantaleão *et al*., 2011; Bueno and Rodrigues, 1995; Magalhães, 1989; Mejía-Ortíz *et al*., 2010, respectively). Molecular analyzes (using mitochondrial 16S and COI genes) indicate that these species are phylogenetically close and are part of the same clade with abbreviated larval development (Pileggi and Mantelatto, 2010; Mantelatto *et al*., 2021). Thus, the reproductive and phylogenetic aspects found lead us to infer that *M. candango* presents abbreviated larval development, a condition that should be investigated in the future with the larval description of the species.

The reproductive period in freshwater shrimps can be characterized in two ways: continuous reproduction throughout the year with reproductive peaks at specific times or the reproductive period is seasonal (Bauer, 1989). Although we do not have enough evidence to state the type of reproductive period for *M. candango* due to the sampling method used in the capture of individuals, the majority of ovigerous females (93.3 %) were collected when there was an increase in rainfall, and it is known that there is a strong relationship between this abiotic factor and the seasonal reproductive period in some species of *Macrobrachium*. This type of reproductive period associated with rainfall has already been observed in some other species of freshwater shrimps, such as *M. iheringi* and *Macrobrachium potiuna* (Müller, 1880) (Mattos and Oshiro, 2009; Nogueira *et al*., 2019, respectively), which could be an indication that *M. candango* has seasonal reproduction. However, in addition to evidence on the type of larval development, further studies are needed to confirm this hypothesis.

Based on the information obtained in the present study, we can state that *M. candango* presents similarities with other species of the genus *Macrobrachium*, *e.g.*, reproductive features such as low fecundity due to abbreviated larval development, along with allometric development patterns. Some characteristics of *M. candango* categorize it as a species at risk of decreasing its already low natural abundance: endemic, occurring in environments with anthropogenic pressures and low fecundity. Thus, the biological aspects studied herein are important and reinforce the previous recommendation regarding the unrestricted protection of the species (Mantelatto *et al*., 2016; 2021), including future projects focused on monitoring populations throughout the area of occurrence.

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