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Reproductive potential of four freshwater prawn species in the Amazon region

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ABSTRACT

The bioecology of freshwater prawns can be understood by studying their reproductive biology. Thus, the aim of this paper was to determine and compare the reproductive potential of four freshwater caridean prawns collected in the Amazon region. For two years, we captured females of *Macrobrachium brasiliense*, *Palaemon carteri*, *Pseudopalaemon chryseus* and *Euryrhynchus amazoniensis* from inland streams in the municipality of Itacoatiara (AM). At the laboratory, we measured the biometric variables total length, carapace length, abdomen length and total weight, and recorded the number of eggs (NE) by direct counting. There was a significant difference for all variables between the species. The females of *M. brasiliense* were the most abundant and had the largest sizes and NE. However, the fecundity index shows that *P. carteri* has the highest reproductive potential of the four species. Despite the differences in size and weight, all the species showed low fecundity, which is a characteristic of continental palaemonidean K strategist prawns.

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Introduction

The order Decapoda comprises crustaceans of ecological importance (Whiteley 2011) that play a key role in several trophic levels (Collins et al. 2007). It is known that the larger and most abundant species are used as food by humans (Magalhães et al. 2006), but there is a great variety of small species that contribute to the functioning of ecosystems in which they live (Moulton et al. 2004), although they have no commercial value.

Regarding the abundance of freshwater prawn species, the family Palaemonidae Rafinesque, 1815 is among the most abundant in Brazil (Melo 2003). Of this family, the genus *Macrobrachium* Bate, 1862 is the most abundant, with 18 species throughout Brazil. The genera *Palaemon* Weber, 1795 and *Pseudopalaemon* Sollaud 1911 are less representative, both with five species (Melo 2003). The family Euryrhynchidae Holthuis, 1950 has five freshwater species of the genus *Euryrhynchus* Miers, 1877 that inhabit the Amazon region (De Grave and Franssen 2011).

Freshwater prawns of the genus *Macrobrachium* can grow and mate in freshwater environments, but most species require brackish water for their larval development (Pinheiro and Hebling 1998). In these environments, caridean prawns produce many eggs of a small volume. Their offspring hatch in an initial stage and complete 12 larval stages as described for *Macrobrachium carcinus* (Linnaeus,

1758) in Choudhury (1971). However, the prawns that inhabit inland streams adapted their bioecology to a system with cyclic flood pulses (Walker and Ferreira 1985; Junk et al. 1989; Bittencourt and Amadio 2007) and their reproductive strategies are related to the hydrological regime of the Amazon region described by Junk et al. (1989). Moreover, these animals produce few eggs of a large volume that hatch juveniles in advanced development stages (see Magalhães and Walker 1988).

The freshwater prawns *Macrobrachium brasiliense* (Heller, 1862), *Palaemon carteri* (Gordon, 1935), *Pseudopalaemon chryseus* Kensley and Walker, 1982 and *Euryrhynchus amazoniensis* Tiefenbacher, 1978 have full ontogeny in freshwater environments with epimorphic development in abbreviated larval stages (Magalhães and Walker 1988). They are commonly found in blackwater rivers (Walker and Ferreira 1985) and in submerged litter. Some of these species are associated with macrophytes (Montoya 2003; Paschoal et al. 2013).

Genetic and environmental factors determine the absolute number of eggs carried in all the clutches of females, and the relative number of eggs carried in a single spawn – individual fecundity – has a linear relationship with the size of females (Valenti et al. 1989; Bilgin and Samsun 2006). According to Corey and Reid (1991), fecundity is related to environmental adaptations, variations in the animal's

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size and geographic location. Furthermore, there may be considerable loss of eggs, which can result in a better adjustment of egg mass in the pleura (Nazari et al. 2003).

García-Dávila et al. (2000) and Pereira and Chacur (2009) conducted studies on the reproductive biology of *M. brasiliense*. Moreover, the reproductive strategy of *P. carteri* was investigated in the Rio Negro by Collart and Enriconi (1993), as well as fecundity including a comparison of egg volume between embryonic stages of development (Santos and Vieira 2016). Studies on *Ps. chryseus* and *E. amazoniensis* are scarce and we only found information on the larval development of both species (Magalhães 1986a, 1988; Odetz-Collart and Magalhães 1994).

The evident scarcity of studies on the reproductive biology of prawns in the Amazon region can be associated with the difficulty of capturing some species and the lack of specialists in the area. Thus, the aim of this paper was to fill the information gaps on the reproductive biology of freshwater caridean prawns. We investigated the reproductive potential of four prawn species of the Amazon region, namely *M. brasiliense*, *P. carteri*, *Ps. Chryseus* and *E. amazoniensis* captured at inland streams in the Middle Amazon region and compared the fecundity of the species and the relationship between the size and fecundity of females.

Material and methods

Study area and data collection

The females of all four species were collected in the municipality of Itacoatiara, AM, Brazil, from July 2011 to August 2013. Ovigerous females of *Macrobrachium brasiliense* and *Pseudopalaemon chryseus* were caught in river Carú (03°02'39"S, 58°37'32"W). Females of *Palaemon carteri* were captured in lakes Serpa (03°07'23.3"S, 58°27'0.10"W), Poranga (03°07'11.4"S, 58°27'13.0"W), Centenário (03°08'24.5"S, 58°27'24.60"W) and Aeroporto (03°07'23.53"S, 58°27'0.25"W). Ovigerous females of *Euryrhynchus amazoniensis* were collected only in Lake Poranga.

With no exception, all these floodplains are influenced by the periodic flood pulses and water volume ranges from around 10 to 12 m every six months (Bittencourt and Amadio 2007). The muddy water largely affects these water bodies in the flood period. The river margin has grass as well as weeds, which are associated with the studied crustaceans.

All the samples were collected by two people for one hour in each lake. They used a 70 × 30-cm rectangular dip nets (2 mm diameter mesh) and a 1 × 2-m trail-net (2 mm diameter mesh) near the edge of the stream vegetation. The captured animals were frozen for 15 min at -20 °C,

fixed in 70% alcohol and transported to the laboratory. Subsequently, the prawns were examined under a stereomicroscope coupled to an imaging system for identification, according to Melo (2003).

Biometry and statistical analysis

After identification, the samples were measured for total length (TL), which is from the base of eyestalk to the distal end of the telson, and carapace length (CL) with a caliper (0.05 mm). Abdomen length (AL) was obtained by calculating the difference between TL and CL. Later, the females were weighed to determine total wet weight (TW) on a digital scale (0.001 g). The eggs were removed from the pleopods of each female and directly counted to record the total number of eggs (NE).

The sizes of the females and absolute fecundity of the four species were compared separately using analysis of variance (ANOVA) followed by the Tukey test (Zar 2010). The biometric variables (TL, CL, AL, TW) were considered independent and confronted by the variable NE (dependent) by simple analysis of linear regression. The most suitable mathematical model to represent the relationship between the number of eggs and the other variables was determined by adjusting the coefficient of determination (R^2). The F test verified the significance of each regression. Analysis of covariance (ANCOVA) was used to compare the slope and the intercept of the obtained straight in the regression analysis between species (Zar 2010), considering the size and fecundity as variables. The fecundity index (FI) was calculated according to the ratio $FI = NE/CL$ (Mansur and Hebling 2002), and the ratio $FI = NE/TW$. Then, ANOVA followed by the Tukey test were used to compare the FI among the species. It was then possible to compare the fecundity of the species excluding the effect of the size and weight. For all analyses, we adopted a significance level of $p < 0.05$ (Sokal and Rohlf 1995).

Results

During the study period, we captured 158 females of *Macrobrachium brasiliense*, 69 of *Palaemon carteri*, 63 of *Pseudopalaemon chryseus* and 18 of *Euryrhynchus amazoniensis*. Table 1 shows the variation of size and weight and the number of eggs of each species.

Regarding the size comparison between the species, there was a significant difference: TL ($F_3 = 45.4656$; $p < 0.0001$), CL ($F_3 = 85.3882$; $p < 0.0001$), AL ($F_3 = 45.6521$; $p < 0.0001$). The same pattern was detected for weight (TW) ($F_3 = 14.0987$; $p < 0.0001$) and the number of eggs (NE) ($F_3 = 6.1724$; $p = 0.0007$) among the females of the four species. There was no difference in size (TL) between *P. carteri* and *Ps. Chryseus*; however, these two species were

Table 1. Results of sampling and values for the biometric variables of the four species evaluated in the present study.

	Species	N	Min	Max	Mean ± SD
TL	<i>Macrobrachium brasiliense</i>	158	7.12	47.65	30.18 ± 7.57 ^a
	<i>Palaemon carteri</i>	69	18.20	30.50	25.82 ± 2.52 ^b
	<i>Pseudopalaemon chryseus</i>	63	16.50	32.00	25.93 ± 3.39 ^b
	<i>Euryrhynchus amazoniensis</i>	18	11.75	19.48	15.17 ± 2.53 ^c
CL	<i>Macrobrachium brasiliense</i>	158	3.72	22.30	13.79 ± 3.94 ^a
	<i>Palaemon carteri</i>	69	5.95	9.95	8.43 ± 0.81 ^b
	<i>Pseudopalaemon chryseus</i>	63	9.20	18.00	12.68 ± 2.01 ^c
	<i>Euryrhynchus amazoniensis</i>	18	4.11	7.32	5.83 ± 1.05 ^d
AL	<i>Macrobrachium brasiliense</i>	158	3.88	26.00	16.38 ± 4.11 ^a
	<i>Palaemon carteri</i>	69	12.25	22.50	17.4 ± 2.27 ^a
	<i>Pseudopalaemon chryseus</i>	63	6.55	17.30	13.25 ± 1.97 ^b
	<i>Euryrhynchus amazoniensis</i>	18	6.82	12.76	9.34 ± 1.62 ^c
TW	<i>Macrobrachium brasiliense</i>	158	0.22	2.26	0.61 ± 0.53 ^a
	<i>Palaemon carteri</i>	69	0.18	0.61	0.38 ± 0.08 ^b
	<i>Pseudopalaemon chryseus</i>	63	0.24	0.50	0.37 ± 0.05 ^b
	<i>Euryrhynchus amazoniensis</i>	18	0.04	0.41	0.14 ± 0.09 ^b
NE	<i>Macrobrachium brasiliense</i>	158	8	116	33 ± 26 ^a
	<i>Palaemon carteri</i>	69	9	50	28 ± 11 ^a
	<i>Pseudopalaemon chryseus</i>	63	13	49	26 ± 7 ^{ab}
	<i>Euryrhynchus amazoniensis</i>	18	6	23	14 ± 5 ^b

Notes: N = number of individuals; Min = minimum; Max = maximum; SD = standard deviation; TL = total length; CL = carapace length and AL = abdomen length (mm); TW = total weight (g); NE = number of eggs. Means followed by different letters are significantly different ($P < 0.05$).

smaller than *M. brasiliense* and larger than *E. amazoniensis*. With regard to mean of the CL, all species differed significantly, the largest being *M. brasiliense* followed by *Ps. chryseus*, *P. carteri* and *E. amazoniensis*. There was no

significant difference between *M. brasiliense* and *P. carteri* regarding AL, but they were larger than *Ps. chryseus* and *E. amazoniensis*, which also differed from one another since *Ps. chryseus* was larger than *E. amazoniensis*. The females of *M. brasiliense* were heavier than *P. carteri*, *Ps. Chryseus* and *E. amazoniensis*, but these last three species did not differ in TW. Absolute fecundity did not differ between *M. brasiliense*, *P. carteri* and *Ps. chryseus*, but *M. brasiliense* and *P. carteri* had more eggs than *E. amazoniensis*.

Table 2 shows the equations and adjustments (R^2) of the relationship between the biometric variables and fecundity of the four studied species. Despite the significance between the sizes (TL, CL, AL, and TW) and fecundity, only *M. brasiliense* exhibited a high coefficient of determination $R^2 = 0.85$, following the same pattern for the CL ($R^2 = 0.77$), AL ($R^2 = 0.72$) and $R^2 = 0.91$ for TW (Table 2). The covariance between the lines of biometric relations of the prawns and fecundity showed a significant difference among the species here studied (NExTL: $F = 10.41$, $p < 0.0001$; NExCL: $F = 8.41$, $p < 0.0001$; NExAL: $F = 12.06$, $p < 0.0001$; NExTW: $F = 12.52$, $p < 0.0001$) (Figure 1). Based on the slope of the curve, *M. brasiliense* showed a tendency to increase fecundity in relation to its biometric variables.

Although *M. brasiliense* is the largest and most fecund species, the *FI* excluding the CL was higher for *P. carteri* and *E. amazoniensis* (Table 3). Excluding the effect of size, *P. carteri* had the greatest reproductive potential of the four species. However, when comparing *FI* and excluding the effect of TW, *M. brasiliense* exhibited the highest reproductive potential (Table 3).

Discussion

The CL of ovigerous females of *Macrobrachium brasiliense* was similar to the CL found by García-Dávila et al. (2000) for specimens of the Peruvian Amazon, and it could not

Table 2. Equations of the linear regression for modelling the relationships between the biometric variables and the number of eggs of each species under study.

Relationship	Species	N	Equations	R^2	F	P
TLxNE	<i>Macrobrachium brasiliense</i>	158	NE = 3.15TL - 62.28	0.85	870.55	<0.0001
	<i>Palaemon carteri</i>	69	NE = 3.06TL - 50.56	0.53	75.90	<0.05
	<i>Pseudopalaemon chryseus</i>	63	NE = 1.58TL - 14.77	0.55	74.70	<0.05
	<i>Euryrhynchus amazoniensis</i>	18	NE = 1.01TL - 0.27	0.17	3.31	0.97
CLxNE	<i>Macrobrachium brasiliense</i>	158	NE = 3.15CL - 62.28	0.77	524.57	<0.0001
	<i>Palaemon carteri</i>	69	NE = 2.64CL + 6.30	0.04	2.87	0.63
	<i>Pseudopalaemon chryseus</i>	63	NE = 2.80CL - 9.43	0.61	95.51	<0.05
	<i>Euryrhynchus amazoniensis</i>	18	NE = 1.47CL + 6.41	0.06	1.08	0.45
ALxNE	<i>Macrobrachium brasiliense</i>	158	NE = 5.33AL - 54.45	0.72	402.54	<0.0001
	<i>Palaemon carteri</i>	69	NE = 3.44AL - 31.36	0.54	79.74	<0.05
	<i>Pseudopalaemon chryseus</i>	63	NE = 1.76AL + 2.81	0.23	18.33	0.61
	<i>Euryrhynchus amazoniensis</i>	18	NE = 1.85AL - 2.24	0.24	4.91	0.78
TWxNE	<i>Macrobrachium brasiliense</i>	158	NE = 46.07TW + 5.03	0.91	1540.86	<0.0001
	<i>Palaemon carteri</i>	69	NE = 96.53TW - 8.05	0.57	88.70	<0.05
	<i>Pseudopalaemon chryseus</i>	63	NE = 95.52TW - 8.89	0.50	60.02	0.60
	<i>Euryrhynchus amazoniensis</i>	18	NE = 11.00TW + 13.51	0.02	0.41	0.54

Notes: N = number of individuals; R^2 = determination coefficient; F = results of ANOVA; P = significance; TL = total length; CL = carapace length; AL = abdomen length; TW = total weight; NE = number of eggs.

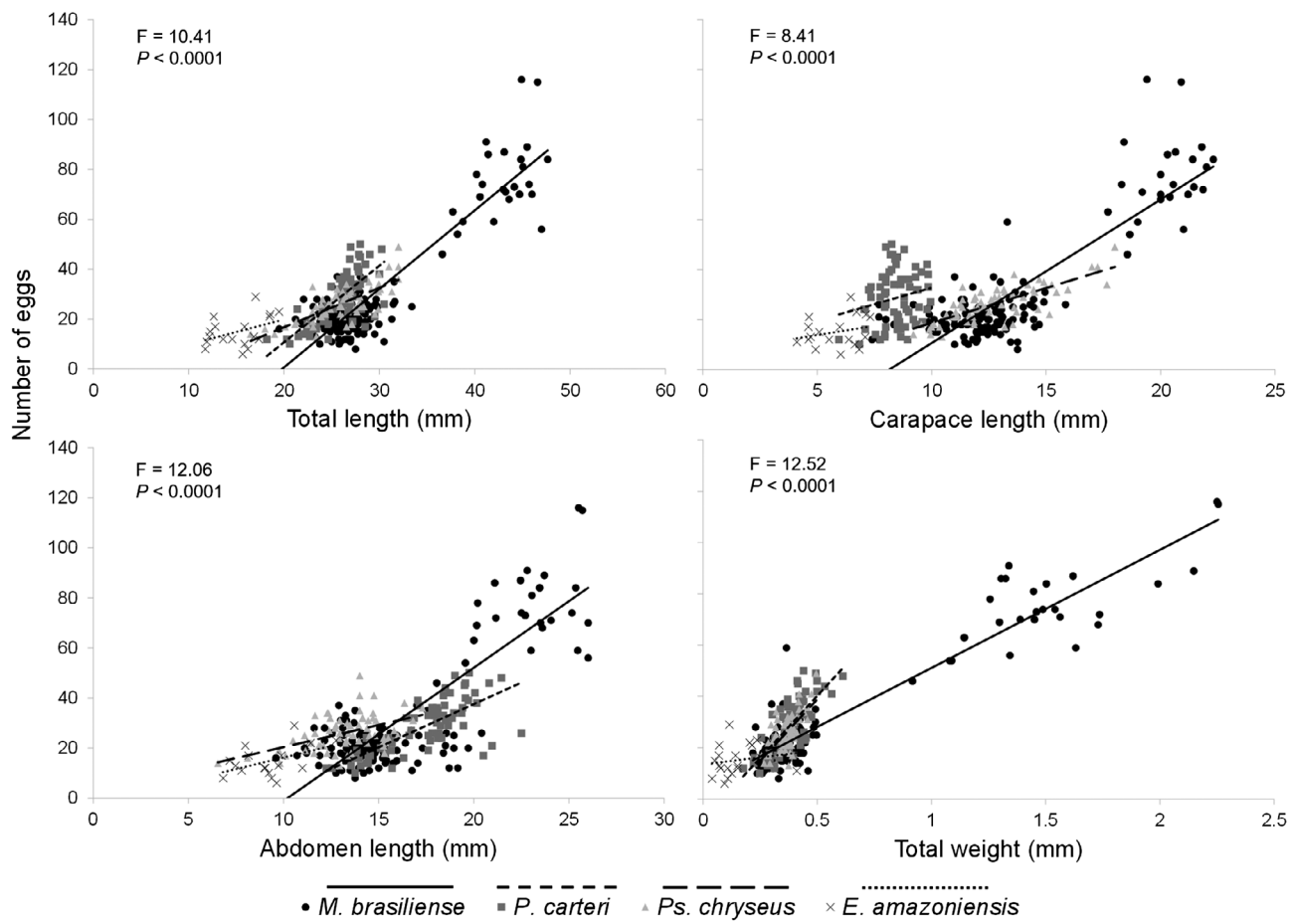


Figure 1. Dispersion points of the relationship between the biometric variables and the number of eggs of the investigated prawn species, with respective analysis of covariance results showing the heterogeneity of slopes.

Table 3. Results for the fecundity indexes for each of the four species.

		<i>M. brasiliense</i>	<i>P. carteri</i>	<i>Ps. chryseus</i>	<i>E. amazoniensis</i>
$IF=NE/CL$	Min	0.58	1.34	1.24	1.00
	Max	5.98	6.13	2.91	4.53
	Mean \pm SD	2.16 ± 1.01^a	3.40 ± 1.25^b	2.04 ± 0.37^a	2.61 ± 1.02^a
$IF=NE/TW$	Min	0.006	0.009	0.009	0.003
	Max	0.042	0.026	0.029	0.105
	Mean \pm SD	0.018 ± 0.005^a	0.015 ± 0.004^b	0.015 ± 0.003^b	0.016 ± 0.023^{ab}

Notes: Min = minimum; Max = maximum; SD = standard deviation; NE = number of eggs; TW = total weight (g). Means followed by different letters are significantly different ($P < 0.05$).

be compared with the results of Pereira and Chacur (2009) that captured only one ovigerous female. *Palaemon carteri* had different CL sizes to the other three species evaluated in this study, and different CL sizes to those recorded by Collart and Enrico (1993). However, the TL of *P. carteri* was similar to the TL obtained by Santos and Vieira (2006). This species had 5–39 eggs in Central Amazon (Collart and Enrico 1993) and 4–29 in Eastern Amazon (Santos and Vieira 2016). The fecundity of *Ps. chryseus* and *E. amazoniensis* was similar to the results found by Magalhães and Walker (1988), that is 14 to 47 and 9 to 30 eggs, respectively. For other amphidromous *Palaemon* species,

fecundity is higher than that of hololimnetic species of the same genus. Paschoal et al. 2016 found that average fecundity of *Palaemon pandaliformis* (Stimpson, 1871) was 139 eggs. The mean fecundity of *Palaemon adspersus* Rathke, 1837 and *Palaemon elegans* Rathke, 1837 was 1963 and 1057, respectively (Bilgin and Samsun 2006). Factors such as food availability may influence the growth rate of caridean prawns. Due to the environments inhabited by the species studied here, fecundity corroborates that of other hololimnetic prawns, which tend to have few large yolky eggs hatching lecithotrophic larvae in advanced stages (Collart and Enrico 1993; García-Dávila et al. 2000;

Magalhães 2016). These results are expected for species living in blackwater that is typically poor in nutrients (Junk et al. 1989).

The freshwater prawn species studied here are not occurring in estuarine or marine environments to complete their ontogenetic cycle, like *P. pandaliformis* (see Paschoal et al. 2016). These animals developed reproductive strategies, such as the incubation of a few yolky eggs (Magalhães and Walker 1988; Collart and Enriconi 1993), due to the evolutionary process that led to the continentalisation of these species (Jalihal et al. 1993). *Macrobrachium brasiliense* and *Ps. chryseus* showed maximum fecundity of 156 and 49 eggs, respectively, and both went through three larval stages (Magalhães and Walker 1988). In contrast, *E. amazoniensis* only completes one stage (Magalhães 1988) and in this study, it produced up to 23 eggs. *Palaemon carteri* had up to 50 eggs and no studies were found on larval development. Magalhães (1986b) found that the congeneric species *Palaemon ivonicus* (Holthuis, 1950) has three larval stages. Moreover, Santos and Vieira (2016) showed that *P. carteri* has a low number of eggs, but the volume is relatively larger than the volume of typical marine and estuarine prawns, such as *Palaemon pugio* Holthuis, 1949 and *Palaemon vulgaris* (Say, 1818) (Hong-Young 1987). Based on this evidence, it is likely that *P. carteri* uses a similar reproductive strategy since the two species may occur concomitantly in the same environment. Consequently, we propose that the number of eggs is directly related to the number of larval stages. In general, the higher the number of eggs, the greater the number of larval stages in caridean prawns.

Fecundity in some species of freshwater prawns increases with growth (Bond and Buckup 1982; Lobão et al. 1985; Valenti et al. 1989). This study shows that the large size and weight of the females are associated with a greater number of eggs per individual. The reproductive investment is related to a morphometric intraspecific variation in the populations (Lima et al. 2015), where larger females produce more eggs. The abdominal cavities of the larger females are large enough to hold large quantities of eggs, as seen in *Macrobrachium olfersii* (Wiegman, 1836) and *Macrobrachium potiuna* (Müller, 1880) in Nazari et al. (2003) and *Macrobrachium surinamicum* (Holthuis, 1948) in Lima et al. (2015). However, these prawns have higher fecundity compared to the freshwater species evaluated in this study, mainly because of the environment they inhabit.

The sampling sites of *M. brasiliense* and *Ps. chryseus* are areas of nutrient-poor blackwaters (Horbe and Santos 2009) subjected to periodical flood pulses and relatively acidic pH ranging from 6.69 to 6.99 (6.85 ± 0.16) (unpublished data). The sites where *P. carteri* and *E. amazoniensis*

were collected are subjected to dynamic flood pulses (Junk et al. 1989), with the substantial influence of the Amazon River, and receive sedimentation and nutrients from this river of muddy water. In general, species that live in estuaries or marine environments tend to have high fecundity, zooplanktonic larvae and complete metamorphosis (Williamson 1972), which does not occur in Amazonian freshwater prawns, such as *Macrobrachium inpa* Kensley and Walker, 1982 described by Magalhães (2016) and *Macrobrachium nattereri* (Heller, 1862) in Magalhães (1989) living in nutrient-poor blackwater rivers.

The fecundity index in *Potimirim glabra* (Kingsley, 1954) is proportional to the size of the female (Hoffmann and Negreiros-Fransozo 2010), which was not observed for the four species in this study. The two populations of *P. pandaliformis* (Stimpson, 1871), one in Ubatumirim and the other in river Comprido, did not differ in fecundity index, showing that these two populations in different environments have the same breeding strategy (Mortari et al. 2009). The fecundity index of the caridean prawns in this study, considering the size, shows that although *M. brasiliense* is the largest species, with the highest absolute number of eggs, their reproductive potential is lower than that of *P. carteri* and similar to *Ps. chryseus* and *E. amazoniensis*. However, these prawns show similar reproductive strategies due to the environment in which they live, probably associated with the chemical characteristics of the water. The fecundity index excluding the effect of weight corroborated the higher fecundity presented by *M. brasiliense*. Consequently, this measurement may be the most appropriate to determine the reproductive potential of a freshwater prawn excluding the effect of biometry.

The species of palemonidean prawns evaluated in this study are small animals with low fecundity compared to other caridean prawns. *Macrobrachium brasiliense* was the largest and most fecund species, followed by *P. carteri*, *Ps. chryseus* and *E. amazoniensis*. However, the fecundity index showed that *P. carteri* had the highest reproductive potential. These animals exhibit K-strategists characteristics, meaning that they invest in quality over quantity of eggs.

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Disclosure statement

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