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Morphometry of the freshwater prawn *Macrobrachium brasiliense* (Caridea: Palaemonidae) and its relationship with reproductive strategy

Morfometría del camarón de agua dulce *Macrobrachium brasiliense* (Caridea: Palaemonidae) y su relación con la estrategia reproductiva

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ABSTRACT

During ontogeny, the allocation of energy can differ throughout the life cycle of a species, especially from juvenile to adult. The present study aimed to describe the relative growth, heterochely, and laterality patterns of the freshwater prawn *Macrobrachium brasiliense*. Carapace length (CL), abdomen length (AL), left cheliped length (LCL), right cheliped length (RCL), and abdomen width (AW) of males and females were measured. Differences in the morphometric relationships between juveniles and adults were evaluated using analysis of covariance (ANCOVA) and linear regressions. Heterochely was tested using the Mann-Whitney test. Only the relationships LCL *vs* CL for males and AL *vs* CL for females were significantly different between adults and juveniles ($P < 0.05$); these were used to calculate morphological sexual maturity, estimated at 10.3mm CL for males and 8.1mm CL for females. Individuals did not present laterality ($P > 0.05$) or heterochely ($P > 0.05$). The average length of the largest and smallest cheliped in males was 9.9 ± 4.8 and 9.2 ± 4.26 mm, while for females it was 7.3 ± 2.4 and 6.8 ± 2.3 mm, respectively. The variation in size and developmental rate of structures suggests that the species follow a mate guarding reproductive strategy since males have well-developed chelipeds to be able to court and guard females during copulation.

Keywords: chelipeds, laterality, heterochely, morphological sexual maturity, relative growth.

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RESUMEN

Durante la ontogenia, la asignación de energía puede diferir a lo largo del ciclo de vida de una especie, especialmente entre la fase juvenil y adulta. El presente estudio tuvo como objetivo describir el crecimiento relativo y los patrones de heteroquelia y lateralidad del camarón de agua dulce *Macrobrachium brasiliense*. Se midieron la longitud de: caparazón (CL), abdomen (AL), quelípodo izquierdo (LCL), quelípodo derecho (RCL) y ancho del abdomen (AW) de machos y hembras. Las diferencias en las relaciones morfométricas entre juveniles y adultos se estudiaron mediante análisis de covarianza (ANCOVA) y regresiones lineales. La heteroquelia se probó utilizando una prueba de Mann-Whitney. Solo la relación LCL *vs* CL para machos y AL *vs* CL para hembras fue significativamente diferente entre adultos y juveniles (P < 0.05), medidas usadas para calcular la madurez sexual morfológica, estimada en 10,3 mm CL para machos y 8,1 mm CL para hembras. Los individuos no presentaron lateralidad (P > 0,05) ni heteroquelia (P > 0,05). La longitud promedio del quelípodo mayor y menor en los machos fue de 9,9 ± 4,8 y 9,2 ± 4,26 mm, mientras que en las hembras fue de 7,3 ± 2,4 y 6,8 ± 2,3 mm, respectivamente. La variación en el tamaño y la tasa de desarrollo de las estructuras indica que la especie sigue una estrategia reproductiva de *mate guarding*, ya que los machos tienen quelípodos bien desarrollados con los que cortejan y protegen a las hembras durante la cópula.

Palabras clave: crecimiento relativo, heteroquelia, lateralidad, madurez sexual morfológica, quelípodos.

INTRODUCTION

Palaemonidae is one of the largest families of decapods. It includes the genus *Macrobrachium*, an important group of prawns from fresh or brackish waters (Holthuis 1952). Researching population aspects of such species can provide information on biodiversity and the development and life history of species in their natural environments (Bauer 2004). Population studies of some *Macrobrachium* species have become more frequent due to their ecological and economical importance, as they belong to the base of the food chain in aquatic environments and can be marketed as food (Maciel and Valenti 2009, Pantaleão *et al.* 2012, Pescinelli *et al.* 2015, Taddei *et al.* 2017, Martinelli-Filho *et al.* 2019).

Morphological investigations of decapods are essential to understand the species as a whole. The variation in its morphology can directly influence the way of life, and can shed light on biological characteristics such as reproductive strategies within congeneric species (Hartnoll 1974, 1978, Bauer 2004). In some genera, females are larger than males and present a mating system called "pure search"; in this system, males do not have exaggeratedly developed chelipeds and do not show aggressive behavior or dispute over sexual partners (Correa and Thiel 2003). In other species, males are larger than females, presenting a mating system named "mate guarding"; these males have exaggerated-sized chelipeds, present aggressive behavior, and compete with other males for sexual partners (Correa and Thiel 2003, Bauer 2004). Both of these reproductive strategies are observed in species of the genus *Macrobrachium* (Holthuis 1952, Bauer 2004, Karplus and Barki 2019). Therefore, understanding the morphological variations of species and their influence over their life cycle can clarify the reproductive features of this commercially and ecologically important genus.

Several species of the genus *Macrobrachium* occur in Brazil (Dos Santos *et al.* 2013, Pileggi *et al.* 2013, Rossi *et al.* 2020), including *Macrobrachium brasiliense* (Heller, 1862), that inhabits first-order streams, far from coastal regions (Mantelatto and Barbosa 2005, Pereira and Chacur 2009, Oliveira *et al.* 2019). This species is widely distributed in the Brazilian territory, occurring in most states (Coelho and Ramos-Porto 1984). It is also present in other countries such as Venezuela, Colombia, Ecuador, and Peru (Holthuis 1980, Coelho and Ramos-Porto 1984). Few studies have analyzed the particularities of populations of *M. brasiliense*, especially regarding morphology (Mantelatto and Barbosa 2005, Taddei *et al.* 2017, Nogueira *et al.* 2019a, Nogueira *et al.* 2020). In these studies, authors usually address length/weight ratio, relative growth with emphasis on the second pair of chelipeds, and the presence of social hierarchy among males.

Given that morphological variations can be found in populations of the species throughout their geographic distribution (García-Davílla *et al.* 2000, Pereira and Chacur 2009, Oliveira *et al.* 2019, Nogueira *et al.* 2019a, 2020), we analyzed the relative growth of the body structures, heterochely, and laterality of a population of *M. brasiliense* in southeastern Brazil and correlated the results of morphometric relations to its reproductive strategy.

MATERIAL AND METHODS

Sampling site and animal collection

Individuals of *M. brasiliense* were collected in two tributaries that flow into the Pardo River, both located in the municipality of Serrana, São Paulo state (Fig. 1). The first sampling site was located in Tamanduá stream (21°08'48.1"S, 47°38'51.9"W) and the second in the Prata stream (21°08'52.2"S, 47°37'36.5"W). Sites are two kilometers apart but with connectivity between them.

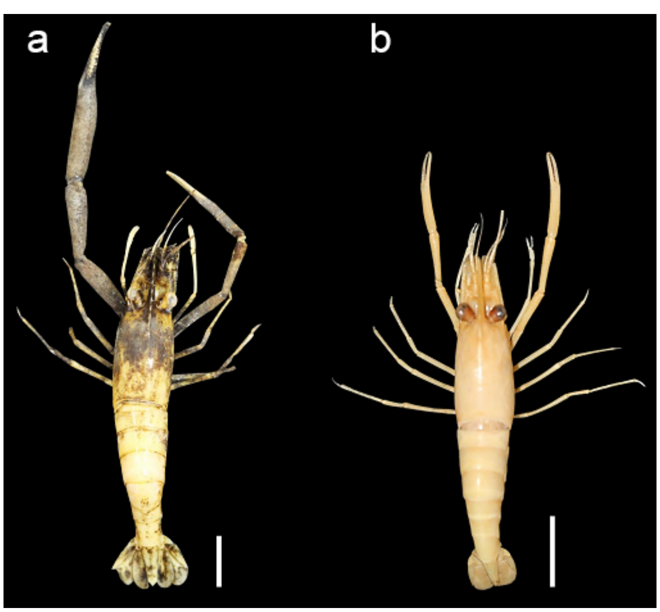

Figure 1. *Macrobrachium brasiliense* (Heller, 1862) **a**. Male and **b**. female. Scale = 7 mm.

Sieves with 3.0 mm mesh and 50.0 cm in diameter were used on the banks of the streams close to the marginal vegetation for sampling. Animals were sampled in the months of June, September, December/1987, and March/1988. Three collectors sampled *M. brasiliense* for 30 minutes, totaling 90 minutes of sampling effort per site per month. Samples were sorted and prawns were packed in plastic bags and kept in iceboxes for transportation to the laboratory. After euthanasia, animals were stored in flasks with 70 % ethanol for further analysis. Prawns were identified following Melo (2003) and sexed with the aid of a stereomicroscope, following the protocol suggested by Mantelatto and Barbosa (2005) for the presence (male) or absence (female) of the appendix masculina in the second pair of pleopods.

The following measurements were obtained with the aid of a digital caliper (0.01 mm): carapace length (CL, distance between the eye socket and the posterior margin of the carapace), abdomen length (AL, distance between the anterior and posterior margin of the abdomen), abdomen width (AW, distance between the left and right anterior margin of the abdomen), left and right cheliped length (LCL and RCL, distance between the anterior margin of the dactyl and the posterior margin of the ischium) (Fig. 2). The second pair of pereopods was chosen for cheliped analysis since they are used on disputes over resources such as sexual partners, shelter, or food (Karplus and Barki 2019). We considered as sexually undifferentiated those individuals with carapace length lower than the smallest individual with visible appendix masculine and were thus excluded from the analyses.

Laterality and heterochely

Male and female laterality patterns were investigated using chi-square tests ($\alpha = 0.05$), based on the measurements of LCL and RCL.

Heterochely's analysis was based on the result of the laterality test, using Mann-Whitney. In cases of laterality, a comparison between the right and the left sides followed. When laterality was absent, heterochely analysis was standardized considering the comparison between the length of the largest and smallest chelipeds, regardless of side. The normality of data was verified before statistical analysis using the Shapiro-Wilk test ($\alpha = 0.05$). When distribution was non-normal, data were log-transformed and non-parametric tests were considered (Zar 2010).

Relative growth analysis

Non-hierarchical analysis of K-means clustering (Sokal and Rohfl 1979) was used to separate juveniles and adults of both sexes. This analysis consists of distributing the dataset into previously established groups by an interactive process, which minimizes variance within groups and maximizes variance among these pre-established groups. After the K-means analysis, discriminant analysis was performed accounting for the overlapping interval to refine results for final categorization (Sampedro *et al.* 1999).

Analysis of covariance (ANCOVA) was used to test the angular and linear coefficients between demographic groups (juveniles and adults). This test verifies whether the data for each morphometric relationship can be grouped into a single equation or separate equations. Thus, changes in the allometric coefficient during the growth of body structures (dependent variables) in relation to the carapace length (independent variable) were analyzed. The CL was used as an independent variable since it is the structure that best represents the overall size of a prawn (Hartnoll 1982).

Data were linearized to the equation log y = log a + b × log x, in which "y" is the dependent variable, "x" the independent variable, "a" the coefficient of the intersection of the axis "y" and "b" the allometric (angular) coefficient that represents the slope and angulation of the line. The allometric constant "b" was calculated for each morphometric relationship and the null hypothesis (H0: b= 1) was tested with the Student test ($\alpha = 0.05$). The allometric constant values correspond to isometric growth (b= 1), positive allometry (b> 1), or negative allometry (b< 1) (Zar 2010). Only individuals with left chelipeds were used in this analysis. K-means and discriminant analysis were performed in PAST 1.8 software and ANCOVA and linear regressions were performed in Statistica 7.0 software (Hammer *et al.* 2001, StatSoft© 2004).

The size at which animals reach morphological sexual maturity was defined by morphometric relationships of structures that play an important biological role. These were the relationship LCL *vs* CL for males and AL *vs* CL for females. The importance of these structures for the reproductive behavior of caridean prawns have been discussed in previous studies (Mossolin and Bueno 2003, Mantelatto and Barbosa 2005, Nogueira *et al.* 2019b).

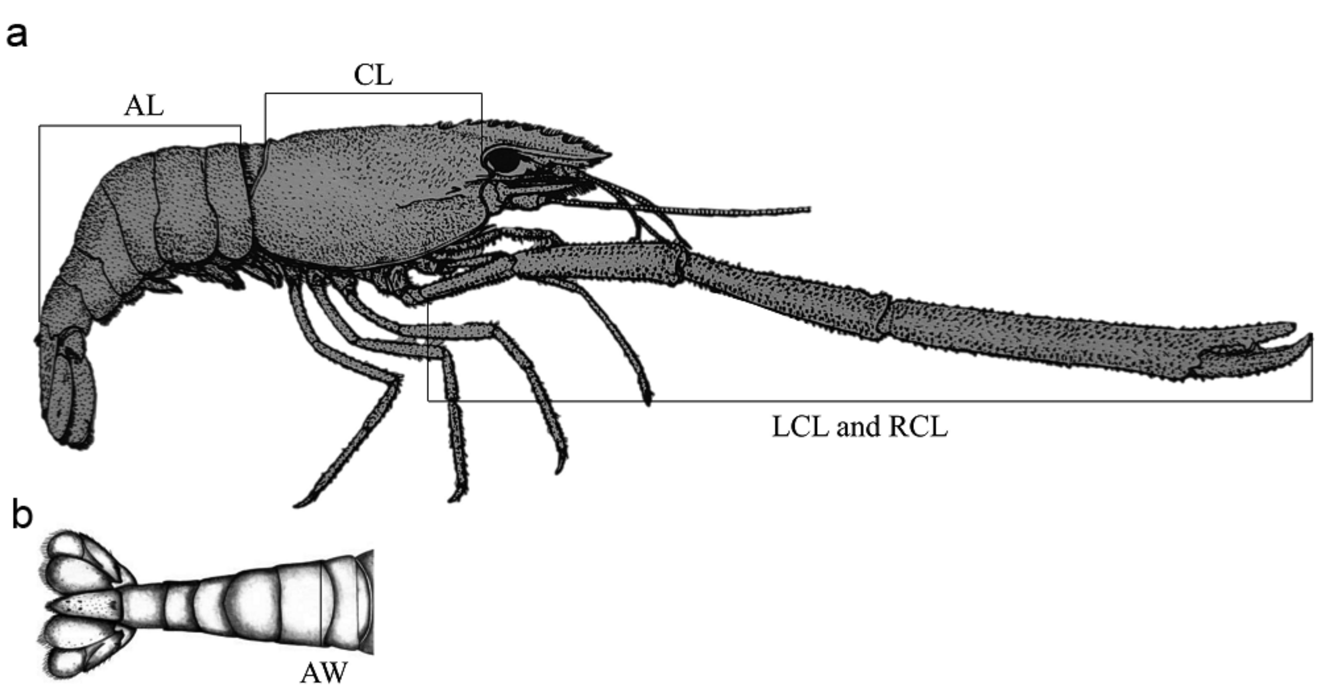

Figure 2. Body dimensions of the freshwater prawn *Macrobrachium brasiliense* (Heller, 1862) used in the morphometric analysis. **a**. Illustration modified from Melo (2003). **b**. Illustration modified from Nogueira ***et al.*** (2020). CL = carapace length, AW = abdomen width, AL = abdomen length, LCL = left cheliped length, RCL = right cheliped length.

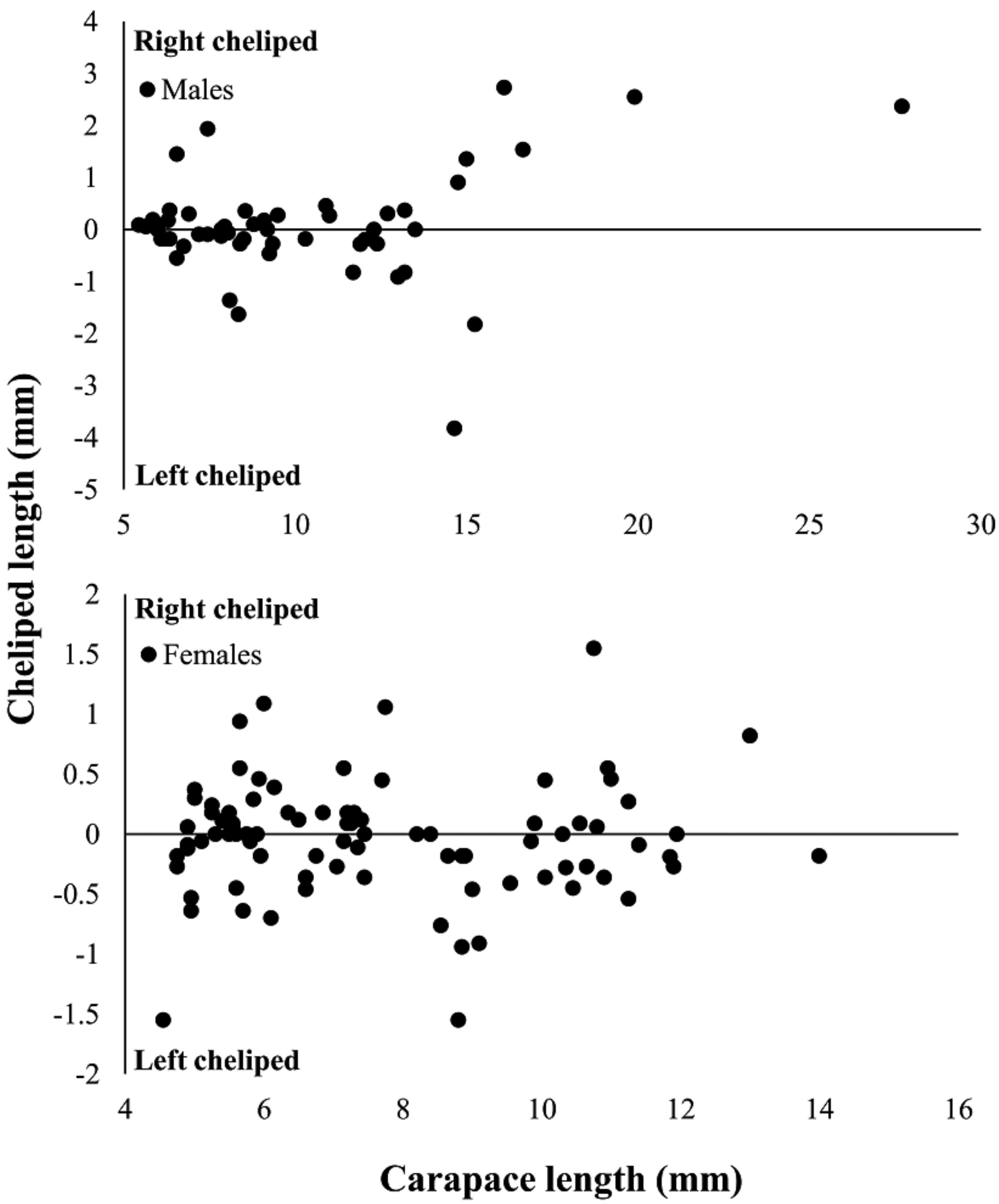

Figure 3. Laterality was observed from the frequency of the largest cheliped length of *Macrobrachium brasiliense* (Heller, 1862). The distribution of points for males and females indicates that there is no pattern of laterality between the left or right chelipeds.

RESULTS

A total of 394 individuals were analyzed, 131 males with CL ranging from 4.2 to 19.9 mm (10.14 ± 4.17 mm), and 263 females with CL ranging from 4.2 to 20.0 mm (7.68 ± 2.34 mm).

Laterality and heterochely

There was no indication of laterality in both males and females (Females, $\chi2 = 1.4$, $P = 0.49$; Males, $\chi^2 = 0.39$, $P = 0.82$, Fig. 3). In males, the length of the largest cheliped ranged from 4.64 to 25.64 mm (9.91 ± 4.8 mm) and the smallest ranged from 3.91 to 23.09 mm (9.22 ± 4.26 mm). In females, the length of the largest and smallest cheliped ranged from 3.11 to 13.36 mm (7.28 ± 2.42 mm) and 2.47 to 13.18 mm (6.8 ± 2.31 mm), respectively. No significant differences were observed when comparing the length of the largest and smallest chelipeds (heterochely) of either sex (Mann-Whitney; Males: U = 1073.5, $P = 0.36$; Females: U = 2.587, $P = 0.17$).

Relative growth analysis

As there was no significant size difference between the largest and smallest chelipeds, the left cheliped length (LCL)

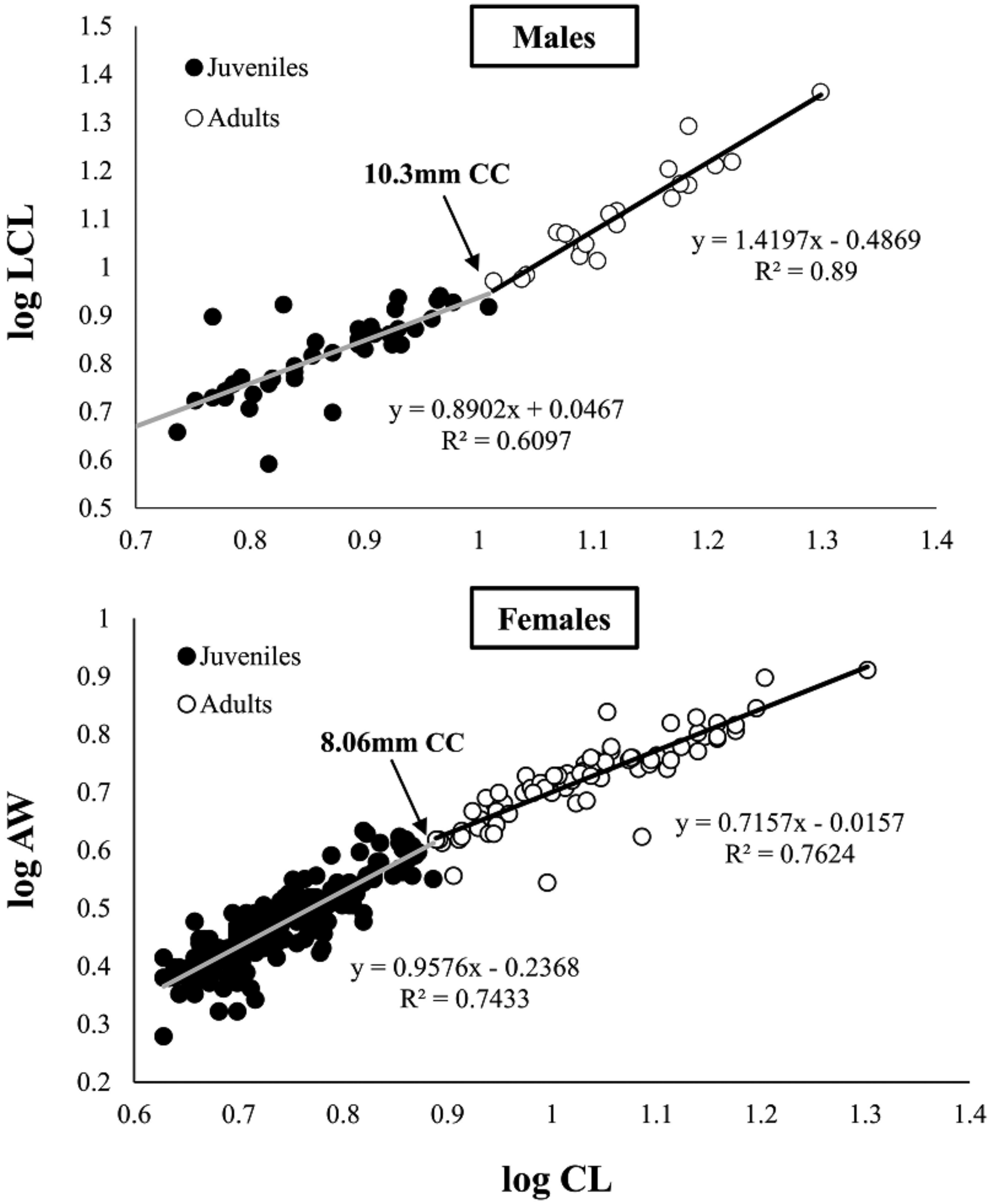

Figure 4. Scatterplots of the morphometric relationships for males and females of *Macrobrachium brasiliense* (Heller, 1862). CL = carapace length, AW = abdomen width, LCL = left cheliped length.

was used for relative growth analysis. Only the relationships LCL *vs* CL for males and AW *vs* CL for females differed between juveniles and adults as shown by the ANCOVA results ($P < 0.05$, Table 1). The same relationships were used for morphological sexual maturity, which was estimated at 10.3 mm CL for males and 8.06 mm CL for females (Fig. 4).

The morphometric relationships AL *vs* CL and AW *vs* CL were characterized by a negative allometric development in both male demographic groups, while the LCL *vs* CL relationship presented positive allometry for adults and isometry for juveniles (Table 2). For females, negative allometric development was observed for AL *vs* CL and positive allometric for LCL *vs* CL. For AW *vs* CL, there was a negative allometric development for adults and isometric for juveniles (Table 2).

DISCUSSION

Structures related to reproductive behavior are commonly used to estimate sexual morphological maturities, such as cheliped total length or propodus length for males, and the abdomen length or width for females (Mossolin and Bueno 2003, Pantaleão *et al.* 2012, Nogueira *et al.* 2019b). These measurements were related to sexual morphological maturity in *M. brasiliense*, as observed for other palaemonid prawns (Mossolin and Bueno 2003, Mantelatto and Barbosa 2005, Pantaleão *et al.* 2012, Paschoal *et al.* 2013, Nogueira *et al.* 2019b).

The absence of laterality and the isochely pattern observed in the present study may be related to the size (CL) of the individuals. In the investigated population, most individuals were not within the largest size classes reported for *M. brasiliense* (García-Davílla *et al.* 2000, Pereira and Chacur 2009, Oliveira *et al.* 2019). Mossolin and Bueno (2003) observed a lack of laterality for *Macrobrachium olfersii* (Wiegmann, 1836). However, they found significant heterochely, which gradually increased with CL. Mossolin and Bueno (2003) argued that laterality is not likely to be genetically determined since the most developed chelipeds can either be the left or the right. According to our results on laterality, the same seems to be true *for M. brasiliense*.

While some structures developed in a similar pattern in juveniles and adult males of *M. brasiliense*, cheliped development was notably different between these demographic categories. There was a greater investment in the development of this structure among adult males (positive allometry), whereas juvenile males developed chelipeds in the same pattern as the carapace (isometry). Variations in the growth pattern of this structure may be related to agonistic behavior. In adults of this species, more developed chelipeds can assist them in disputes over sexual partners and food resources (Nagamine and Knight 1980, Karplus and Barki 2019). Positive allometry in the development of chelipeds, or articles that comprise it, of adults and negative allometry/isometry for juvenile individuals, have been found in other *Macrobrachium* species (Moraes-Riodades and Valenti 2002, Mossolin and Bueno 2003, Mantelatto and Barbosa 2005, Nogueira *et al.* 2019a, 2019b).

On the other hand, the abdomen tends to be less developed in males than in females. Negative allometry in male abdomen development has been characterized in several studies (Darnell 1956, Flexa *et al.* 2005, Mantelatto and Barbosa 2005, Sethi *et al.* 2013, Nogueira *et al.* 2019a, 2019b). During somatic growth, lower amounts of energy are directed toward the development of structures such as the abdomen in males since this structure does not play the same role in reproduction as it does in females (Peiró et al. 2011, Ahamed and Ohtomi 2014).

For females, in general, the morphometric relationships between juveniles and adults were mostly similar, with some exceptions. A negative allometric developmental pattern in the AL vs CL morphometric relationship was observed, regardless of demographic category. This means that the abdomen length develops less than the carapace

Table 1. Results of the covariance analyses (ANCOVA). (J) Juveniles (A) Adults. CL= carapace length; AL = abdomen length; AW = abdomen width; LCL = left cheliped length. *Significant difference at 0.05.

Morphometric relationship	Group	Regression parameter	F	*P*
AL *vs* CL	Male J *vs* A	*A*	0.04	0.86
		B	0.32	0.56
	Female J *vs* A	*A*	0.22	0.63
		B	0.06	0.79
AW *vs* CL	Male J *vs* A	*A*	0.06	0.8
		B	0.38	0.53
	Female J *vs* A	*A*	-	-
		B	15.84	< 0.01*
LCL *vs* CL	Male J *vs* A	*A*	-	-
		B	8.17	< 0.01*
	Female J *vs* A	*A*	3.7	0.057
		B	0.01	0.89

Table 2. Regression analyses of morphometric data. (AF) Adult females, (JF) Juvenile females, (AM) Adult males, (JM) Juvenile males. CL = carapace length; AL = abdomen length; AW = abdomen width; LCL = left cheliped length.

Relationship	Sex	N	*a*	*b*	r^2	*P*	t (H0: b=1)	Allometry
AL *vs* CL	Males	131	0.3834	0.7864	0.89	> 0.001	8.9	-
	Females	263	0.3434	0.8313	0.91	> 0.001	10.78	-
AW *vs* CL	Males	131	-0.1632	0.8574	0.91	> 0.001	6.39	-
	AF	76	-0.0157	0.7157	0.76	> 0.001	6.3	-
	JF	187	-0.2368	0.9576	0.74	> 0.001	1.02	=
LCL *vs* CL	AM	21	-0.4869	1.4197	0.89	> 0.001	3.66	+
	JM	43	0.0467	0.8902	0.6	> 0.001	0.98	=
	Females	103	-0.1341	1.0932	0.91	> 0.001	2.79	+

length in both juveniles and adults. Regarding chelipeds, a positive allometric development pattern was observed for females. This type of allometry might be relevant for all life stages in both sexes since chelipeds can perform many tasks, such as helping in the search, dispute, and manipulation of food (Nagamine and Knight 1980, Karplus *et al.* 1992).

The sexual morphological maturity of females was estimated through the morphometric relationship AW *vs* CL. This relationship differed significantly between demographic categories, being isometric for juveniles and negatively allometric for adults. The development of this structure is attenuated in comparison to the development of the carapace in adults. Meanwhile, this structure develops at the same rate as the carapace in juveniles. Similar results were observed for *Macrobrachium iheringi* (Ortmann, 1897) (Nogueira *et al.* 2019b) and another population of *M. brasiliense* (Nogueira *et al.* 2019a). This seems to be a pattern in species with abbreviated larval development. There is a possibly greater investment in the development of this structure during the juvenile phase, as it needs to be developed before female sexual morphological maturity for reproduction (egg incubation). In adults, this structure can grow at a slower pace.

Different patterns were observed in the morphometry between males and females of *M. brasiliense*. On average, males are larger than females (CL) and have larger chelipeds. Importantly, chelipeds of males were developed in adults more than in juveniles, whereas no difference in the development of this appendix was found in adult and juvenile females. These characteristics are related to the reproductive strategy of *M. brasiliense* known as mate guarding (García-Davílla *et al.* 2000, Bauer 2004, Mantelatto and Barbosa 2005). In this mating system, males are larger than females and their chelipeds are exaggeratedly developed due to the selective pressures exerted by disputes over sexual partners.

In this study, we added information on the relative growth of *M. brasiliense*, presented estimated values of morphological sexual maturity, and provided relevant information on laterality and heterochely. These previously unexplored morphological characters can contribute to future studies on other populations of this species or other congeneric species.

AUTHORS PARTICIPATION

CSN – conception, design, data analysis, and writing. ACA – design, writing, and supervision.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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