Papéis Avulsos de Zoologia
Museu de Zoologia da Universidade de São Paulo

ARTICLE

Relative growth and population dynamics of *Macrobrachium iheringi* (Decapoda, Palaemonidae)

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Abstract. During the ontogenetic development of crustaceans, the relative growth of some structures may change, especially during the transition from juvenile to adult. This study describes the relative growth of body structures of *Macrobrachium iheringi,* and provides information on its population dynamics, such as structure, fecundity, and morphological sexual maturity. The sampling of *M. iheringi* was carried out in "Ribeirão da Hortelã", in Botucatu (SP, Brazil). The length of the carapace (CL), abdomen (AL), and ischium (IL), merus (ML), carpus (CrL), propodus (PpL), and dactyl (DcL) of the second right pereopod were measured. In addition, the width of the second abdominal pleura (PW) and propodus height (PpH) were included in analyses. The relationships that best demonstrated the changes in the allometric coefficient were CL *vs* PpL in males and females. The CL, in which males and females reach morphological sexual maturity, was estimated as 13.3 mm and 11.1 mm, respectively. The sex-ratio differed from the expected 1:1 and was skewed towards females. Precipitation and temperature influenced the abundance of different demographic classes. *Macrobrachium iheringi* has few but large eggs, which is expected since this species has an abbreviated larval development. Based on these results, we conclude that the propodus are good indicators of the size at onset of morphological sexual maturity. In addition, important information was obtained on the biology of *M. iheringi,* including its life cycle pattern, reproduction and influence of abiotic factors.

Key-Words. Allometry; Freshwater; Caridea; Populations; Sex-ratio.

INTRODUCTION

In Brazil, currently, 35 species of freshwater prawns are known, belonging to three families: Atyidae, Euryrhynchidae and Palaemonidae (Magalhães *et al.,* 2016). Among the Palaemonidae, 19 species of *Macrobrachium* Spence Bate, 1868 are known, which, besides being the most abundant genus (Mantelatto *et al.,* 2016), is of great commercial interest. Even though, the biological aspects of only a few species are known, especially the ones of economic importance (Mantelatto *et al.,* 2016). Among these species, *M. iheringi* (Ortmann, 1897) is an endemic Brazilian prawn found in cold continental waters (Fransozo *et al.,* 2004) in the states of Goiás, Espirito Santo, São Paulo, Minas Gerais, Rio de Janeiro, Mato Grosso and Paraná (Pileggi *et al.,* 2013). Previous studies addressed the geographical distribution (Coelho & Ramos-Porto, 1984; Gomes-Correa, 1977), behavior (Volpato & Hoshino, 1984), ecophysiology (Favaretto, 1973), reproductive period (Fransozo *et al.,* 2004), growth and longevity (Lobão *et al.,* 1986), and larval development (Bueno & Rodrigues, 1995) of *M. iheringi.*

During development, after the embryonic stage, ontogenetic changes in habits, and sexual differentiation and maturation can lead to differences in the relative growth of different structures. Knowledge on these relationships can provide important information on the different life cycle stages, for example, the size at the onset of

Pap. Avulsos Zool., 2019; v.59: e20195908
http://doi.org/10.11606/1807-0205/2019.59.08
http://www.revistas.usp.br/paz
http://www.scielo.br/paz
Edited by: William Ricardo Amâncio Santana
Received: 08/07/2018
Accepted: 14/02/2019
Published: 27/03/2019

ISSN On-Line: 1807-0205
ISSN Printed: 0031-1049
ISNI: 0000-0004-0384-1825

morphological sexual maturity and/or the presence of sexual dimorphism (Hartnoll, 1978, 1982). The growth of these body structures may also vary according to sex and life stage. For example, juveniles invest more in somatic growth to achieve sexual maturity than they invest in the growth of specific structures related to the mating behavior, as adults (Paschoal *et al.,* 2013; Moraes-Riodades & Valenti, 2002).

The population structure of species of *Macrobrachium* has a similar pattern: the majority of individuals belonging to the smaller size classes, with fewer individuals in the larger ones (Barros-Alves *et al.,* 2012; Pereira & Chacur, 2009; Pescinelli *et al.,* 2016; Taddei *et al.,* 2017). Part of this is due to the relative growth of structures related to agonistic behaviors, such as the second pair of chelipeds. In this way, the aggressiveness displayed by some species can, to a certain extent, shape the population structure of a community (Peebles, 1977, 1979; Valenti, 1985; Valenti *et al.,* 1993). Knowledge of the reproductive biology of palaemonid prawns is an important tool to establish biodiversity conservation strategies (Mossolin & Bueno, 2002). Reproductive characteristics may vary according to individual intrinsic aspects, such as female size and age, as well as according to environmental conditions, and may influence fertility and recruitment (Sastry, 1983; Pereira *et al.,* 2017).

The present study describes the relative growth and population dynamics of *M. iheringi* by identifying the structures that best represent the transition between the juvenile and adult phases and determining the size at the onset of morphological sexual maturity. In addition, we report the size frequency distribution, size of the smallest ovigerous female, sex-ratio, reproductive period, recruitment, and fecundity.

MATERIAL AND METHODS

Study area and sampling of specimens and environmental factors

Specimens of *M. iheringi* were collected for two years, from July 1991 to June 1992, and July 1993 to June 1994. The samplings were carried out in "Ribeirão da Hortelã", a first-order stream of the Paranapanema River upper basin, located 880 m above sea level, in the municipality of Botucatu, central region of the state of São Paulo (22°57'S, 48°26'W) (Fig. 1). The riverbed consists of sand and mud with about 80% shade cover by the surrounding riparian forest (except in some sections cleared for cattle grazing. In the early morning, for 90 minutes, two collectors used 2 mm mesh sieves in the aquatic vegetation near the river bank to obtain both juvenile and adult prawns. The sampling covered a 200-meter long section of the stream.

The prawns were stored in plastic bags and kept frozen until they were taken to the laboratory, where they were preserved in 70% ethanol until analysis. Specimens were identified at species level according to Melo (2003), separated by sex by the presence of the male appendix on the endopod of the second pleopod (Mantelatto & Barbosa, 2005) and measured with a digital caliper (0.01 mm). The body structures of males and females measured and used in the morphometric analysis were

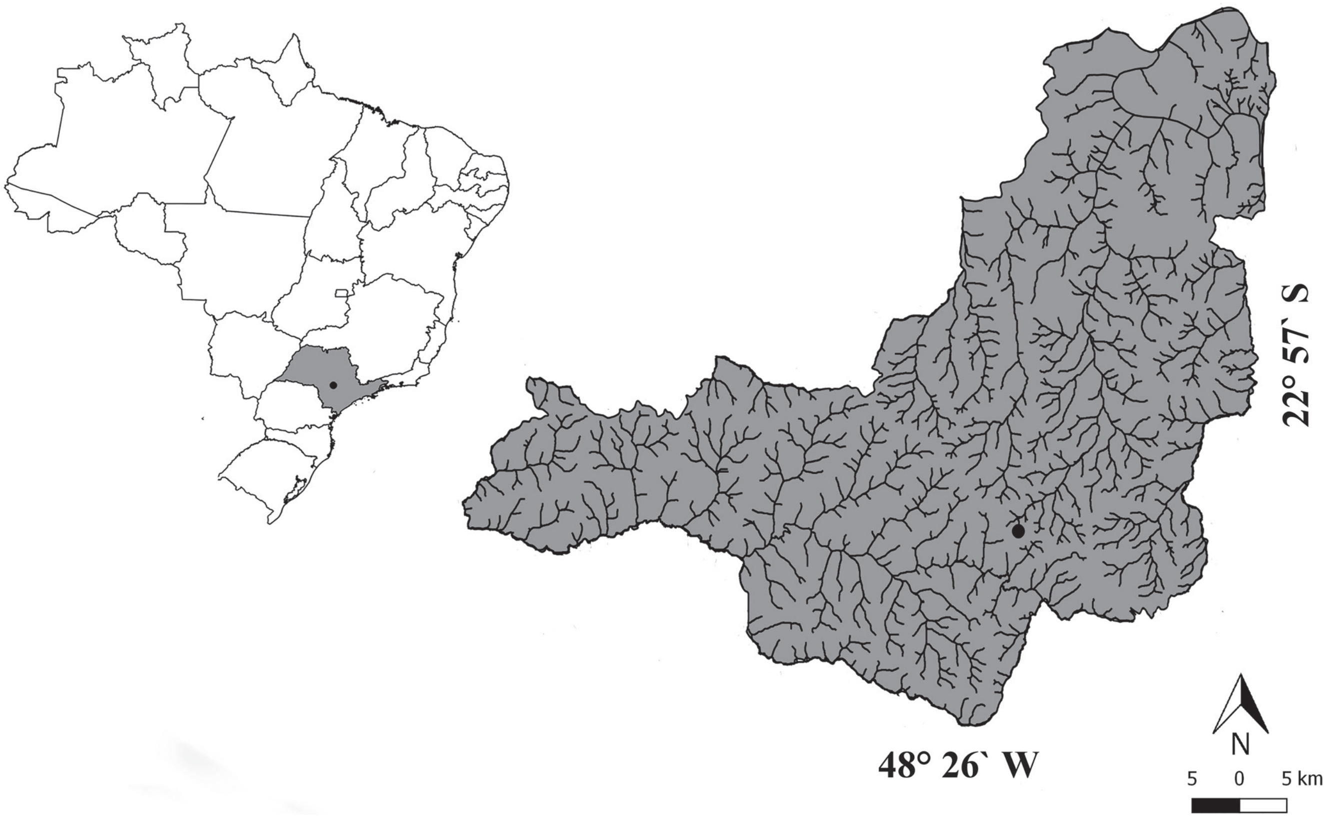

Figure 1. Map showing the sampling site, Ribeirão da Hortelã (22°57'S and 48°26'W), in Botucatu, São Paulo.

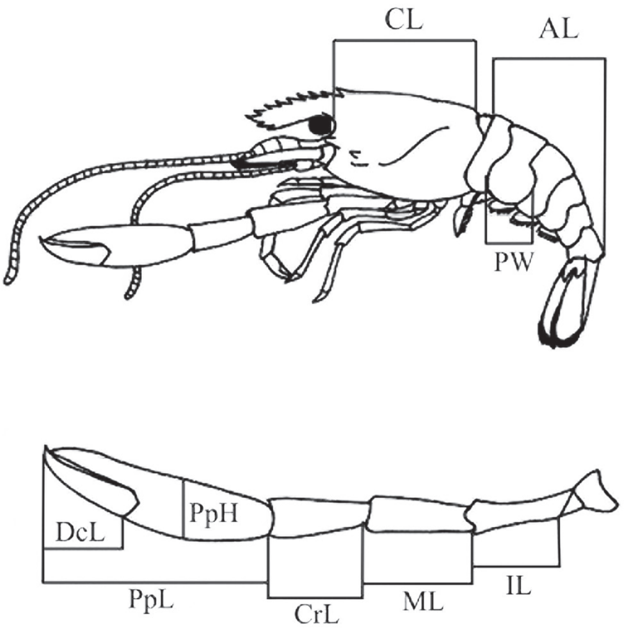

Figure 2. Measurements taken from each specimen of *Macrobrachium iheringi* (Ortmann, 1897) (CL = carapace length, PW = pleura width, AL = abdomen length. IL = ischium length, ML = merus length, CrL = carpus length, PpL = propodus length, DcL = dactyl length and PpH = propodus height).

the carapace length (CL), pleura width (PW), abdomen length (AL), and ischium length (IL), merus length (ML), carpus length (CrL), propodus length (PpL), dactyl length (DcL), and propodus height (PpH) of the second right pereopod (Fig. 2). Individuals smaller than the smallest recognizable male were considered as sexually undifferentiated and used only in the population structure analyses. The temperature of the water was obtained with a mercury thermometer (0.1°C), and the rainfall was obtained from the Integrated System of Management of Water Resources of the State of São Paulo.

Analysis of morphotypes (males)

To check for the presence of different morphotypes in the population, we initially searched for macroscopic morphological differences between the individuals, such as the ornamentation of the chelipeds and the angulation of the spines, as observed in *M. amazonicum* (Heller, 1862) and *M. rosenbergii* (De Man, 1879) (Kuris *et al.,* 1987; Moraes-Riodades & Valenti, 2004; Pantaleão *et al.,* 2014). Then, an exploratory analysis (principal component analysis – PCA) was used with the morphometric data, to verify whether the population could be separated into distinct morphological groups based on the structures analyzed.

Relative growth and determination of morphological sexual maturity

The Mann-Whitney test was used to investigate the existence of heterochely in the population, a factor that could directly influence the analysis of relative growth. Then, changes in the growth of different body structures in relation to the independent variable (CL) were verified using the relative growth analysis. The data were plotted and fit to the allometric equation $y = ax^b$, where y is the size of a given body structure, x is the length of the carapace, and b is the allometric coefficient (angular) that reflects the angulation of the curve. (Hartnoll, 1974, 1978, 1982). The values of the allometric constant correspond to isometric growth ($b = 1$), positive allometry ($b > 1$) or negative allometry ($b < 1$). To calculate b for each biometric relationship, the data were converted to the linear form by means of natural logarithm transformation (Zar, 2010). The null hypothesis (H_0: $b = 1$) was tested with the Student T-test ($\alpha = 95\%$). Only individuals who had all the previously mentioned structures were used in the analyses. Sexually undifferentiated individuals (UJ) were not considered. After the measurements, the individuals were classified as juveniles or adults, from the differential growth of body structures in relation to the CL. For this, the non-hierarchical K-means analysis was used with the morphometric relationships of males and females separately. This analysis distributes the data into previously established groups (juveniles and adults in our case), by an interactive process that minimizes the variation within groups and maximizes the variation between them. For data overlap, a discriminant analysis was performed with individuals within the overlap range to refine the data for categorization. Both analyzes were based on Sampedro *et al.* (1999) and Hirose *et al.* (2013). The breaking point between the groups identified by the discriminant analysis was considered the beginning of morphological sexual maturity. After refining the data, they were subjected to a covariance analysis to compare the angular and linear coefficients between juveniles and adults. This showed whether the data for each relationship were better adjusted in a single line or if juveniles and adults should be represented by different linear equations.

Population structure

The prawns were distributed in 12 size classes which were established with the method of Sturges (1926). The sex-ratio in adults of the two periods was compared with the Chi-square test (χ^2) ($p < 0.05$). The mean total length (TL) of males and females of different demographic classes was compared with the Mann-Whitney test ($\alpha < 0.05$) (Zar, 2010). All statistical analyses were performed using the statistical software PAST v2.17.

Reproductive aspects

The reproductive period was based on the monthly observation of ovigerous females in sampling years. For the analysis of fecundity, 15 females with an intact egg mass were considered. Spent females were taken into account in the population structure analysis. They were classified by the macroscopic observation of the pleopod region, were it was noticed a recent spawn and reminiscent egg mass. The embryonic development of eggs was classified as Early (homogenous color, no visible eye pigments) or Late (eyes completely developed) (Wehrtmann, 1990; García-Guerrero & Hendrickx, 2009). Ten eggs of each female were carefully removed from the parental pleopods and measured for length and width using a microscope with magnification of 10x. Then, the females were immersed in a solution of hypochlorite (0.05%) and all eggs were carefully extracted with fine tweezers and counted. The fecundity of each female was calculated as F = number of eggs per female. Egg volume (VO) was calculated as: $VO = \pi * l * h * (h)^2$; where l is the length in mm; h is the width in mm and $\pi = 3.14$ (Wehrtmann, 1990). The relationship between fecundity and CL was tested by Simple Linear Regression (Software R, $\alpha = 0.05$). To investigate a possible influence of environmental factors (water temperature and rainfall) on fecundity and presence of UJ, a time series analysis was used (Cross-correlation, Statistica 7,0, StatSoft, Inc) with $\alpha = 0.05$ (Zar, 2010).

RESULTS

Environmental factors

During the first sampling year, the highest temperatures were observed in spring and summer, and during the second year in spring, summer and early autumn. The lowest temperatures were recorded in August and September of 1991 and June 1992 in the first sampling year, and in the second in July 1993 and June 1994 (Fig. 3). The highest precipitation was observed in February and March of 1992, and in January and February of 1994. July and August of 1991 and June of 1992 had the lowest precipitation in the first year, and July 1993 and June 1994 in the second (Fig. 3).

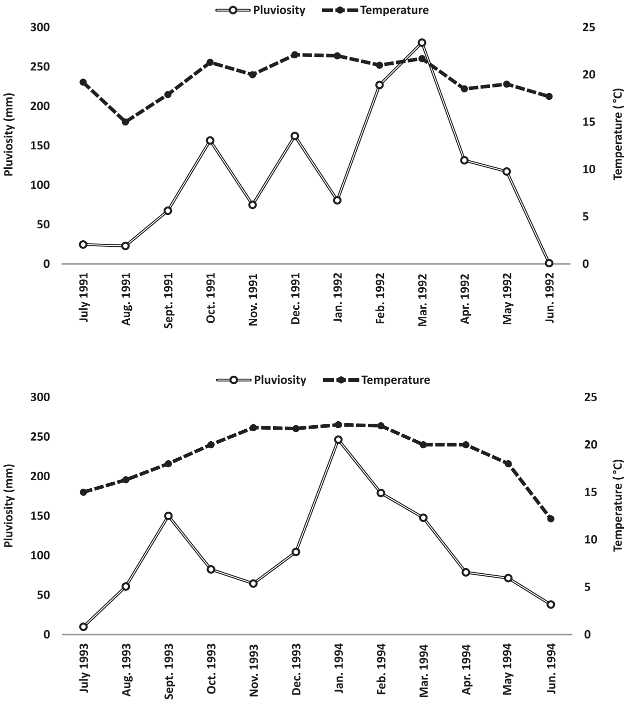

Figure 3. Monthly variation of water temperature and pluviosity during the two sampling periods, July 1991 to June 1992 and July 1993 to June 1994, in Botucatu, state of São Paulo, Brazil.

General data

Overall, 1478 prawns were captured, but for the screening of potential morphotypes and the analysis of relative growth, only the sexually differentiated individuals with intact articles from the second pair of pereopods were used in the statistical analysis, resulting in 171 males and 197 females. According to the Mann-Whitney test, there was no significant difference ($p > 0.05$) between the size (mm) of left and right chelipeds, therefore, the right cheliped was chosen to analysis performance.

Regarding the analysis of relative growth, the K-means analysis showed a significant difference ($p < 0.01$) in the PpL *vs* CL relationship between juveniles and adults males. The relationship PpL *vs* CL was positively allometric in adults and isometric in juveniles, thus, in the adults the propodus grows faster than the CL. Based on this relationship, the size at onset of sexual maturity of males was estimated at 13.23 mm CL (Fig. 4). As in PpL *vs* CL, the relation CrL *vs* CL was positively allometric to adult males and negatively to juveniles. All other biometric relationships related to the second pair of chelipods (IL *vs* CL; ML *vs* CL; DcL *vs* CL) showed isometry for adult males and negative allometry for juveniles, with the exception of the PpH *vs* CL relation, which showed positive allometric development for both demographic classes. In relation to the abdomen, AL *vs* CL and PW *vs* CL presented negative allometry in both demographic classes.

The size at onset of morphological sexual maturity in females was estimated to be 11.1 mm CL (Fig. 5). In females, a few relationships were significantly different ($p < 0.05$) between juveniles and adults: AL *vs* CL, PpL *vs* CL, PpH *vs* CL, DcL *vs* CL (Table 2). Regarding the abdomen, the relationship AL *vs* CL and PW *vs* CL, was isometric in adults and juveniles. For the second right cheliped, the relationships IL *vs* CL, ML *vs* CL, CrL *vs* CL showed the same development pattern between demographic classes, being characterized as negatively allometric. It was observed in the relations PpL *vs* CL and PpH *vs* CL different development patterns between demographic classes, being, positively allometric to adults and negatively allometric and isometric to juveniles, respectively. The relation DcL *vs* CL was characterized by the same development pattern between the demographic classes, being isometric.

No macroscopic evidence of different male morphotypes was found in this population. The same result was obtained by the morphometric analysis: the PCA showed no separation of morphological groups in the adult males. Principal component (PC1) (Table 1, Fig. 6) explained most of variation (93.56%), and was related to propodus length (PpL). The wide distribution of individuals along the PC1 suggests a high variation in propodus size from juveniles to adults.

Populational structure

A total of 1,478 individuals were collected during the two sampling periods, of which 759 females (with 19 of them carrying eggs), 494 males, and 225 undifferentiated juveniles. The TL range was 16.5-63.5 mm in non-ovigerous females, 47.4-61.5 mm in ovigerous females, 19.2-72.0 mm in males, and 8.6-19.2 mm in undifferentiated juveniles.

Prawns were distributed in 12 TL size classes of 5.3 mm intervals. Undifferentiated juveniles were found in the first two size classes, being more abundant in the second (Table 4). The highest absolute frequency of undifferentiated juveniles was found in size class 13.9 [19.2 (Table 4). Females were more abundant in the size classes of 19.2 [24.5, followed by 24.5 [29.8 and 35.1 [40.4 mm. Males were more abundant in the classes 24.5 [29.8, followed by 29.8 [35.1 and

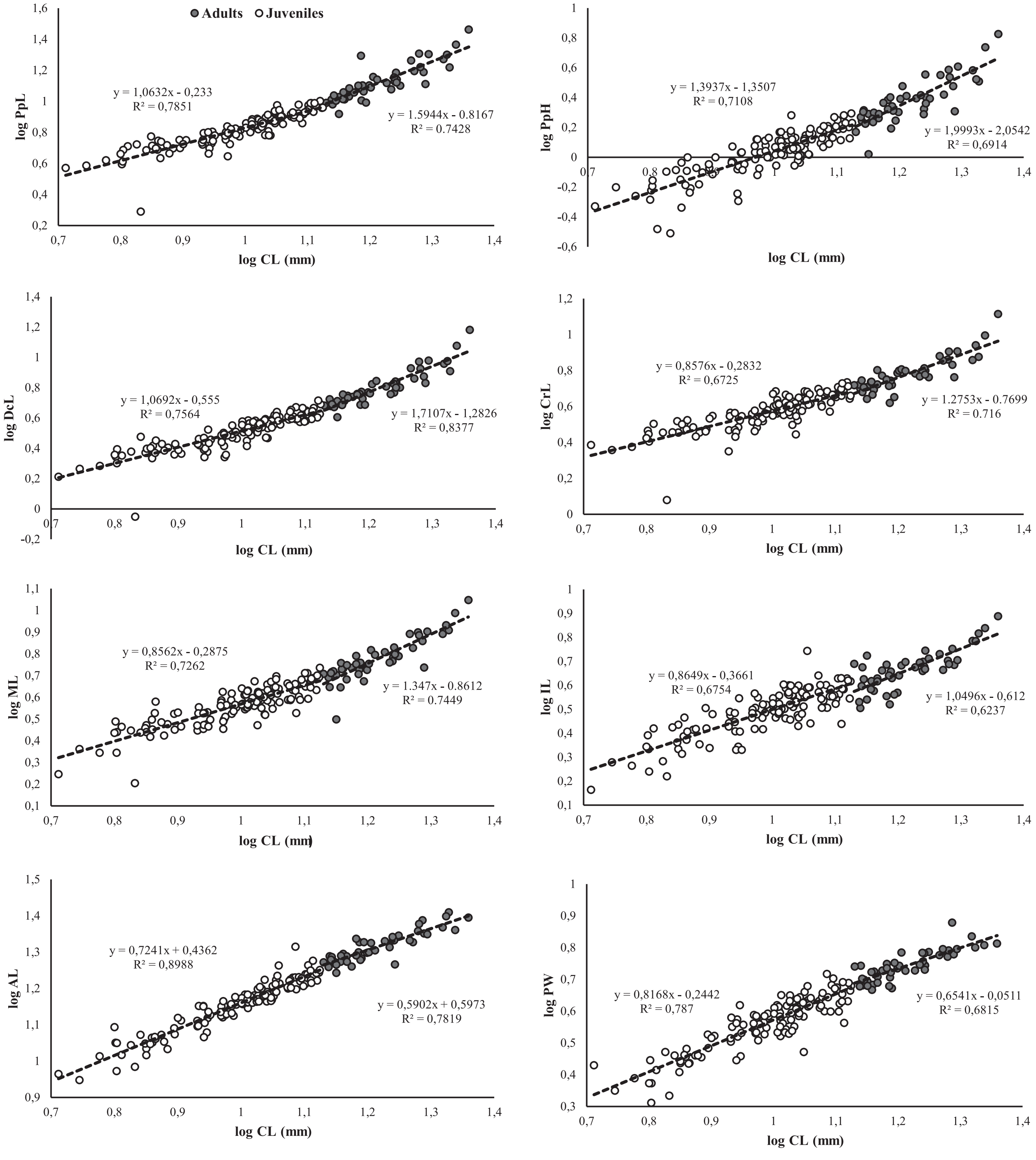

Figure 4. Estimation of the size at onset of morphological sexual maturity of *Macrobrachium iheringi* (Ortmann, 1897) males. The estimated size is the carapace length (CL) of the smallest adult individual, obtained after the distinction of juvenile (open circles) and adult (black circles) equations. PW = pleura width, AL = abdomen length, IL = ischium length, ML = merus length, CrL = carpus length, PpL = propodus length, DcL = dactyl length and PpH = propodus height.

35.1 [40.4 mm (Table 4). Comparing the two sampling years, 1991/1992 and 1993/1994, males and females were found all over the year, yet, abundance in rainy months was higher than in the drier ones. In 1991/1992 the abundance of males and females was similar, whereas in 1993/1994 females were more abundant (Figs. 7 and 8).

Regarding the sex ratio, there was a significant bias towards males in the larger size classes, in both years. For females, there was no significant bias in classes 13.9 [9.2, 19.2 [24.5, 45.7 [50 and 69.9 [72.2 mm (Table 4).

Reproductive aspects

The reproductive period was seasonal: in the period of July 1991 to June 1992 ovigerous females occurred only in October and February (Fig. 7). In the period of

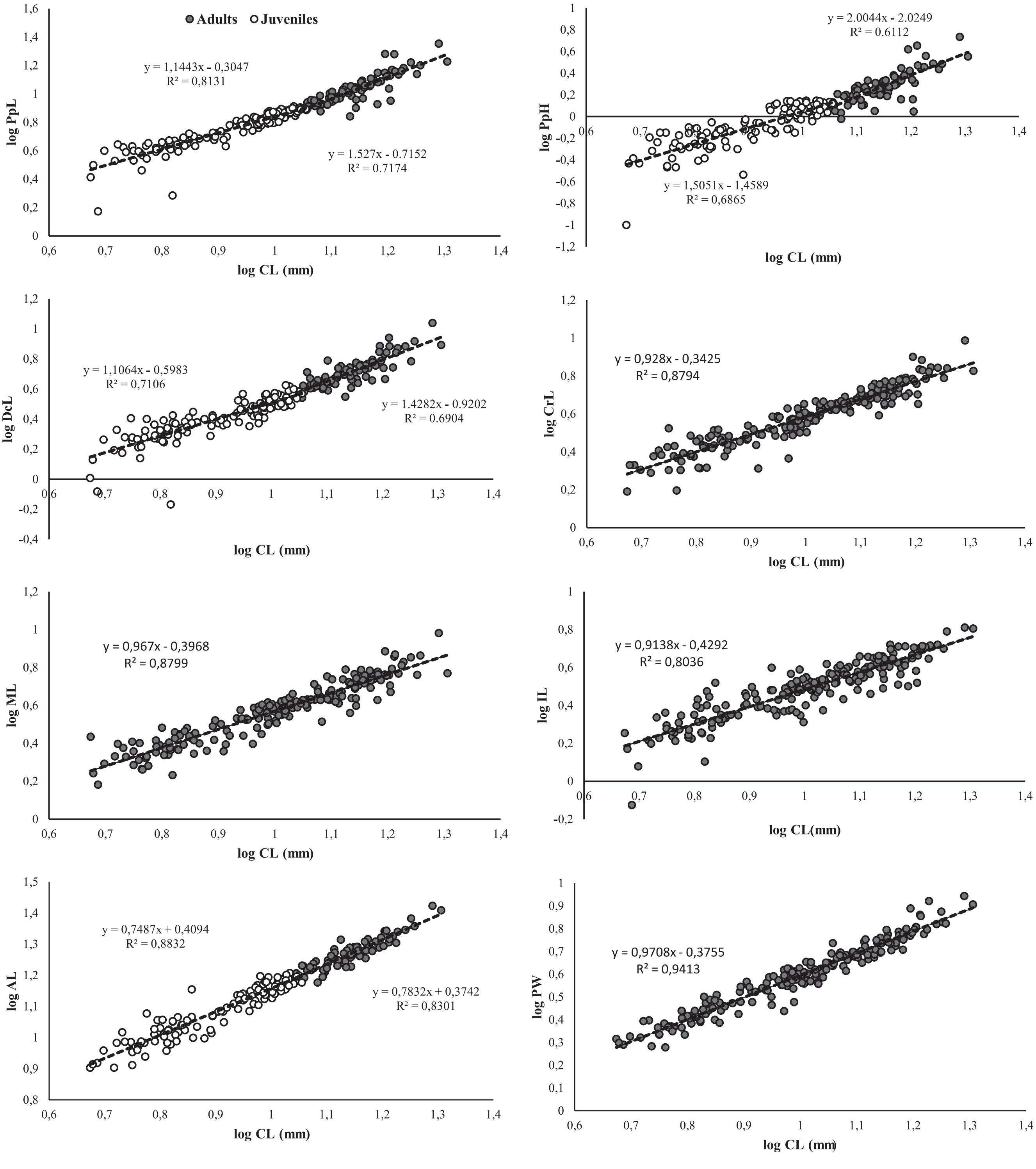

Figure 5. Estimation of the size at onset of morphological sexual maturity of *Macrobrachium iheringi* (Ortmann, 1897) females. The estimated size is the carapace length (CL) of the smallest adult individual, obtained after the distinction of juvenile (open circles) and adult (black circles) equations. PW = pleura width, AL = abdomen length, IL = ischium length, ML = merus length, CrL = carpus length, PpL = propodus length, DcL = dactyl length and PpH = propodus height.

Table 1. Scores of the nine morphometric measurements of the first two axes of the principal component analysis. The structure with the highest score in PC1 is shown in bold.

Variable	PC 1	PC 2
CL	0.5212	-0.33307
PW	0.00866	-0.010452
Ab	0.48881	-0.62735
IL	0.13366	0.006380
ML	0.20113	0.14011
CrL	0.20474	0.17258
PpL	**0.5534**	0.59567
PpH	0.11616	0.15663
DcL	0.2635	0.25824

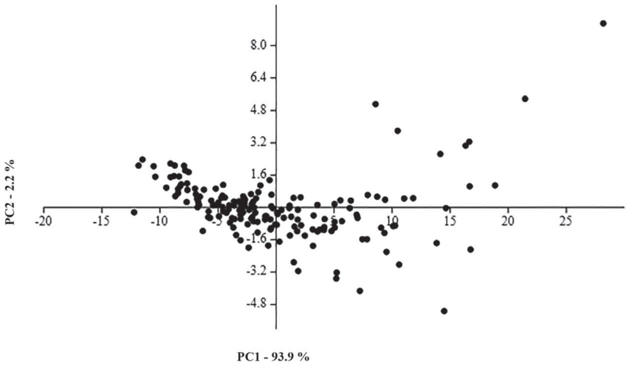

Figure 6. Projection scores of first and second principal components, generated with the principal components analysis of *Macrobrachium iheringi* (Ortmann, 1897) males' morphometric data.

July 1993 to June 1994, there was a higher abundance of ovigerous females in November and December, and a lower from January to March (Fig. 8).

Fecundity varied from 57 to 107 eggs, in females with CL ranging from 51 to 56 mm, with a mean of 76 eggs per female. There was a significant positive relationship between CL and fecundity (p = 0.005, F = 11.2, df = 13) (Fig. 9).

Egg size varied with development. In the early stage, width was 1.41-1.61 mm and length was 2.02-2.2 mm, with a mean width of 1.49 mm and mean length of 2.13 mm. Egg volume ranged from 2.22 to 2.9 mm^3, with a mean of 2.48 mm^3. In the late stage, egg width was 1.5-1.66 mm, and length was 2.11-2.24 mm, with a mean width of 1.59 mm and mean length of 2.19 mm. Egg volume in the late stage ranged from 2.55 to 3.14 mm^3, with mean of 2.91 mm^3. There was an increase of nearly 17% in egg volume between the early and late stages.

A time series analysis (Cross-correlation) of the period 1993/1994 indicated a positive correlation ("lag -2") between pluviosity and number of ovigerous females (Fig. 10A), meaning that two months after pluviosity increased there was a higher abundance of ovigerous females. A positive correlation between temperature and ovigerous females ("lag 0") was also observed (Fig. 10B), indicating that abundance increased with temperature. However, there was no correlation between the abundance of ovigerous females and environmental factors in 1991/1992.

Table 2. *Macrobrachium iheringi* (Ortmann, 1897). Results of covariance analysis (ANCOVA). (J) juveniles and (A) adults.

Relationship	Group	Coefficient (log)	F	P
PW *vs* CL	Male J *vs* A	a	—	—
		b	13.63	< 0.001*
	Female J *vs* A	a	0.22	0.638
		b	1.10	0.296
AL *vs* CL	Male J *vs* A	a	—	—
		b	31.32	< 0.001*
	Female J *vs* A	a	—	—
		b	10.24	< 0.001*
IL *vs* CL	Male J *vs* A	a	5.42	0.021*
		b	1.31	0.254
	Female J *vs* A	a	0.38	0.540
		b	1.17	0.282
ML *vs* CL	Male J *vs* A	a	—	—
		b	10.93	< 0.001*
	Female J *vs* A	a	0.25	0.618
		b	0.99	0.32
CrL *vs* CL	Male J *vs* A	a	—	—
		b	8.75	< 0.001*
	Female J *vs* A	a	0.31	0.578
		b	0.24	0.632
PpL *vs* CL	Male J *vs* A	a	—	—
		b	15.88	< 0.001*
	Female J *vs* A	a	—	—
		b	4.33	0.039*
PpH *vs* CL	Male J *vs* A	a	—	—
		b	18.77	< 0.001*
	Female J *vs* A	a	—	—
		b	12.16	< 0.001*
DL *vs* CL	Male J *vs* A	a	—	—
		b	28.20	< 0.001*
	Female J *vs* A	a	—	—
		b	5.04	0.026*

During the first sampling period undifferentiated juveniles were found in December 1991, and March-June 1992 (Fig. 7), whereas in the second period they were found in July-October 1993 and January-June 1994 (Fig. 8). There was a positive correlation ("lag 1") between pluviosity and number of undifferentiated juveniles in 1991/1992 (Fig. 11A); thus, one month after pluviosity increased there was a higher abundance of juveniles. There was also a negative correlation ("lag -3") between temperature and undifferentiated juveniles in 1993/1994 (Fig. 11B); three months after a rise in temperature their abundance decreased.

DISCUSSION

Previous studies (Mantelatto & Barbosa, 2005; Mossolin & Bueno, 2002; Pantaleão *et al.,* 2012) indicated the second pair of chelipeds as good indicators of morphological sexual maturity. In this study, we observed the second pair of chelipeds and the second abdominal pleura as indicators of juveniles and adults of *M. iheringi,* corroborating the previously mentioned studies. The pleura width is commonly used as an indicator of mor-

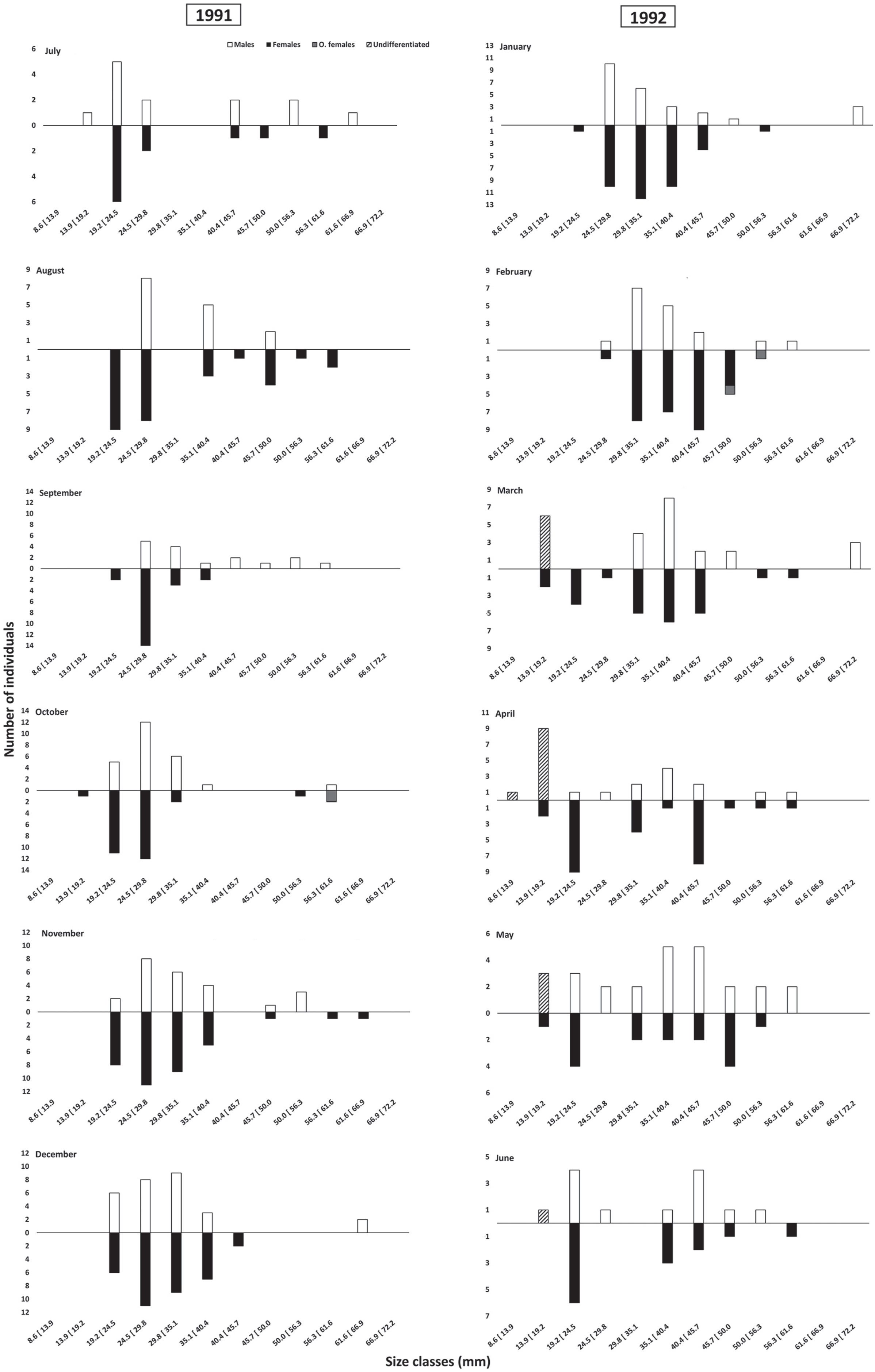

Figure 7. Monthly distribution of individuals of *Macrobrachium iheringi* (Ortmann, 1897) by size classes, captured from July 1991 to June 1992.

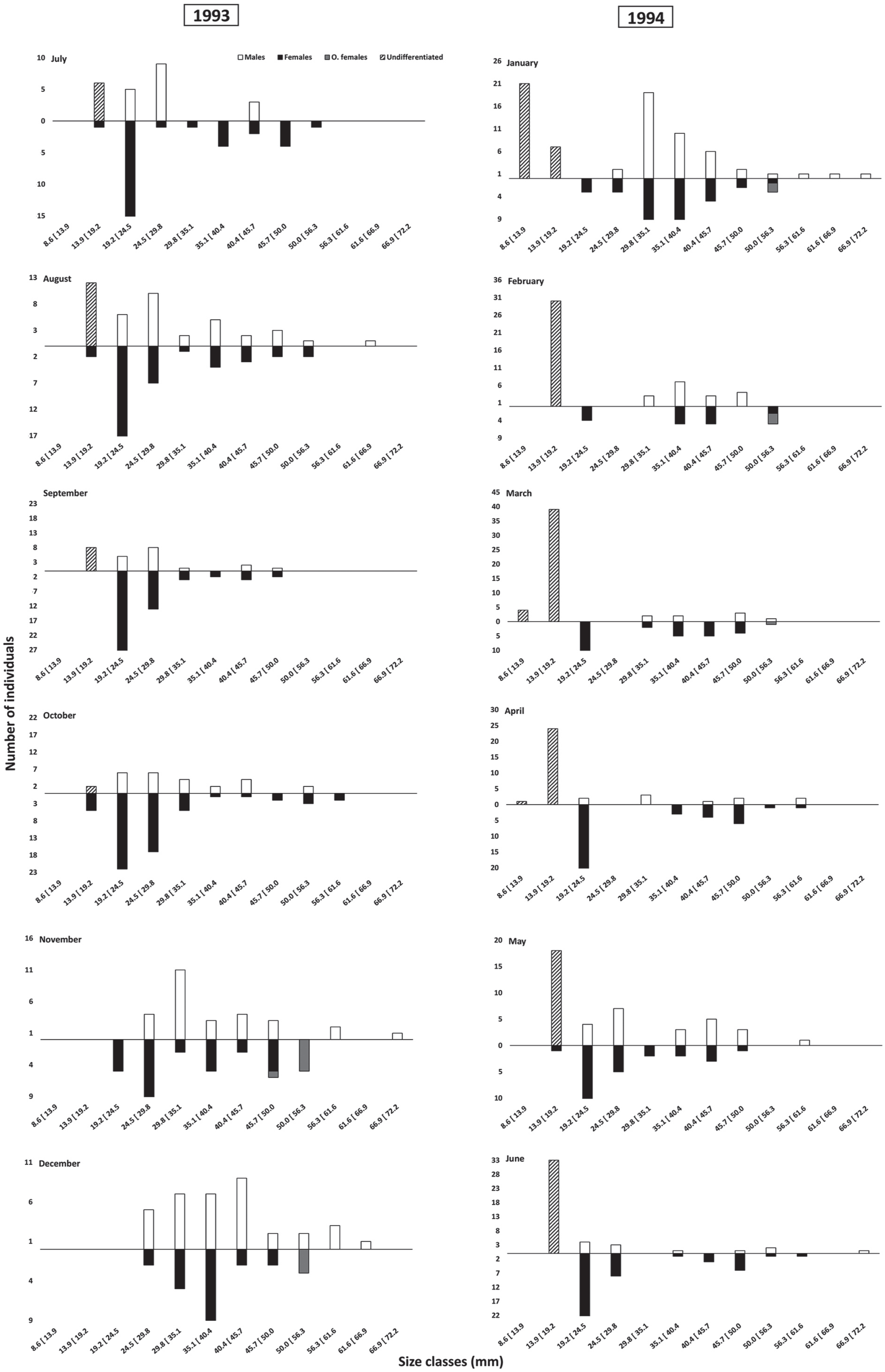

Figure 8. Monthly distribution of individuals of *Macrobrachium iheringi* (Ortmann, 1897) by size classes, captured from July 1993 to June 1994.

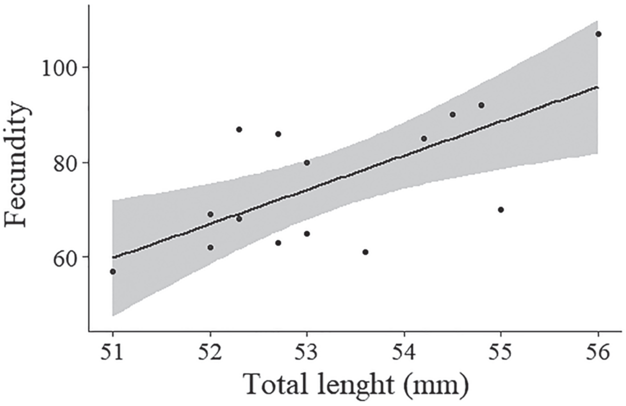

Figure 9. *Macrobrachium iheringi* (Ortmann, 1897). Relationship between fecundity and total length of females.

phological sexual maturity for females; however, the ANCOVA results showed no difference in the size of this structure among the demographic classes of the studied population. Therefore, cheliped was used as an indicator of morphological maturity in both sexes.

Based on the relative growth of males, different growth patterns were observed from juveniles to adults. Almost all analyzed morphometric relationships differed between juveniles and adults, being allometric negative in juveniles and allometric positive or isometric in adults. With the exception of the relations AL *vs* CL, PW *vs* CL and PpH *vs* CL, where both classes presented during development negative allometry in the first two relations and positive allometry in the last relation. These results emphasize the different energy investments during development. Juveniles invest in somatic growth to achieve sexual maturity and to be able to reproduce, while adults invest more in structures related to reproductive success. For example, males need to compete for females with the help of chelipeds (Correa & Thiel, 2003; Hartnoll, 1978, 1982). To females, pereopods relationships were similar, as described above, since almost all relationships were identical among demographic classes. As the second pereopod can have several functions in these prawns, such as feeding and sexual and agonistic behaviors, this structure may develop in a similar way, presenting different functionalities in different demographic classes (Karplus *et al.,* 1992; Nagamine & Knight, 1980; Volpato & Hoshino, 1984; Valenti *et al.,* 1989).

In abdominal structures, the development of both pleura and abdomen, was shown as negative allometric in the two phases of life, therefore, these structures are

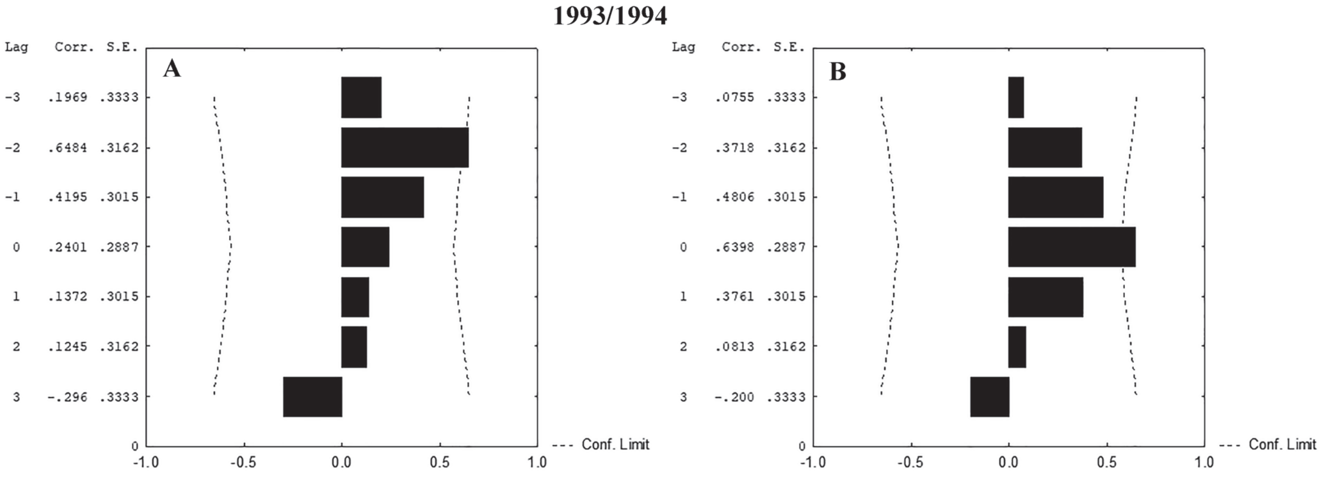

Figure 10. *Macrobrachium iheringi* (Ortmann, 1897). Time series analysis of ovigerous females and (A) rainfall (mm) and (B) temperature (°C) from July 1993 to June 1994 in Botucatu, Brazil. Lag = time; Corr = correlation value; S.E. = standard error; Conf. Limit = confidence limit.

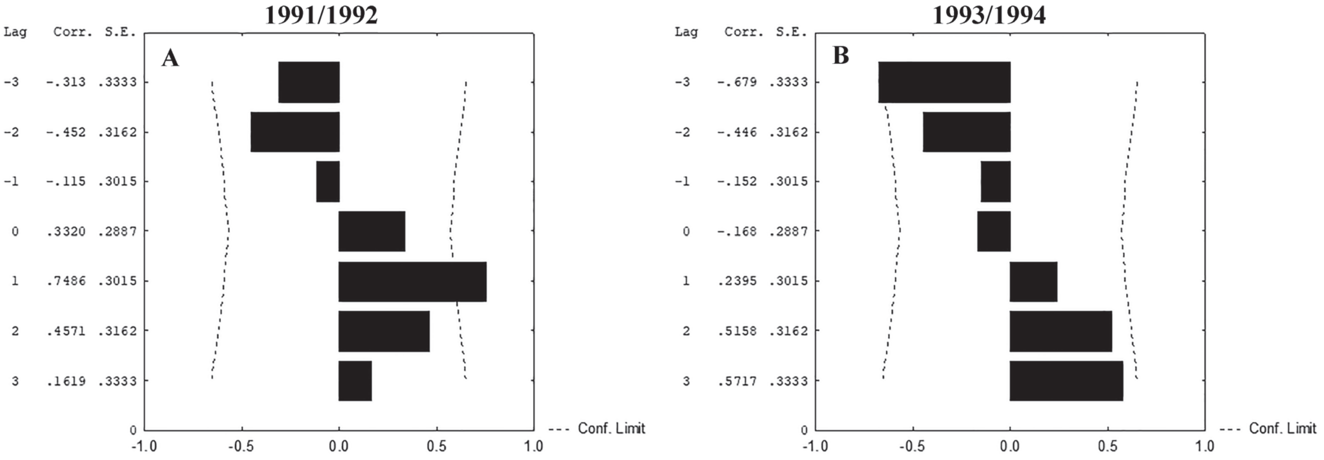

Figure 11. *Macrobrachium iheringi* (Ortmann, 1897). Time series analysis of undifferentiated individuals and (A) rainfall (mm) from July 1991 to June 1992 and (B) temperature (°C) from July 1993 to June 1994 in Botucatu, Brazil. Lag = time; Corr = correlation value; S.E. = standard error; Conf. Limit = confidence limit.

Table 3. *Macrobrachium iheringi* (Ortmann, 1897). Regression analysis of morphometric data. CL was used as the independent variable. (AM) adult males, (JM) juvenile males, (AF) adult females and (JF) juvenile females.

Relation	Sex	N	*a*	*b*	r^2	*T* (b=1)	*p*	Allometry
PW vs CL	AM	45	-0.0511	0.6541	0.6815	-2.974	<0.001	—
	JM	124	-0.2442	0.8168	0.787	2.021	<0.001	—
	AF and JF	190	-0.3755	0.9708	0.9413	1.649	<0.001	—
AL vs CL	AM	46	0.5973	0.5902	0.7819	-7.269	<0.001	—
	JM	125	0.4362	0.7241	0.8988	-7.633	<0.001	—
	AF	76	0.3742	0.7832	0.8301	-4.696	<0.001	—
	JF	117	0.4094	0.7487	0.8832	-6.096	<0.001	—
IL vs CL	AM	46	-0.612	1.0496	0.6237	1.622	0.53	=
	JM	125	-0.3661	0.8649	0.6754	-1.687	<0.01	—
	AF and JF	193	-0.4292	0.9138	0.8036	2.638	<0.001	—
ML vs CL	AM	46	-0.8612	1.347	0.7449	2.764	0.08	=
	JM	125	-0.2875	0.8562	0.7262	2.611	<0.01	—
	AF and JF	193	-0.3968	0.967	0.8799	1.275	<0.001	—
CrL vs CL	AM	46	-0.7699	1.2753	0.716	2.788	0.09	=
	JM	125	-0.2832	0.8576	0.6725	2.876	<0.01	—
	AF and JF	193	-0.3425	0.928	0.8794	2.894	<0.001	=
PpL vs CL	AM	46	-0.8167	1.5944	0.7428	2.729	<0.05	+
	JM	125	-0.233	1.0632	0.7851	5.254	0.06	=
	AF	76	-0.7152	1.527	0.7174	7.670	<0.01	+
	JF	117	-0.3047	1.144	0.8131	2.255	0.09	=
PpH vs CL	AM	46	-2.0542	1.9993	0.6914	4.604	<0.01	+
	JM	125	-1.3507	1.3937	0.7108	15.685	<0.001	+
	AF	76	-0.462	1.034	0.6409	5.580	<0.001	+
	JF	117	-0.301	0.8808	0.746	19.460	<0.001	—
DcL vs CL	AM	46	-1.2826	1.7107	0.8377	4.273	<0.001	+
	JM	125	-0.555	1.0692	0.7564	7.892	0.12	=
	AF	76	-0.7152	1.527	0.7174	2.859	0.12	=
	JF	117	-0.3047	1.1443	0.8131	8.15	0.21	=

developing at the same rhythm independent of phase of life. Mantelatto & Barbosa (2005) found a similar result in their study with *M. brasiliense* (Heller, 1862) and hypothesized that the pleura would not develop much due to its abbreviated larval development, which also occurs in *M. iheringi.* Due to the increase of the embrionic stages that occur within the eggs, and because females have a small number of eggs, the pleura need not be as developed as in species with longer larval stages (Mantelatto & Barbosa, 2005).

The reproductive period was considered seasonal as the presence of ovigerous females occurred only in the warmer months. In the second sampling period, the presence of ovigerous females was related with higher pluviosity and higher temperatures, their abundance increased in rainy periods and when water temperature reached 20°C. According to Alekhnovich & Kulesh (2001), the occurrence of reproduction when temperature reaches between 18 and 20°C is apparently a general pattern for *Macrobrachium.* Reproductive peaks after an increase in pluviosity and temperature were also observed in other species of the genus, *M. olfersii* (Wiegmann, 1836), *M. hainanense* (Parisi, 1919) and *M. jelskii* (Miers, 1877) (Mossolin & Bueno, 2002; Mantel & Dudgeon, 2005; Mossolin *et al.,* 2013; Soares *et al.,* 2015; Rocha & Barbosa, 2017). The recruitment of undifferentiated juveniles occurs in the months after the appearance of ovigerous females, therefore, it is suggested that the reproductive period of *M. iheringi* is seasonal.

Table 4. Total number *Macrobrachium iheringi* (Ortmann, 1897) males, females and undifferentiated juveniles per size class (mm), and the sex ratio (M:F). The chi-square value (χ^2) indicates the comparison with the expected 1:1 ratio, and P is the statistical significance.

Size classes	Males	Females	Undifferentiated Juveniles	M:F	χ^2	P
8.6 [13.9	0	0	27	—	—	—
13.9 [19.2	1	15	198	1:15	12.25	> 0.001
19.2 [24.5	58	247	0	1:3.31	71.82	> 0.001
24.5 [29.8	112	139	0	1:1.24	2.90	0.088
29.8 [35.1	98	87	0	1:0.88	0.65	0.419
35.1 [40.4	80	97	0	1:1.21	1.63	0.201
40.4 [45.7	60	74	0	1:1.23	1.46	0.227
45.7 [50.0	34	54	0	1:1.58	4.55	> 0.05
50.0 [56.3	21	32	0	1:1.52	2.28	0.131
56.3 [61.6	15	13	0	1:0.86	0.14	0.705
61.6 [66.9	6	1	0	1:0.16	3.57	0.06
66.9 [72.2	9	0	0	9:00	9.00	> 0.05
Total	494	759	225	1:1.42	36.81	> 0.001

Regarding fecundity, *M. iheringi* had a lower amount of eggs but they were larger than in other species of the genus (*e.g., M. potiuna* (Müller, 1880) and *M. brasiliense*) (Nazari *et al.,* 2003; Oliveira *et al.,* 2017), reflecting the reproductive strategy of this species. As *M. iheringi* has an abbreviated larval cycle, the larval development occurs mostly inside the eggs and larvae hatch in an advanced stage (Bueno & Rodrigues, 1995; Magalhães & Walker, 1988). When compared to other species of *Macrobrachium* that have abbreviated larval development, we observe similar results: *M. brasiliense* has on average 33 eggs per female, with fecundity varying between 8 and 116 eggs, and in *M. potiuna,* fecundity is 35 eggs on average and ranges from 19 to 65 eggs. In addition, for *M. iheringi,* egg size was similar to those of *M. potiuna,* which were 1.41 mm wide and 2.17 mm long (Nazari *et al.,* 2003; Oliveira *et al.,* 2017). Even though the fecundity of *M. iheringi* was twice that of *M. brasiliense* and *M. potiuna;* however, it can still be considered low and similar to other *Macrobrachium* species with abbreviated larval cycle, considering that species with extended larval cycle can carry 1,500 eggs on average, as observed in *M. olfersii* and *M. amazonicum* (Nazari *et al.,* 2003; Silva *et al.,* 2004).

According to Bauer (2003), in crustacean species that display mate guarding behavior, males are bigger than females, due to agonistic interactions that this behavior induces. In the population studied here, males reached a larger size than females, following the pattern shown by most caridean prawns with mate guarding behavior (Bauer, 2003; Gualberto *et al.,* 2012). It may be possible that these morphological variations occur due to genetic variations between populations and different environmental conditions, which may stimulate differential growth between sexes (Weiss *et al.,* 2015).

The sex ratio observed in the studied population was skewed towards females, which is a common pattern in caridean prawns and in *Macrobrachium* spp., as noted in studies of *Macrobrachium acanthurus* (Wiegmann, 1836) (Román-Contreras & Campos-Lince, 1993), *M. amazonicum* (Montoya, 2003), *M. brasiliense* (Mantelatto & Barbosa, 2005) and *M. jelskii* (Barros-Alves *et al.,* 2012). This variation may be influenced by differences in size, mortality, birth rates between males and females, ecdysis frequency, larval dispersion, and differential migration. The reproductive pattern of *M. iheringi* can be reflected in the sex ratio, since, in species that display mating guarding behavior, sexual deviance for females is usually greater. (Bauer, 2003; Wilson & Pianka, 1963; Botelho *et al.,* 2001).

Information on *M. iheringi* is scarce when compared to other species of the genus. Unlike several *Macrobrachium* species of Brazil, *M. iheringi* is not cultivated, and it also differs regarding its life cycle patterns. Since this prawn is part of a unique group in which the life cycle occurs exclusively in freshwater, studies on the biology of this species are important to better comprehend their adaptations to this environment. Our results provide important information on its population structure, relative growth in juveniles and adults, and size at maturity. Also, studies on other forms of sexual maturity, such as gonadal, physiological, and functional, may also help to better understand this species reproductive cycle.

ACKNOWLEDGMENTS

The authors are thankful to CNPq (Conselho Nacional de Deenvolvimento Cientifico e Tecnológico) for financial support during field work. All sampling in this study has been conducted in compliance with current applicable state and federal laws. We are also thankful to the anonymous reviewers and to Bernard Sainte-Marie for the contributions and improvement of our manuscript.

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Published with the financial support of the Committee of
"Programa de Apoio às Publicações Científicas Periódicas da USP" (SIBi-USP)