



Evaluation of population dynamics of *Macrobrachium olfersii* (Palaemonidae) along ~150 km extension of the Lower Ribeira de Iguape River, São Paulo, Brazil

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Abstract: This study aimed to verify the spatial and temporal population parameters of *Macrobrachium olfersii* over of ~150 km of the Ribeira de Iguape River (SP). Prawns were collected monthly (January to December 2007) in Eldorado, Sete Barras, Registro, and Iguape, using traps and sieves. We analyzed 9,691 individuals with carapace length (CL) from 2.2 to 25.4mm. In our results, smaller individuals were found close to the estuary, i.e., Iguape, whereas larger individuals were recorded as they moved away from the estuary. Reproduction was continuous but more intense in the summer, when temperature and rainfall were higher. The total sex ratio differed from the expected favoring males (1:0.73), and this deviation was also observed in Eldorado, Registro, and Iguape. Female sexual maturity was at 10.9 mm CL, without significant variation along the river. The regions closer to the estuary (Iguape/ Registro) presented lower CL^∞ and longevity, and higher k , due to the greater number of juveniles. In conclusion, the results suggest that the variation in size, recruitment, sexual maturity, and growth of individuals are related to the population structure along ~150 km of the river, and are triggered by the upstream migration of juveniles after larval development, which takes place in the estuarine region.

Key words: upstream migration, sexual maturity, sex ratio, longevity, Vale do Ribeira.

Avaliação da dinâmica populacional de *Macrobrachium olfersii* (Palaemonidae) ao longo de ~150km de extensão do Baixo Rio Ribeira de Iguape, São Paulo, Brasil. Resumo: Este estudo verificou espacialmente e temporalmente os parâmetros populacionais de *Macrobrachium olfersii*, ao longo de ~150km do Rio Ribeira de Iguape (SP). Os camarões foram coletados mensalmente com armadilhas e peneira, de janeiro a dezembro de 2007, nas regiões de Eldorado, Sete Barras, Registro e Iguape. Analisou-se 9.691 indivíduos com comprimento de carapaça (CC) de 2,2 a 25,4 mm. Os resultados indicam que os menores indivíduos estão na região próxima ao estuário (Iguape) e a medida que se afastam deste ambiente ficam maiores. A reprodução foi contínua, mas com maior intensidade no verão, quando a temperatura da água e o índice pluviométrico foram maiores. A proporção sexual total diferiu da esperada favorecendo os machos (1:0,73), sendo o mesmo observado nas regiões de Eldorado, Registro e Iguape. A maturidade sexual das fêmeas foi de 10,9 mm CC, sem grandes variações ao longo do rio. As regiões mais próximas ao estuário (Iguape/Registro) apresentaram menor CC^∞ e longevidade e maior k , devido ao maior número de juvenis. Como conclusão,

este estudo sugere que a variação no tamanho dos indivíduos, recrutamento, maturidade sexual e crescimento estão relacionados com a estrutura populacional ao longo do rio, desencadeada pela migração dos juvenis após o desenvolvimento larval na região estuarina.

Palavras-chave: Migração, maturidade sexual, razão sexual, longevidade, Vale do Ribeira.

Introduction

In recent years, the freshwater communities have suffered a considerable increase in human activities resulting in overexploitation, pollution, modification or blocking of river flow through dams, habitat destruction or degradation, and invasion by exotic species (Dudgeon *et al.* 2006).

Caridean shrimp are among the most important taxa in freshwater communities (Bauer 2011, Jardine 2014). Their populations put pressure on macroinvertebrate communities in streams through predation (Mantel & Dudgeon 2004, Ramirez & Hernandez-Cruz 2004). They can also modify the properties of the bottom, which affect the communities by removing the sediment (Pringle *et al.* 1993); by acting on leaf litter decomposition and nutrient cycling (Crowl *et al.* 2001, Benstead *et al.* 2010); and by being critical species in aquatic food webs (Mantel & Dudgeon 2004, Cross *et al.* 2008, Novak *et al.* 2017). Many species of the genus *Macrobrachium* (Caridea, Palaemonidae) are commercially exploited and are often targeted by subsistence, recreational and commercial fisheries (Hoarau *et al.* 2018). For this reason, studies on the population biology of freshwater prawns can help define strategies for managing and preserving these ecologically important species (Dudgeon *et al.* 2006, Hoarau *et al.* 2018).

Macrobrachium olfersii, like other freshwater prawns from the Ribeira de Iguape watershed (Rocha & Bueno 2004, Bertini *et al.* 2014), are migratory species vulnerable to anthropic changes along the river. They exhibit amphidromous migration, in which the larvae hatch in freshwater and move to the estuarine with the river current, where they stay during their entire larval development; after undergoing metamorphosis, the juveniles return to the river, where they will grow, mature, and reproduce (McDowall 2007, Bauer 2013).

Previous population studies in Brazil with *M. olfersii* were conducted in short rivers (Müller & Prazeres 1992, Barros 1995, Ammar *et al.* 2001, Mossolin & Bueno 2002, Teixeira & Couto 2012, Pescinelli *et al.* 2016). In these locations, individuals do not travel great distances from the river mouth as the inhabitants of the Ribeira de Iguape River.

According to Ribeiro *et al.* (2020), the abundance and spatiotemporal distribution of *M. olfersii* along the Ribeira de Iguape River are related to its amphidromous habit and regional rainfall regime. However, there are no studies on this species along the river extension to verify if there are changes in its population dynamics. Thus, the hypothesis was tested to evaluate if there is a spatial (along the ~150 km extension of the Lower Ribeira de Iguape River) and temporal difference (over the seasons) on the population parameters of *M. olfersii* as the individuals migrate upstream, after their larval period in the estuarine region of this river.

To accomplish this goal, the population dynamic of *M. olfersii* was assessed in a region close to the estuary (72 km from the mouth) and upstream of the Lower Ribeira de Iguape River, covering ~150 km of its extension. Several population biology aspects were analyzed, such as size structure, sex ratio, reproductive period, recruitment, female size at first sexual maturity, and growth. This information will expand the knowledge on the life cycle of this prawn in large rivers and serve as a basis for future management plans regarding the sustainable use of this natural resource.

Material and methods

Description of the study area: The Ribeira de Iguape River watershed (23°50'S 46°50'W; 25°30'S 50°00'W) has approximately 25.000 km² of area, being one of the largest on the Brazilian coast (Mahiques *et al.* 2014). It is the main river in the basin. It has its source in the State of Paraná, traveling about 470 km until it flows into the Atlantic Ocean in Barra do Ribeira, in the municipality of Iguape (Veneziani *et al.* 2019). The Ribeira de Iguape River can be divided into three sections: upper, middle, and lower. In the upper and middle courses, rapids occur, while in the lower portion of the basin, the lands are flatter and more floodable, where the river meanders down until it flows into the coastal region near Iguape (Diegues 2007, Veneziani *et al.* 2019, Cunha-Lignon *et al.* 2021). The river plain observed up to Eldorado has an average altitude of 17m (above sea level) (Veneziani *et al.* 2019).

The present study included four municipalities in the lower section of the Ribeira de Iguape River plain. The Iguape region is about 72 km away from the estuary. The other areas are located farther upstream: Registro (114 km), Sete Barras (138 km), and Eldorado (155 km) (Fig. 1). According to Ribeiro *et al.* (2020), the river margins are similar in these four regions, surrounded by pastures and banana plantations. The vegetation on the banks mainly comprises grasses (*Brachiaria subquadripara*, *Brachiaria platyphylla*, and *Panicum dichotomiflorum*). In Iguape, there are many aquatic macrophytes (*Eichhornia crassipes*).

Data Collection: Specimens of *M. olfersii* were collected monthly from January to December 2007

in four regions (Fig. 1). We followed the collection method proposed by Ribeiro *et al.* (2020). In each area, samples were obtained using traps and sieves in two locations, 2 km apart. Twelve traps (1 m length, 30 cm diameter, and 8mm mesh) were baited with small pieces of banana and/or pieces of cow bones. They were installed within the marginal vegetation (n=6 traps) and at each region's river bottom (n=6 traps) and retrieved after 24 h. Two researchers collected prawns from the vegetation along the riverside using a single sieve (0.5 m², 5 mm mesh size) for a 20-min period (against the current). All samples were identified following Melo (2003).

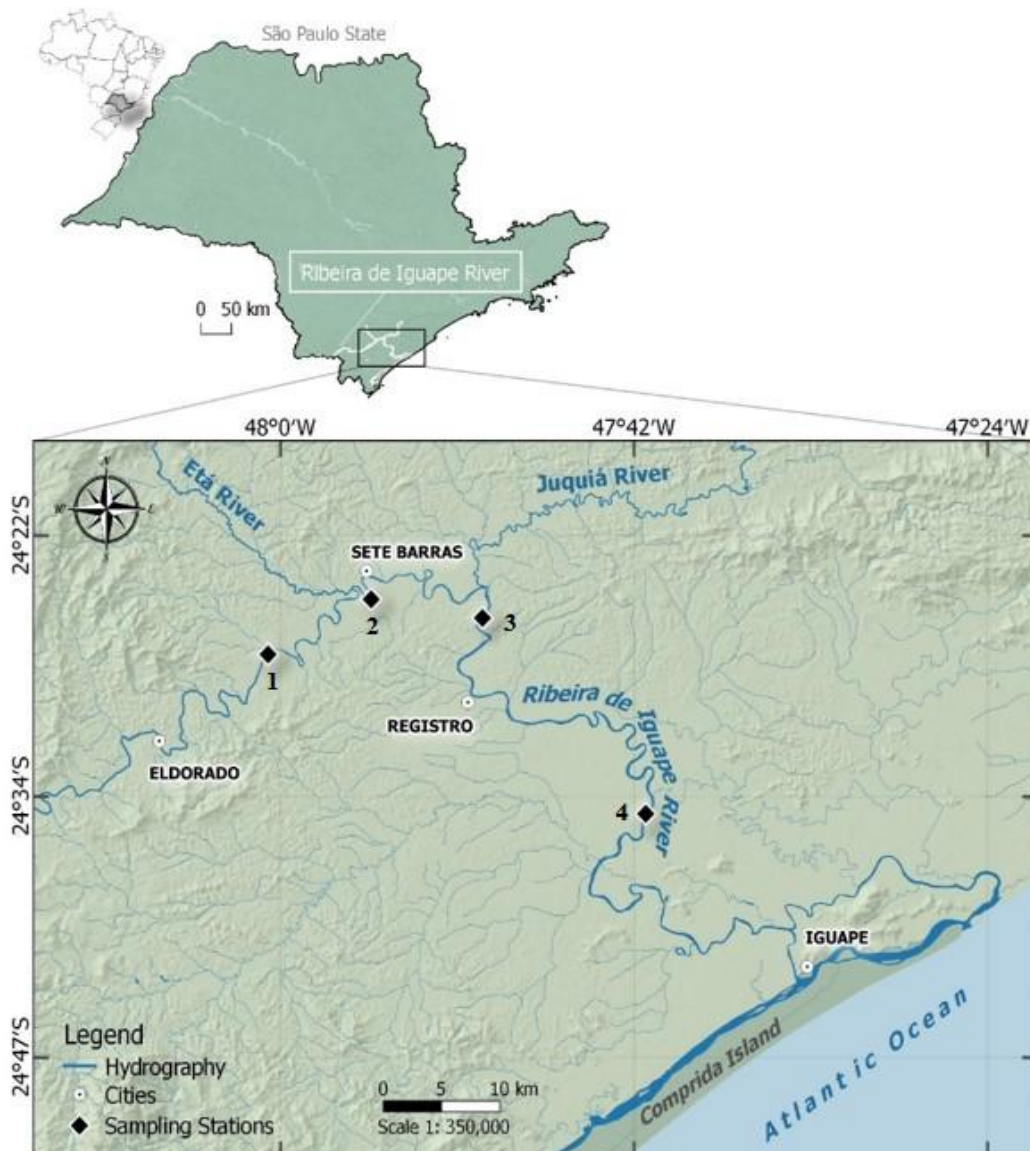


Figure 1. Map of the Ribeira de Iguape River basin, São Paulo, Brazil, showing the sampling regions of *Macrobrachium olfersii*, collected monthly from January to December 2007. 1 - Eldorado, 2 - Sete Barras, 3 - Registro, and 4 - Iguape.

Water temperature and salinity were measured in each region with a thermometer and a refractometer, respectively. Precipitation data for 2007 were obtained from the Integrated Center for Agrometeorological Information (CIIAGRO) of the Agronomic Institute (IAC).

Subsampling was used to analyze the size of *M. olfersii* in samples over 80 specimens, following the procedures of Bertini *et al.* (2014). In samples of up to 80 prawns, all individuals were analyzed. In samples with more than 80 prawns, specimens were randomly selected with the following proportion: a) samples from 80 to 160 prawns, 80 individuals were selected; b) 160 to 320, 50% of individuals were analyzed; c) 320 to 500, 25% were analyzed; and d) more than 500 prawns, 10% were analyzed.

All individuals from subsamples were measured and sexed based on secondary sexual characteristics, with males being recognized by the presence of the appendix masculine in the endopodite of the second pair of pleopods and females by the absence of it. Carapace length (CL) was measured as the distance between the carapace's orbital angle and the posterior margin. In individuals >10.0 mm, CL was measured with a caliper (to the nearest 0.1mm). In individuals with 10.0 mm or less, CL was measured (to the nearest 0.025 mm) under a stereomicroscope using a graduated ocular micrometer. All prawns smaller than 4 mm CL that lacked masculine appendix were considered juveniles (sexually undifferentiated), following Ribeiro *et al.* (2020).

The ovarian development stage of adult females (considered from the minor ovigerous female) was determined following Mossolin & Bueno (2002) with modifications: rudimentary (RU): Small ovaries, straw-yellow in color, with many chromatophores in the dorsal surface, impossible to see through the carapace; in development (ID): turgid ovaries, with color ranging from light green to olive-green and presence of few chromatophores on their dorsal surface, located behind the stomach, covering the entire region of the hepatopancreas; developed (DE): turgid and voluminous ovaries, filling the entire dorsal cephalothorax, of a dark green color with a dorsal surface filled with chromatophores; spent (SP): ovaries with a flaccid consistency and yellow-brown, with the presence of many chromatophores on the entire surface, located only on the hepatopancreas, not reaching the stomach region. This last stage is found only in ovigerous females who have recently laid eggs.

Females were also classified according to embryos' presence or absence (ovigerous or non-ovigerous, respectively). The embryos' developmental stage (early, intermediate, and late) beneath the abdomen was classified as follows: early-stage embryos were those that had been spawned recently, with no eyes and a uniformly distributed yolk; intermediate-stage embryos had visible but not well-developed eyes; late-stage embryos had little yolk, well-developed eyes, chromatophores, and appendages (Bertini & Baeza 2014).

Statistical analyses: Data were tested for homoscedasticity (Levene, $\alpha=0.05$) and normality (Shapiro-Wilk, $\alpha=0.05$) for choosing proper statistical tests (Sokal & Rohlf 1995).

Population structure and sex ratio: Population structure was characterized to verify variability among regions (Eldorado, Sete Barras, Registro, and Iguape) and seasons. Seasons were determined as follows: summer (January to March), autumn (April to June), winter (July to September), and spring (October to December). Prawns were divided into size classes, based on carapace length, according to the method by Sturges (1926). Size distributions of males and females were compared using the Kolmogorov–Smirnov test (Sokal & Rohlf 1995).

The sex ratio was calculated as the ratio of males to the total number of individuals. The observed proportion of males and females was tested for deviations from the 1:1 ratio for each month, region of sampling, and the whole population using the binomial test (Wilson & Hardy 2002) at a significance level of 5%.

Breeding cycle and recruitment: Reproductive period and recruitment were also compared among regions and seasons. Recruitment was examined using the percentage of juveniles in relation to the whole population. The reproductive period was based on the rate of ovigerous females in regard to the total number of adult females in the population. Permutational multivariate analysis of variance (two-way PERMANOVA) (Anderson 2001) was used for both comparisons (region and season). Pairwise comparisons were performed using a t-test ($p<0.05$). The occurrence of females with developed gonads (ID and DE) in each season was recorded.

Spearman's rank correlation coefficient at a 5% probability level was used to verify the association between the percentage of ovigerous females and water temperature and between the rate of ovigerous females and monthly rainfall in the region.

Sexual maturity size: Sexual maturity size was determined as the CL of the smallest ovigerous female captured. The average size in which 50% of females reach sexual maturity was determined by adjusting the logistic model-L50 (Fonteles-Filho 2011). This analysis was performed for the whole female population in each region. The analysis included females larger than the smallest ovigerous female collected. These individuals were distributed in size classes with an amplitude of 1 mm, where CL was considered the independent variable and the relative frequency of the size classes was considered the dependent variable. The data were fitted to a sigmoid function, following the results of the logistic equation ($Y=1/(1+e^{-(CL-CL_{50})})$), where CL 50% is the CL in which 50% of individuals reach maturity, and r is the slope of the curve. An adjustment equation was carried out using the least squares method (Vazzoler 1996).

Growth pattern and longevity: Growth analyses were performed based on the Von Bertalanffy (1938) growth model following the methodology for decapods crustaceans adopted by Fonseca & D’Incao (2003), Miazaki *et al.* (2019) and Pescinelli *et al.* (2020). The analyses were performed separately for males and females, excluding juveniles. A modal analysis was performed for each sampled region and the whole population, and the monthly frequency distribution of CL in 1 mm size classes. The modes were calculated and adjusted using the software PeakFit® (Peak Fit version 4.06). The mode peak values were plotted on a scatter plot (time versus age), from which the growth rate of the population cohorts was analyzed.

To estimate growth parameters, all chosen cohorts were adjusted to the Von Bertalanffy (1938) growth model, given by $CL_t = CL_{\infty}[1 - e^{-k(t-t_0)}]$ where CL_t is the estimated size at age t , CL_{∞} is the asymptotic size, k is the growth coefficient, and t_0 is the theoretical age at which the organism would have a measure equal to zero. Growth parameters (CL_{∞} , k , and t_0) were estimated for the different cohorts using the Solver package, available as a Microsoft Excel® Add-in. In addition, cohorts with

a coherent biological rhythm regarding longevity, growth coefficient, and asymptotic size (CL_{∞}) were selected. Finally, the growth curves of males and females were compared using the F-test ($p < 0.05$) (Cerrato, 1990).

Longevity was calculated by the inverse of the Von Bertalanffy growth function, based on modifications suggested by D’Incao & Fonseca (1999), with $t_0=0$ and $CL/CL_{\infty} = 0.99$. The longevity equation was $t = (t_0 - (1/k) \ln[1 - CL_t/CL_{\infty}])$.

Results

Overall 23,818 *M. olfersii* individuals were sampled and 9,691 were analyzed. The population represented in the subsample comprised 68.7% juveniles, 18.0% males, 9.2% females, and 4.10% ovigerous females (Table I). The Kolmogorov–Smirnov results demonstrated significant differences in size-frequency distribution between the males and females (ovigerous or not) ($d_{max}=0.196$; $p < 0.05$). The median size (50 percentile) was 7.5 mm CL in males and 8.7 mm CL in females. All percentiles were higher for males than females.

The regions’ total frequency distribution of *M. olfersii* indicated that the individuals reached larger classes in Eldorado and Sete Barras. A high abundance of individuals was found in the areas of Registro and Iguape, comprising more than 50% of the total number of specimens in the first size class (2 [–4 mm CL) (Fig. 2).

The total sex ratio of the population showed a significant deviation toward males (1:0.73) ($p < 0.05$). This deviation was also observed in Eldorado, Registro, and Iguape ($p < 0.05$), while the ratio was 1:1 ($p > 0.05$) in Sete Barras. Considering the months, there were significant deviations in the 1:1 sex ratio, mainly in months corresponding to spring and summer, usually favoring males ($p < 0.05$) (Fig. 3).

Ovigerous females were found in all regions with no statistical difference (PERMANOVA, $Pseudo-F=1.769$, $p=0.113$). However, there was a significant difference among seasons (PERMANOVA, $Pseudo-F=22.157$, $p=0.000$).

Table I. Carapace length (CL) in mm of *Macrobrachium olfersii* individuals. (N=number of individuals, sd=standard deviation, Min=Minimum; Max=Maximum).

	Juveniles	Male	Non - ovigerous female	Ovigerous female	Total
N	6,655	1,746	889	401	9,691
Min-Max	2.2-3.9	4.0-25.4	4.0-23.7	7.0-19.9	2.2-25.4
Mean±sd	3.2 ± 0.32	9.8 ± 5.2	7.8 ± 4.6	11.2 ± 2.5	5.1 ± 3.9

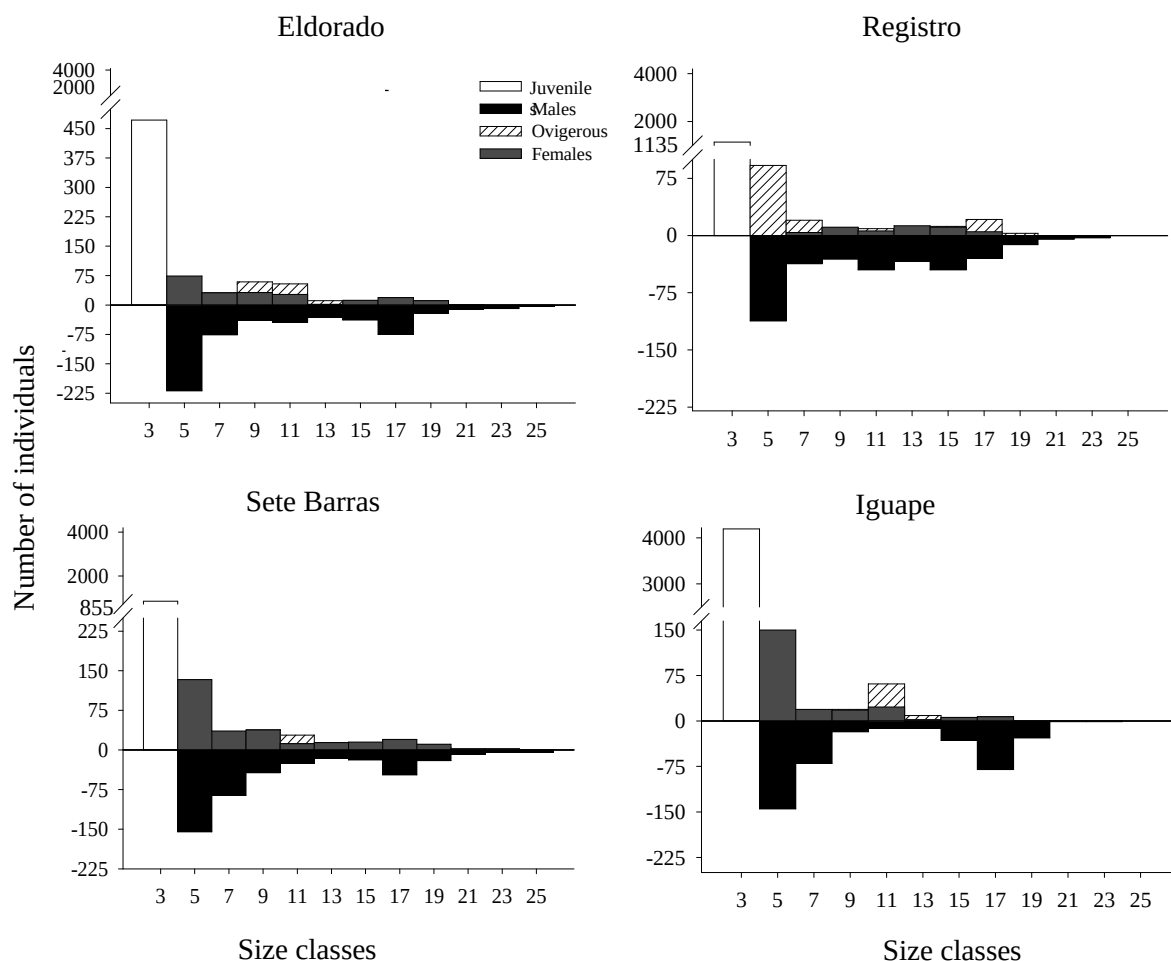


Figure 2. *Macrobrachium olfersii* collected monthly from January to December 2007. Size frequency distribution for the total sample of individuals in the four sampled regions along the Ribeira de Iguape River. The numbers on axis X represent the midpoint of each class.

Almost 60% of the ovigerous females were found in the summer. In winter, reproductive activity was only recorded in Iguape by the presence of ovigerous females. As for the analysis of gonadal development, females with ID and DE gonads began to appear in the spring, peaking in the summer and decreasing again in the autumn (Fig. 4).

The percentage of each ovarian developmental stage with the embryonic egg stage in 383 ovigerous females was compared between regions. It was observed that females present eggs in all stages of embryonic development in all regions, showing that reproduction occurs along the extension of the river (Fig. 5).

The average water temperature in the four regions ranged from 17.9 ± 0.18 °C (July; Iguape) to 30.6 ± 0.07 °C (March; Sete Barras). There was a positive association between temperature and the presence of ovigerous females (Spearman, $r_s=0.85$, $p<0.05$) (Fig. 6). Rainfall varied from 10.6 ± 7.06 mm

(June) to 251.9 ± 52.59 mm (January), also resulting in a positive association with the percentage of ovigerous females ($r_s=0.77$, $p<0.05$) (Fig. 6). In July, a large volume of rain was recorded, with an average of 151.2 ± 25.83 mm, which is considered atypical for the region. Since it was an outlier, July was excluded from Spearman's rank correlation.

Juveniles were recruited more intensely from April to September (autumn and winter). The PERMANOVA results indicate that the percentage of juveniles varied according to the season ($Pseudo-F=10.578$, $p=0.000$), and there was no interaction between factors (region and season) ($Pseudo-F=1.122$, $p=0.339$). The pairwise comparison within seasons revealed that only autumn and winter were not statistically different, as they presented the highest percentages of juveniles ($p>0.05$).

The size of the smallest ovigerous female (individual sexual maturity) was 7.0 mm CL. Females of this size were found in Registro and Sete

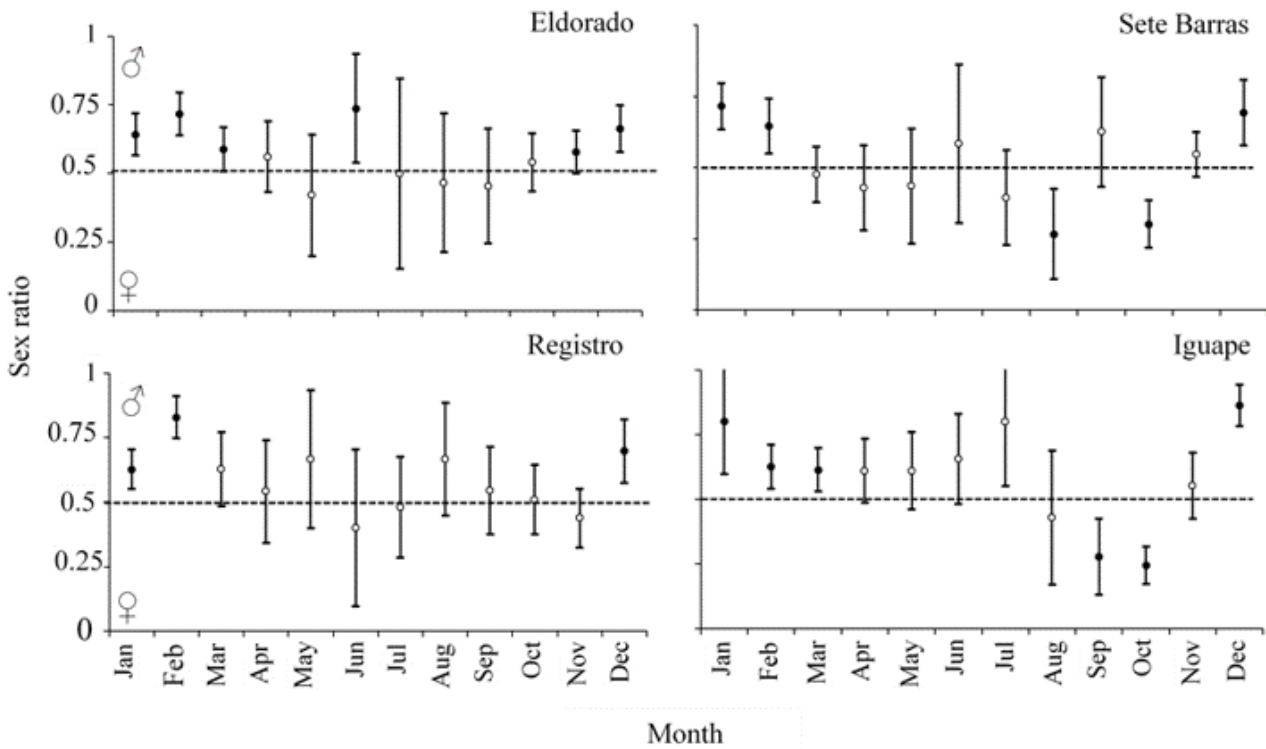


Figure 3. *Macrobrachium olfersii* collected monthly from January to December 2007. Sex ratio (mean ± standard error) from January to December 2007 in the four regions along the Ribeira de Iguape River. Black circles indicate a statistical difference of 1:1 (M:F) (Binomial test, p<0.05).

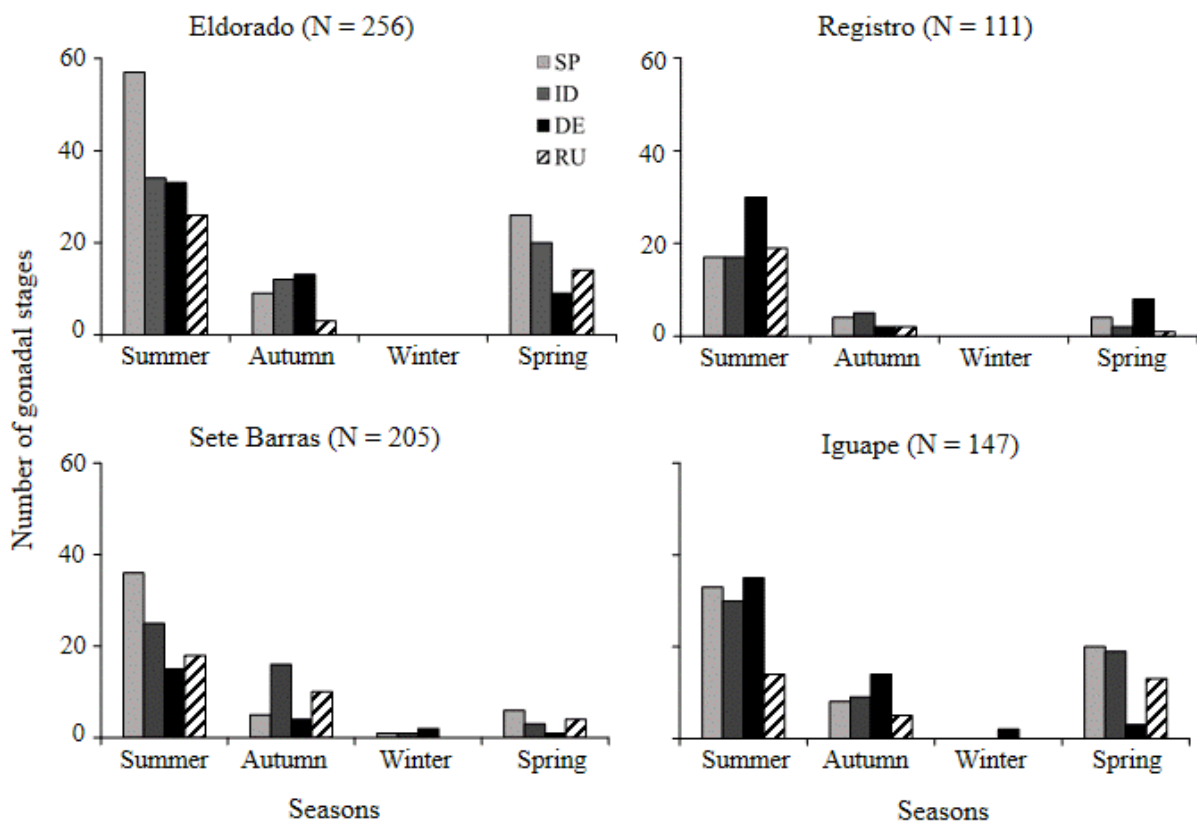


Figure 4. *Macrobrachium olfersii*. Presence of adult females in different gonadal stages by regions and seasons from January to December 2007 on the Ribeira de Iguape River (SP=spent, ID=In development, DE=Developed, RU=rudimentary).

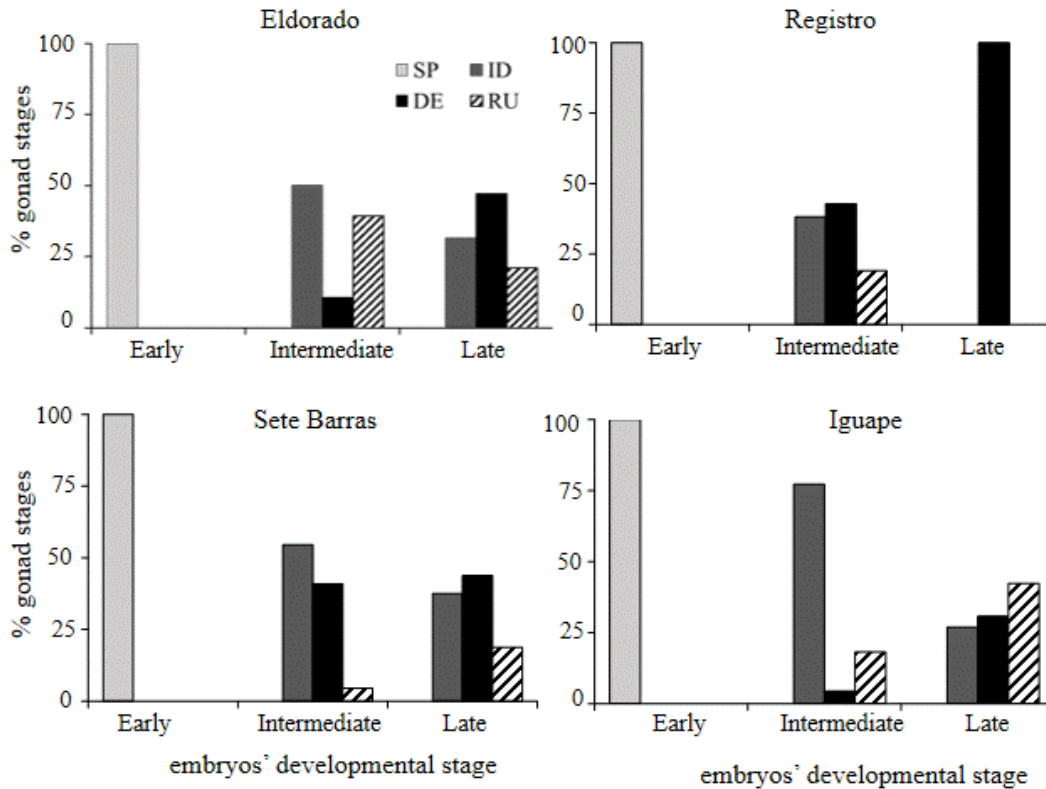


Figure 5. *Macrobrachium olfersii* collected monthly from January to December 2007. Percentage of the stage gonadal development of ovigerous females for each stage of embryonic development of eggs in each sampled region. (SP=Spent; ID=In Development; DE=Developed; RU=Rudimentary).

Barras. The estimated size for sexual maturity (CL50%) was 10.9 mm CL. Female sexual maturity size was similar across regions, with the smallest size in Iguape (10.2 mm CL), followed by Eldorado (10.5 mm CL), Sete Barras (11.2 mm CL), and Registro (12.3 mm CL).

Growth curves were significantly different between sexes ($F_{cal}=126.54 > F_{tab}=2.77$; $p<0.001$) according to the *F*-test. Longevity was similar for males and females, around 2.60 years (Table II). The growth curve per region showed that both males and females reached the smallest asymptotic sizes (CL_{∞}), presenting a slightly decreased longevity (t_{max}) and a slightly greater growth rate (k) in Registro and Iguape. There was no difference in growth among regions in relation to sex ($p>0.05$), except for Iguape ($F_{cal}=28.61 > F_{tab}=3.01$; $p<0.001$) (Table II).

Discussion

The population structure of *M. olfersii* is the more drastic parameter that changed along ~150 km of the Ribeira de Iguape River. Prawn size changes influenced other species parameters. For example, 85% of *M. olfersii* were juveniles in the Iguape

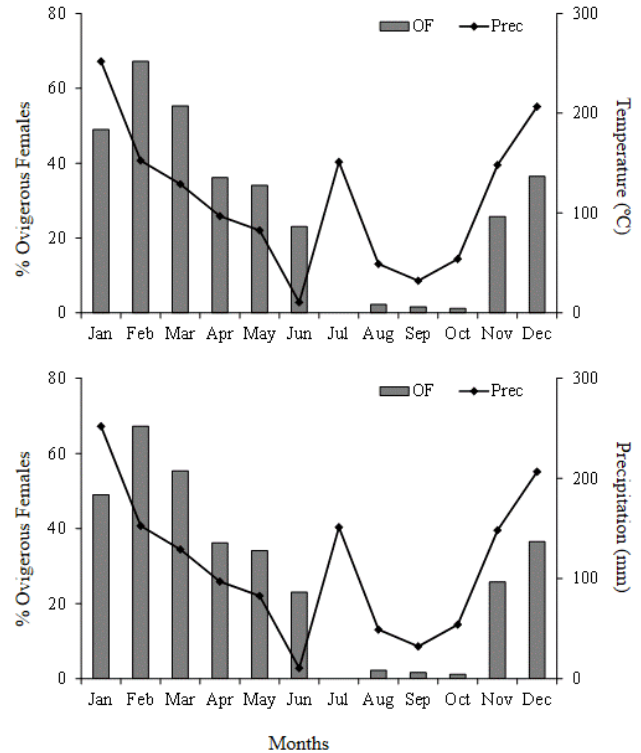


Figure 6. Monthly variation of the frequency of ovigerous females (OF) of *Macrobrachium olfersii* concerning the bottom temperature (BT) and precipitation (Prec) in the Ribeira de Iguape River from January to December 2007.

Table II. Growth parameters of *Macrobrachium olfersii* estimated for males and females in four regions along the Ribeira de Iguape River (CL_{∞} =asymptotic size; k =growth coefficient; t_0 =theoretical age of the organism at size zero; t_{max} =longevity).

	CL_{∞}	k (year ⁻¹)	t_0	t_{max} (years)
Total				
Male	31.85	1.75	0.0032	2.64
Female	23.67	1.75	0.0965	2.62
Eldorado				
Male	30.09	1.38	0.0965	3.25
Female	26.35	1.82	0.6045	2.50
Sete				
Barras				
Male	30.06	1.71	0.6556	2.64
Female	26.71	1.75	0.0032	2.65
Registro				
Male	25.50	1.86	0.0032	2.45
Female	24.46	1.97	0.0032	2.32
Iguape				
Male	25.02	2.04	0.0032	2.24
Female	21.75	1.82	0.7074	2.52

region, decreasing progressively until Eldorado. This indicates the population grows as it migrates upstream, suggesting that *M. olfersii* individuals can migrate about 150 km upstream, reaching the Eldorado region as juveniles after having passed the larval stage in the estuarine area.

The migration of juveniles of *M. olfersii* was mainly observed in the autumn and winter months (April to September), when there is low rainfall in the study region and the river level decreases considerably. Ribeiro *et al.* (2020) found a decrease in the abundance of juvenile prawns during the summer months due to high rainfall when studying the distribution of *M. olfersii* along the Ribeira de Iguape River. The abundance increased significantly upstream in the low ebbing months (autumn and winter), indicating an upstream juvenile migration (Ribeiro *et al.* 2020). Migration of *M. olfersii* juveniles was also observed in the coastal lagoon of Tacarigua, in eastern Venezuela; although followed throughout the year, there was greater intensity from January to February, when juveniles formed parallel bands visible on the channel banks that leads towards the lagoon (Gamba & Rodríguez 1987).

This migratory behavior of juveniles has been observed for other *Macrobrachium* species in different seasons: *M. malcolmsonii* in the Godavari

River (Ibrahim 1962); *M. ohione* in the Atchafalaya River (Bauer & Delahoussaye 2008); and *M. tenellum*, in the El Zarco River (Rodríguez-Urbe *et al.* 2014).

Regarding the reproductive pattern of *M. olfersii* in the Ribeira de Iguape River, females with eggs and mature gonads (ID/DE) were observed in all seasons. This suggests a continuous pattern, despite differences among seasons. First, there is greater activity in the summer. In the winter, ovigerous females and females with mature gonads were found only in the Iguape and Sete Barras regions and in low numbers. This reproductive pattern classification is confirmed by the presence of juveniles throughout the year since individuals comprise a single population. A genetic flow probably occurs among regions due to the migration of larvae to the estuary and the later return of juveniles to the areas farther from the river's mouth. Ovigerous *M. olfersii* females were detected in all months of the year according to monthly samplings carried out from 2014 to 2015 in the Iguape estuarine region (Giovana Bertini, com. pess.), corroborating this population can reproduce continuously.

Reproductive peak is related to higher rainfall, as shown for a sympatric species. For example, the reproductive peak of *M. acanthurus*, a sympatric species of *M. olfersii* in the region, also occurs in the summer, when rainfall is more abundant (Bertini *et al.* 2014). According to these authors, the transportation of *M. acanthurus* larvae is facilitated at this time. There is a great increase in the volume and flow of the Ribeira de Iguape River, with water currents varying from 3.5 to 4.2 km/h⁻¹, so that the larvae that have hatched in the Eldorado region (155 km from the estuary) need approximately 37 hours to reach the estuary in Iguape. As *M. olfersii* and *M. acanthurus* are found in the same environment, it can be considered that the larvae move together to the estuary, where they will find ideal conditions for larval development.

Continuous reproduction has been observed by Mossolin & Bueno (2002) and Pescinelli *et al.* (2016). These authors registered the reproduction of *M. olfersii* throughout the year on the north coast of São Paulo, with peaks in spring and summer. Another study found discontinuous reproduction of the same species in the southern region of Brazil, with the occurrence of ovigerous females only in warmer months (Barros 1995, Ammar *et al.* 2001). Unlike the river we investigated, the rivers analyzed in the studies mentioned above are small, so the

relationship between their flow and the reproduction of *M. olfersii* may not be as intense. Regardless, this factor is predominant for other species of the genus *Macrobrachium* that have a reproductive pattern associated with the hydrological cycle, as observed for *M. amazonicum* by Odinetz-Collart (1993) in the Brazilian Amazon, location with large river dimensions.

Ovigerous *M. olfersii* females were observed bearing eggs at all embryonic and ovarian development stages along the entire river length (~150 km). Even in farther regions (Eldorado and Sete Barras), many females had eggs ready to hatch, which indicates that they release the larvae wherever they are. Later, larvae are transported to the estuary by currents. The same thing has been observed for its congeneric species, *M. acanthurus*, in the same region (Bertini *et al.* 2014). Gamba (1982) also observed that the ovigerous *M. olfersii* females were not found in the estuarine area on the northern coast of Venezuela, showing that they do not migrate for reproduction. Similar behavior has been observed in other congener species, such as *M. carcinus* and *M. heterochirus* (March *et al.* 1998). Meanwhile, females of other species, such as *M. rosenbergii* (John 2009), *M. ohione* (Olivier & Bauer 2011), and *M. tenellum* (Rodríguez-Uribe *et al.* 2014) migrate to the estuarine region for larval release. Variations among species of the genus *Macrobrachium* indicate a great diversity of these prawns' reproductive behavior, which is probably modulated by differences in the hydrodynamics of each place or ecosystem.

The sex ratio of *M. olfersii* favored males for the whole population and in the three regions. In Sete Barras, a 1:1 ratio was found. The deviations also favored males in most months in each region. The sex ratio of *M. olfersii* is influenced by the capture method; traps capture more males that are known to be territorialists and live preferably on the riverbed (Karplus & Barki 2019), while sieves capture more females which inhabit the marginal vegetation where they find shelter and food (Almeida *et al.* 2008, Ribeiro *et al.* 2020).

The predominance of females in other populations of *M. olfersii* in Brazil (Barros 1995, Mossolin & Bueno 2002, Pescinelli *et al.* 2016) may be related to the capture method, which was sieve only. Similarly, the deviations in favor of *M. olfersii* males by Dornellas *et al.* (2011) may be due to the use of traps only. Combining both methods (trap + sieve) is the best way to study the population biology of freshwater prawns as it can provide a

more accurate overview of population structure (Ribeiro *et al.* 2020). As we combined capture methods in this study, our results likely reflect population parameters.

Males move more during the reproductive peak as they actively look for females. However, they are more likely to be captured in this period, which explains the deviation favorable to males found in the present study, especially during the reproductive period. Deviation in sex ratio was observed for *M. potiuna*, with a greater abundance of males during the reproductive season (Mattos & Oshiro 2009). Although studies have pointed out that the most frequent pattern is deviation towards females (Mossolin & Bueno 2002, Jimoh *et al.* 2012, Sethi *et al.* 2014, Soares *et al.* 2015, Pescinelli *et al.* 2016, Hoarau *et al.* 2018, Costa & Silva *et al.* 2019, Nogueira *et al.* 2019, Oliveira *et al.* 2019), those results should be interpreted with caution, considering the capture method.

The sexual maturity size of *M. olfersii* (7.0 mm CL) was smaller than in other populations of the same species. This was the lowest value recorded for this species since Barros (1995) found 7.3 mm CL, and Pescinelli *et al.* (2016) found 7.9 mm CL. Nonetheless, logistic regression has shown an estimated size at which 50% of females reach sexual maturity of 10.9 mm CL. The estimated value is above the one by Pescinelli *et al.* (2016), who determined a value of 6.7 mm of CL based on female gonad analysis.

CL_{50%} varied slightly (10.2 to 12.3 mm CL) among regions along the Ribeira de Iguape River, probably due to limited female sample size (which can lead to over- or underestimation of CL_{50%}) (Bauer 2002, Costa *et al.* 2016). Prawn maturity comparisons across a gradient are rare in the literature. Bertini *et al.* (2014) did not find significant differences in this parameter in *M. acanthurus* among the same regions and study period. On the other hand, Soares *et al.* (2015) recorded variations in the size at sexual maturity of *M. jelskii* upstream and downstream of the Três Marias hydroelectric plant (state of Minas Gerais, Brazil). Females reached maturity earlier upstream, probably because they were more susceptible to predation due to the reduced availability of marginal vegetation in the area (Soares *et al.* 2015). Since there are no anthropic dams along the river and there is a natural downstream and upstream migration in the study area, the population exhibited similar sexual maturity in all regions.

Asymptotic length (CL_{∞}) is the maximum theoretical size that species can reach in its natural habitat (Etim & Sankare 1998). The maximum size of *M. olfersii* was estimated as 23.7 mm of CL for females and 31.8 mm for males. The estimated sizes were similar to the length of the largest female sampled and slightly larger than the largest male. Both estimates were within the observed for populations from other locations by Müller *et al.* (1999), Ammar *et al.* (2001), Mossolin & Bueno (2003), and Pescinelli *et al.* (2016), indicating that this parameter is within the standard size for this species.

We estimated that males had a longer asymptotic length (CL_{∞}) and, in general, a lower growth rate (k), which is a typical pattern of sexual dimorphism. In this pattern, females and males have similar growth until reaching sexual maturity; then, females begin to direct most of their energy towards reproduction (egg production and arranging the incubator chamber), while males invest in somatic growth, becoming the most prominent individuals in

the population (Ammar *et al.* 2001, Mossolin & Bueno 2003, Nwosu & Wolfi 2006). Sexual dimorphism related to the larger size of males in the population is very common among prawns of the genus *Macrobrachium* (Fransozo *et al.* 2004, Mantelatto & Barbosa 2005, Mattos & Oshiro 2009, Bertini *et al.* 2014, Iketani *et al.* 2016), as well as in other *M. olfersii* populations studies by Barros (1995), Ammar *et al.* (2001), and Mossolin & Bueno (2002, 2003).

As for the longevity of the *M. olfersii* population, there was a variation from 2.24 to 3.25 years. The longevity of shrimp of the genus *Macrobrachium* varies between species since this parameter is directly related to the maximum size reached by individuals (Hayd & Anger 2013; Vogt 2014). Therefore, as it is a small species, the life expectancy of *M. olfersii* is lower when compared to species that reach larger sizes, such as *M. acanthurus*, *M. tenellum*, and *M. hancocki*, among others (Table III).

Table III. Growth rate of species of the genus *Macrobrachium* (L_{∞} CL-asymptotic carapace length (mm), L_{∞} TL-asymptotic total body length (mm), k -growth rate (year^{-1}), t_{max} -longevity, M-males, F-females, T-total).

Species	Sex	L_{∞} CL (mm)	L_{∞} TL (mm)	k	t_{max} (years)	Locality	Reference
<i>M. olfersii</i> (Wiegmann, 1836)	M	31.85		1.75	2.64	Ribeira de Iguape river, São Paulo, Brazil	Present study
	F	23.67		1.75	2.62		
<i>M. amazonicum</i> (Heller, 1862)	T	21.53		0.61		Parananema Lake, Amazonas, Brazil	Taddei <i>et al.</i> (2017)
	T	95.00		0.83		Santana Island and Mazagão Velho, Amapá, Brazil	Silva <i>et al.</i> (2016)
	T	47.83		0.31	4.00	Flexal and Curral Velho, Pará, Brazil	Freire <i>et al.</i> (2012)
	M	50.40		0.30			
	F	45.26		0.33			
<i>M. acanthurus</i> (Wiegmann, 1836)	M	75.70		0.49	6.00	Ribeira de Iguape river, São Paulo, Brazil	Bertini <i>et al.</i> (2014)
	F	71.40		0.42	6.40		
	T		212.00	0.24		Palizada river, Campeche, Mexico	Román-Contreras & Campos-Lince (1993)
<i>M. potiuna</i> (Müller, 1880)	M	9.70		0.15		Arroio Sapucaia, Rio Grande do Sul, Brazil	Souza & Fontoura (1995)
	F	9.20		0.21			
<i>M. carcinus</i> (Linnaeus, 1758)	F		210.00	0.49		Ribeira de Iguape river, São Paulo, Brazil	Valenti <i>et al.</i> (1994)
<i>M. equidens</i> Dana, 1852	T		107.10	1.25	2.50	Cross river estuary, Nigeria	Nwosu (2008)
<i>M. intermedium</i> (Stimpson, 1860)	M				1.50	New South Wales, Australia	Gray (1991)
	F				2.00		
<i>M. macrobrachion</i>	M		141.30	1.21	2.50	Cross river estuary,	Nwosu <i>et al.</i> (2007)

Species	Sex	L_{∞} CL (mm)	L_{∞} TL (mm)	k	t_{max} (years)	Locality	Reference
Herklots, 1851	F		117.50	1.60	2.00	Nigeria	Enin (1995)
	T		129.30	1.79	1.70	Cross river estuary, Nigeria	
<i>M. michoacanus</i> Villalobos and Rodriguez, 1990	T		176.00		3.00	Oaxaca, Mexico	Romero & Silva (2008)
<i>M. rosenbergii</i> De Man, 1879	M		420.00	0.98		Vembanad Lake, India	Harikrishnan & Kurup (1997)
	F		308.00	1.10			
<i>M. vollenhovenii</i> Herklots, 1857	T		120.80	2.70	1.11	Niger Delta, Nigeria	Kingdom (2015)
	T		142.00	1.00	3.00	Dawhenya Impoundment, Ghana	Alhassan & Armah (2011)
	T		236.50	1.14	2.10	Asu river, south - east Nigeria	Okogwu <i>et al.</i> (2010)
	M		213.60	1.24	2.42	Cross river estuary, Nigeria	Nwosu & Wolfi (2006)
F		198.90	1.24	2.40			
<i>M. felicinum</i> Holthuis, 1949	T		102.40	1.40	2.14	Niger Delta, Nigeria	Kingdom & Hart (2012)
<i>M. tenellum</i> (Smith, 1871)	T	85.43		0.26	11.5	Pacific slope, Costa Rica	Ibarra & Wehrtmann (2019)
<i>M. panamense</i> Rathbun, 1912	T	84.82		0.65	4.60	Pacific slope, Costa Rica	Ibarra & Wehrtmann (2019)
<i>M. occidentale</i> Holthuis, 1950	T	38.96		0.75	3.90	Pacific slope, Costa Rica	Ibarra & Wehrtmann (2019)
<i>M. hancocki</i> Holthuis, 1950	T	38.58		0.38	7.90	Pacific slope, Costa Rica	Ibarra & Wehrtmann (2019)
<i>M. digueti</i> (Bouvier, 1895)	T	48.17		0.38	7.70	Pacific slope, Costa Rica	Ibarra & Wehrtmann (2019)
<i>M. americanum</i> (Bate, 1868)	T	98.32		0.28	10.6	Pacific slope, Costa Rica	Ibarra & Wehrtmann (2019)

The prawns living in regions closest to the estuary (Iguape and Registro) presented a smaller asymptotic size (CL_{∞}), lower longevity (t_{max}), and higher growth rate (k), possibly due to the greater number of juveniles. In addition, juveniles have an accelerated growth rate which decreases in adulthood due to the investment of more energy in processes other than somatic growth, such as reproduction and body maintenance (Román-Contreras & Campos-Lince 1993).

In conclusion, the results of this work suggest that the variation in individuals' size, recruitment, sexual maturity, and growth are related to the population structure along ~150 km of the Ribeira de Iguape River. The population structure was mainly triggered by the upstream migration of juveniles after larval development, which takes place in the estuarine region (Iguape). Thus, this study gathered important information that was yet unknown about the *M. olfersii* population, a prawn found in this critical and large river on the south coast of São

Paulo, allowing such data to be used to subsidize management and conservation plans for species in this environment.

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Ethical statement

The present investigation did not involve the use of regulated animals and did not require approval by an ethical Committee.

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