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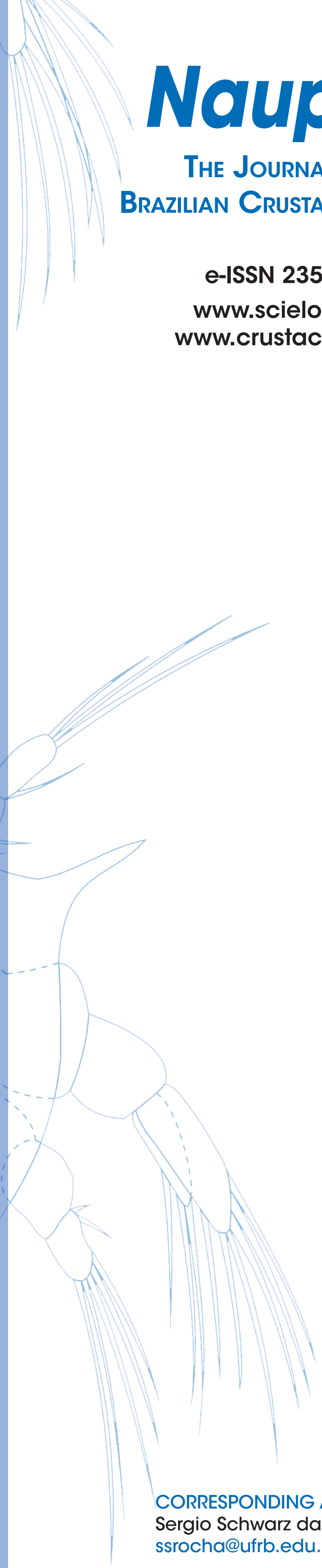

ORIGINAL ARTICLE

Population biology of *Macrobrachium jelskii* (Miers, 1877) (Decapoda, Palaemonidae) from an artificial pond in Bahia, Brazil

Sérgio Schwarz da Rocha[1] orcid.org/0000-0002-2594-2745
Rosiane de Jesus Barbosa[1]

[1] Laboratório de Bioecologia de Crustáceos, Centro de Ciências Agrárias, Ambientais e Biológicas, Universidade Federal do Recôncavo da Bahia. Rua Rui Barbosa, 710. 44380-000 Cruz das Almas, Bahia, Brazil.
SSR E-mail: ssrocha@ufrb.edu.br
RJB E-mail: rosibarbosa4@gmail.com

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CORRESPONDING AUTHOR
Sergio Schwarz da Rocha
ssrocha@ufrb.edu.br

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ABSTRACT

The freshwater prawn *Macrobrachium jelskii* (Miers, 1877) is widely distributed in South America's lentic and lotic habitats. We studied the population structure and reproductive biology of the species in the municipality of Cruz das Almas, state of Bahia, Brazil, to supply information on this ecologically and economically relevant species. Samples were collected monthly, from February 2013 to January 2014, at Laranjeiras pond. The sex ratio was biased towards females (1.4 females : 1 male). The mean carapace length of females and males was respectively 8.08 ± 1.37 mm and 6.61 ± 1.11 mm. Ovigerous females comprised 22.5% of all sampled females, and their reproductive activity, characterized as seasonal-continuous, was positively correlated with precipitation. The average size of females at the onset of functional maturity was estimated at 6.67 mm CL and the mean fecundity was 25.2 ± 8.9 eggs. Egg size, mass and volume increased significantly during embryonic development. Our data strongly indicate that the reproductive strategy that best fits the species is the "pure search" mating system.

KEY WORDS

Reproduction, maturity, population structure, prawn, freshwater.

INTRODUCTION

Most species of freshwater prawns belong to *Macrobrachium* Spence Bate, 1868, a widely distributed genus in tropical and subtropical regions. Currently, there are 246 valid species of *Macrobrachium*, of which 19 occur in Brazil (De Grave and Fransen, 2011; Maciel *et al.*, 2011; Pileggi and Mantelatto, 2012; De Grave and Ashelby, 2013; Santos *et al.*, 2013; Vera-Silva *et al.*, 2016).

Macrobrachium jelskii (Miers, 1877) is popularly known in Brazil as "camarão sossego" (Paiva and Barreto, 1960). It occurs in Trinidad, Venezuela, Guiana, Suriname, French Guiana, Bolivia, Brazil (states of Amapá, Pará, Amazonas, Maranhão, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, Minas Gerais, Rio de Janeiro, Espírito Santo, Mato Grosso, São Paulo and Santa Catarina) (Melo, 2003; Pileggi *et al.*, 2013) and Argentina (Collins, 2000). However, its occurrence at the hydrographic basins of the Brazilian Northeast and Southeast might be considered the result of anthropogenic actions (Magalhães *et al.*, 2005; Soares *et al.*, 2015; Vera-Silva *et al.*, 2016).

Since it can be found in both lentic and lotic environments, from dark to clear waters, among the roots of aquatic plants and grasses, muddy substrates, rocks and sand, *M. jelskii* can be considered a generalist species (Magalhães, 2000; Melo, 2003; Montoya, 2003; Cirilo *et al.*, 2011). The roots of aquatic plants provide nutrition and protection for the ovigerous females and larvae during their development (Montoya, 2003). This prawn is an important component of the food chain in limnetic environments, feeding on insect larvae, diatoms, and other algae, besides sediment grains (Melo, 2003).

In some regions of Brazil, *M. jelskii* is economically relevant in the aquarium trade and used as artisanal fishing bait and food by riverine populations (Cirilo *et al.*, 2011; Vera-Silva *et al.*, 2016). Ramírez *et al.* (2010) and Urbano *et al.* (2010), respectively, analyzed the biochemical composition and growth of the species under culture conditions, aiming to use it as a component of feed for fish and crustacean farming.

In Brazil, studies on the reproductive biology of *M. jelskii* populations were carried out in the Southeast (Barros-Alves *et al.*, 2012; Mossolin *et al.*, 2013; Soares *et al.*, 2015), North (Magalhães, 2000; Lima *et al.*, 2013) and Northeast (Paiva and Barreto, 1960; Nery *et al.*, 2015). However, no studies have investigated the biology of *M. jelskii* populations in the state of Bahia and in an urban artificial environment. Thus, we characterized the reproductive pattern and population biology of *M. jelskii* in the municipality of Cruz das Almas, Bahia State, in order to compare it with other populations from natural environments (lotic and lentic) previously studied. Furthermore, we hope to understand better the correlation between population structure and reproductive strategies of *M. jelskii*. Finally, we believe that the information herein provided will be an important contribution to the knowledge of the biology and ecology of this species, its preservation and sustainable use.

MATERIAL AND METHODS

Specimens of *M. jelskii* were collected monthly from February 2013 to January 2014, at Laranjeiras pond (12°39'59.54"S 039°07'12.06"W), which is located within the city limits of the municipality of Cruz das Almas (Fig. 1A). The sampling site is a lentic environment, without adjacent riparian forest and with high amounts of aquatic weeds, particularly *Cabomba* sp., *Eleocharis* sp., *Eicchornia* sp., *Nymphaea* sp., and *Salvinia* sp. (Fig. 1B). Since the pond is inserted within an urban area, signs of anthropic influence are visible, such as trash at the margins and in the water, houses in the surroundings, and footprints of horses and cattle. Monthly precipitation and temperature during the study period were obtained from the meteorological station at EMBRAPA – Mandioca and Fruticultura, at Cruz das Almas.

Specimens of *M. jelskii* (Fig. 1C) were sampled by sweeping a sieve (diameter 50 cm, mesh 0.5 mm) through the partially submerged vegetation along the riverbanks. The sampling effort consisted of the activity of one collector during 60 minutes.

At the collecting site, we stored the specimens in plastic containers with water from the pond. While still alive, they were transported to the laboratory, where they were maintained at ambient temperature and constant aeration.

In the laboratory, determination of species was based on Melo (2003). Specimens were sexed according to the presence (males) or absence (females) of the appendix masculina on the second pair of pleopods. Furthermore, carapace length (CL = from the post-orbital margin to the posterior margin of the carapace), total body length (TL = from the tip of the rostrum to the end of the telson) and length of the abdomen (AL = from the anterior to the posterior tip of the abdomen, excluding the telson) were measured to the nearest 0.01 mm with a digital caliper. After that, the specimens were dried with a paper towel and weighted using a precision scale (range: 0.01 g). In order to quantify the weight of females and egg masses

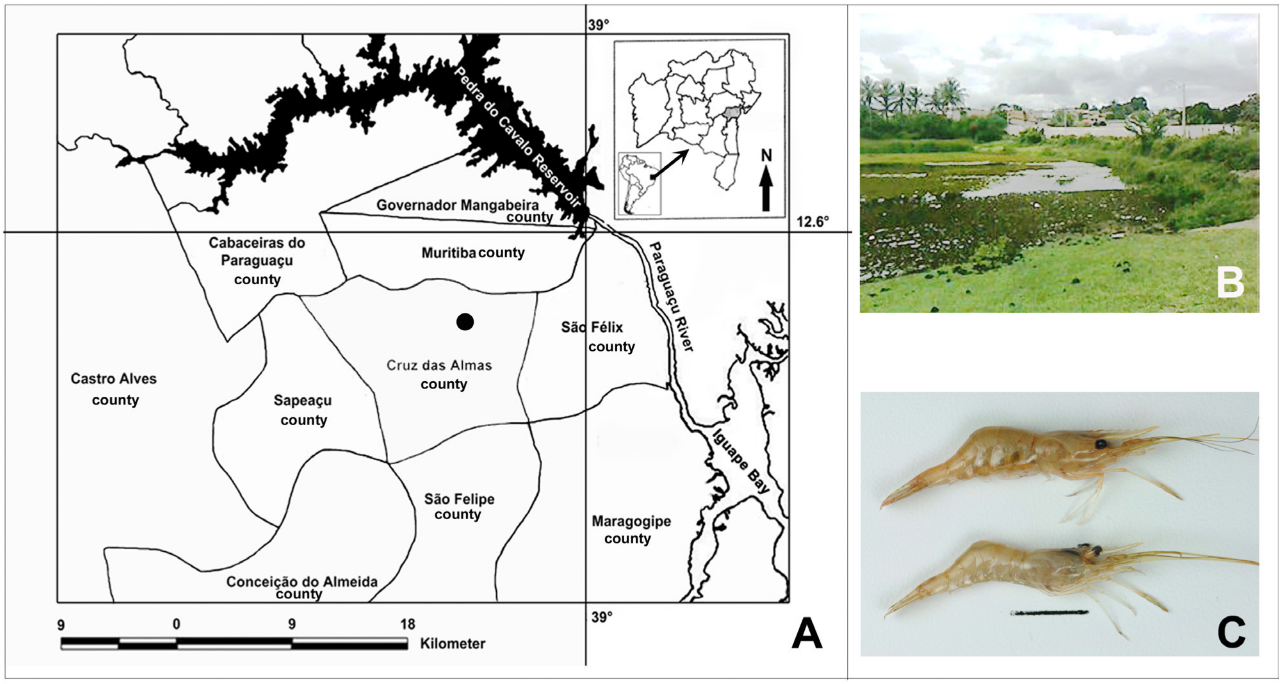

Figure 1. (A) Map of Recôncavo da Bahia. Black area, Pedra do Cavalo Reservoir; black circle, urban area of Cruz das Almas, Bahia. (B) Sampling site (12°39’59.54”S 039°07’12.06”W). (C) *Macrobrachium jelskii*: female (top) and male (bottom). Scale = 10 mm.

separately, ovigerous females were weighted with and without the egg mass. Specimens that had lesions or missing appendages were excluded from the analysis. After taking all biometric data, specimens were stored in 70% ethanol. Voucher specimens were deposited at the Museum of Zoology, Federal University of Bahia, Brazil (MZUFBA, accession number 2732).

Deviations from the 1 : 1 sex ratio were checked with the Yates corrected goodness-of-fit chi square test. The non-parametric Mann-Whitney test was employed to compare carapace length and weight between males and females, since the data sets of both sexes were not normally distributed (Zar, 1996). Sex-ratio analyses of size classes were based on Wenner (1972).

The macroscopic analysis of ovaries was carried out according to Carvalho and Pereira (1981). The reproductive period was determined based on the temporal variation in the relative frequency of ovigerous females (Bueno and Shimizu, 2008; Rocha *et al.*, 2010; Rocha *et al.*, 2013). The average size at the onset of functional maturity was determined as the CL at which 50% of the females sampled during the reproductive period were considered sexually mature (Rocha *et al.*, 2010). The sexual maturity of females was determined based on the following reproductive traits: ovaries at development stage II.2 (*sensu* Carvalho and Pereira, 1981) or beyond, and ovigerous condition. The first criterion was adopted conservatively, since according to Carvalho and Pereira (1981) ovaries at stages II.2 and II.3 (in maturation) may have the same size and macroscopic aspect of stage III (mature). The average size at the onset of functional maturity was determined by interpolation of the equation obtained by performing a logistic regression (Pagano and Gauvreau, 2006) on the maturation stage of the specimen (immature = 0; mature = 1) vs. CL data points. The size at sexual maturity of males could not be determined because all sampled males exhibited a fully developed appendix masculina on the second pleopod.

The eggs of all ovigerous females were removed from the incubating chamber, analyzed under the stereomicroscope, and classified according to their embryonic stage of development as early eggs (embryo showing little or no differentiation, no sign of developing compound eyes and yolk occupying more than two-thirds of egg volume), intermediary eggs (embryo showing little segmentation and developing compound eyes and yolk occupying more than one-third of egg volume) and late eggs (embryo showing appendages and fully developed compound eyes and yolk occupying less than one-third of egg volume) (Anger and Moreira, 1998). After that, the entire egg mass was removed under a stereomicroscope, distributed uniformly on a gridded Petri dish and counted with the aid of a manual counter (Rocha *et al.*, 2013).

Fecundity data were obtained from females bearing early eggs only, since egg loss during incubation had already been observed in pleocyemate decapod crustaceans (Darnell, 1956; Balasundaran and Pandian, 1982; Anger and Moreira, 1998; Galvão and Bueno, 2000; Mossolin and Bueno, 2002). The mean number of late eggs (*i.e.,* actual reproduction *sensu* Anger and Moreira, 1998) was also calculated. Egg loss during incubation was calculated based on the difference between fecundity and actual reproduction (Balasundaram and Pandian, 1982; Anger and Moreira, 1998).

The mean size of eggs was determined based on 50 eggs in each developmental stage, chosen randomly. The major and minor axes of the eggs were measured with the aid of a dissecting Nikon microscope equipped with a Motic digital camera and image manipulation software (Motic Image Plus, v.2.0). Egg volume (EV) was calculated from the formula EV $= \pi lh^{2/6}$, where l is the long axis s and h is the short axis (Odinetz Collart and Rabello, 1996). The values of egg measurements in their initial and final stages were compared with the *t* Student test to verify the significance of the differences between egg sizes and volume throughout the embryonic development. The relationships between the number of eggs and female body measurements (CL, TL and AL) were ascertained by Pearson correlation analysis (Zar, 1996).

All statistical analyses ($\alpha = 0.05$) were based on Zar (1996) and were conducted in the computer program PAST (Paleontological Statistics Software, version 3.0) (Hammer *et al.*, 2001) and Microsoft Office EXCEL® 2003 or later.

RESULTS

We sampled 1,724 individuals, of which 1,013 (58.8%) were females and 711 (41.2%) were males. Among the females captured, 228 (22.5%) were ovigerous. Therefore, females outnumbered males and the resulting overall sex ratio of 1.4 females to 1 male departed significantly from 1 : 1 ($\chi^2 = 52.6$; $p < 0.001$). Females predominated significantly in February, March, June, August, September and October 2013. In the other months, the sex ratio did not deviate significantly from 1 : 1 (Fig. 2).

Carapace length (CL) ranged from 3.58 (21.02 TL) to 11.68 (46.89 TL) mm ($\overline{X} = 8.08 \pm 1.37$ mm; or 35.32

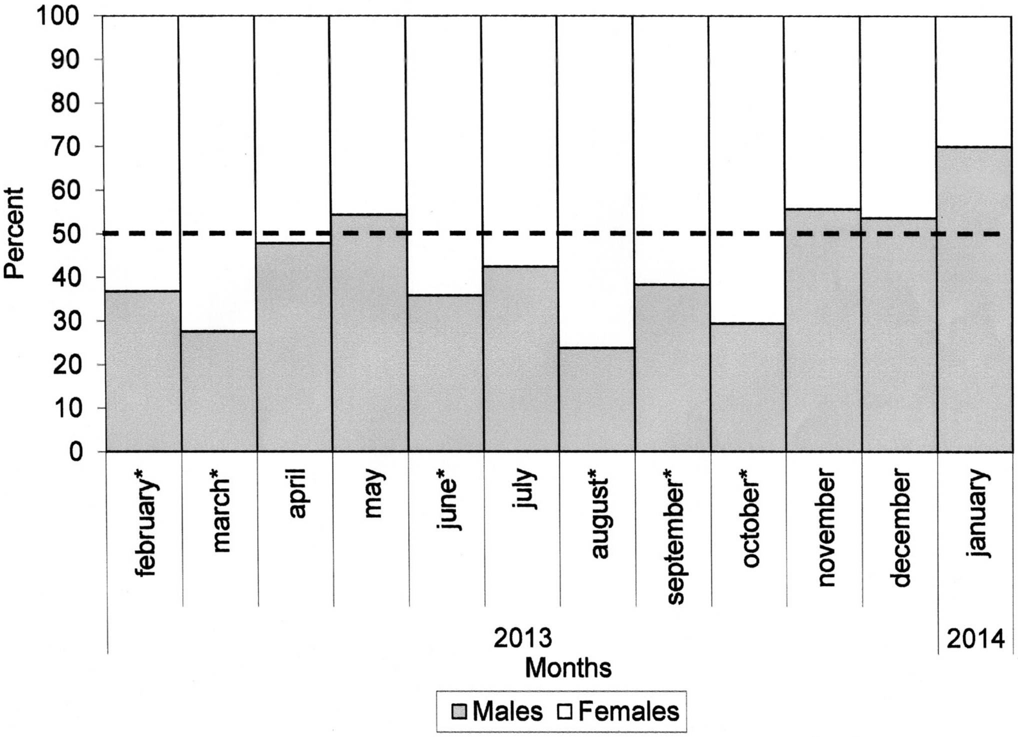

Figure 2. Monthly variation of sex ratio in *Macrobrachium jelskii* collected at Laranjeiras pond, from February 2013 to January 2014. (*) significant difference.

TL) in females and from 3.33 (19.15 TL) to 10.21 (43.03 TL) mm ($\overline{X}$ = 6.61 ± 1.11 mm; or 30.54 TL) in males. The carapace of ovigerous females ranged from 5.96 to 10.80 mm ($\overline{X}$ = 8.50 ± 0.75 mm; or 36.67 TL) (Fig. 3A). Weight ranged from 0.05 to 0.74 g in males and from 0.03 to 0.90 g in females, with means equal to 0.25 ± 0.11 g and 0.42 ± 0.16 g in males and females, respectively. Females were larger (U = 139730; $p < 0.001$) and heavier (U = 140350; $p < 0.001$) than males, characterizing sexual dimorphism. Sex-ratio analysis of CL size classes resulted in a reversal pattern (*sensu* Wenner, 1972), in which males predominate over females in the lower size classes (4.8 |– 7.2 mm) and the opposite condition occurred in the larger size classes (Fig. 3B).

We found females with maturing or mature ovaries throughout the sampling period. Furthermore, we collected ovigerous females in all sampling months, with the exception of January 2014 (Fig. 4), when the fewest number of individuals were collected (n = 20; 6 females). However, it is important to note that collecting in January, 2015 confirmed the presence of ovigerous females during that month.

The highest frequency of ovigerous females occurred in March, characterizing a reproductive peak. March corresponded to the month with the highest rainfall and temperature recorded for the study period (Fig. 5A, B). On the other hand, we observed the lowest frequency of ovigerous females in September, when the dry season starts in the region. Pearson correlation analysis demonstrated that the monthly proportion of ovigerous females was positively correlated ($r = 0.86$; $p < 0.05$) with the average monthly precipitation (Fig. 5A). On the other hand, there was no correlation ($r = 0.22$; $p > 0.05$) with the average monthly temperature, but it was observed that the reproductive peak coincided with the temperature peak during the study period (Fig. 5B).

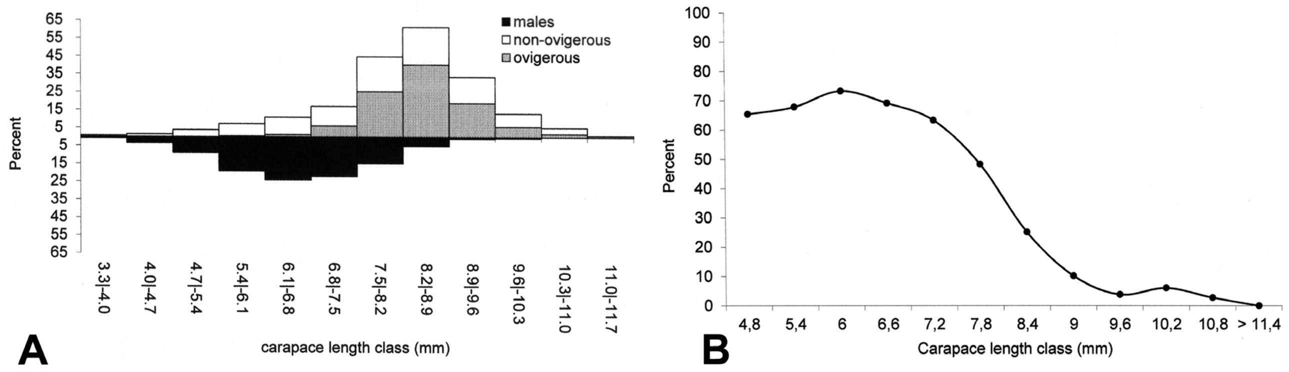

Figure 3. Frequency distribution by size classes of *Macrobrachium jelskii* collected at Laranjeiras pond, from February 2013 to January 2014. (A) Carapace length frequency distribution of males, ovigerous and non-ovigerous females. (B) Proportion of males according to carapace length class.

The smallest ovigerous female measured 5.96 mm CL (TL = 28.10 mm), corresponding to the size class 5.4 |- 6.1. The last immature females and the first females with mature ovaries were also recorded in the same size class. Finally, from this size class onwards the proportion of mature females in the sample gradually increased (Fig. 6A). Thus, we estimated the average size at the onset of functional maturity (L50%) at 6.67 mm CL (TL = 30.78 mm) (Fig. 6B).

Fecundity varied from 5 to 56 eggs ($\overline{X}$ = 25.2 ± 8.9; n = 228) in females with carapace length between 5.96

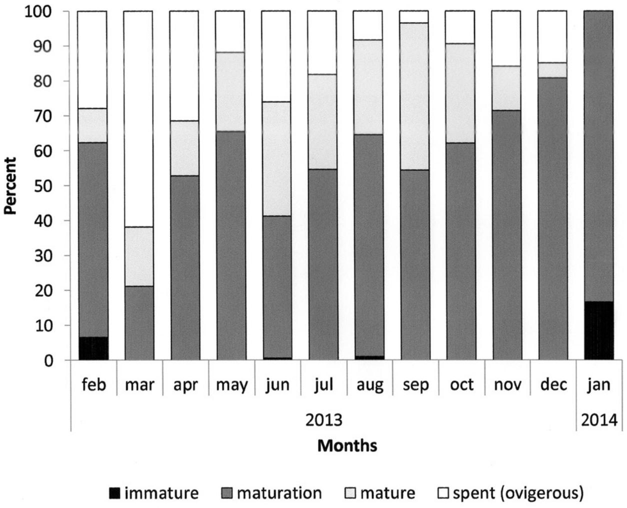

Figure 4. Percentage of immature, maturing, mature and ovigerous females of *Macrobrachium jelskii* collected at Laranjeiras pond, from February 2013 to January 2014.

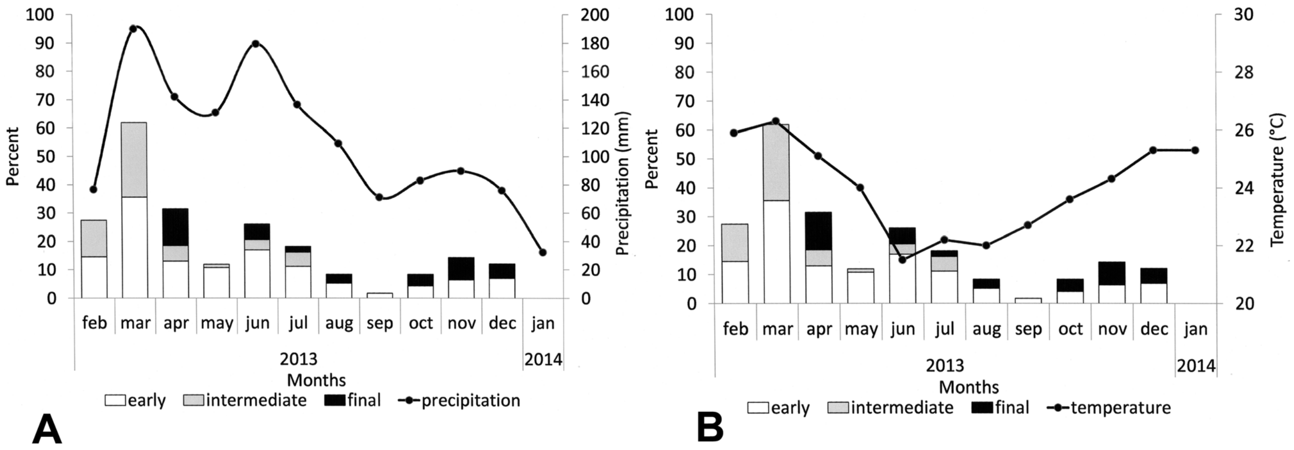

Figure 5. Rain precipitation (A), air temperature (B) and temporal variation in the percentage of ovigerous females (embryonic development of eggs discriminated) of *Macrobrachium jelskii* collected at Laranjeiras pond, from February 2013 to January 2014.

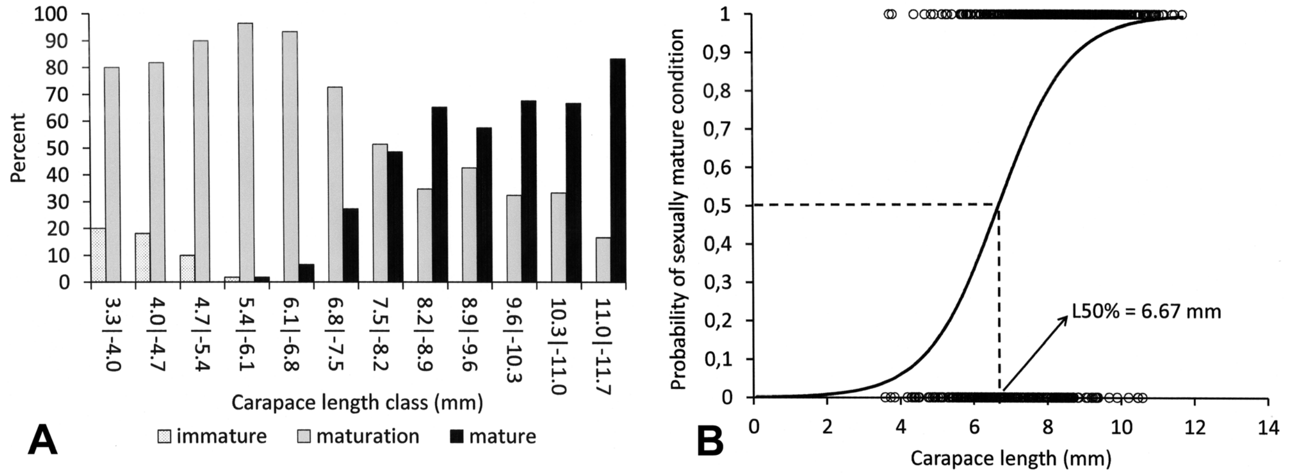

Figure 6. *Macrobrachium jelskii.* (A) Frequency distribution by size classes of females (ovarian developmental stages discriminated). (B) Size at the onset of functional maturity of females estimated by logistic regression based on the absence (0) or presence (1) of discrete reproductive traits plotted against carapace length.

mm (TL = 28.10 mm) and 10.80 mm (TL = 43.06 mm). Ovigerous females predominated in size class 8.40 |- 8.80 ($n = 61$). In addition, there was a wide variation in individual fecundity among females in the same class, with the highest mean fecundity observed in females with carapace length between 9.30 |- 9.80 (Fig. 7). Finally, a comparison between mean fecundity calculated from early and late eggs revealed that the percentage of egg loss during incubation was 4.5%.

Positive correlations were found between the number of eggs in the incubation chamber and carapace length ($r = 0.35$; $p < 0.0001$), total body length ($r = 0.47$; $p < 0.0001$) and length of the abdomen ($r = 0.43$; $p < 0.0001$).

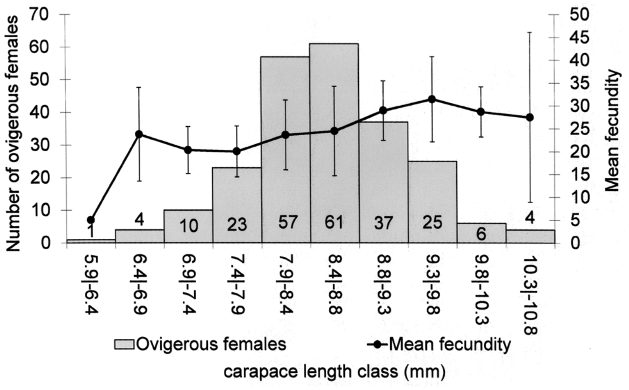

Figure 7. Mean fecundity of ovigerous females distributed by size classes, collected at Laranjeiras pond, from February 2013 to January 2014. Vertical bar: standard deviation.

The weight of the early egg masses varied from 0.02 to 0.23 g ($\overline{X} = 0.07 \pm 0.03$ g), whereas the weight of late egg masses varied from 0.03 to 0.20 g ($\overline{X} = 0.09 \pm 0.05$ g). The Mann-Whitney test detected a significant difference between the weight of egg masses in their initial and final stages ($U = 1810.5$; $p < 0.05$), showing that there was an increase in the weight of eggs during embryonic development, even after considering the 4.5% egg loss.

The eggs of *M. jelskii* were elliptic, with their color varying from olive green (early eggs) to light green (late eggs). Mean egg size was 1.83 ± 0.12 mm × 1.36 ± 0.11 mm and 2.02 ± 0.13 mm × 1.43 ± 0.10 mm in the early and late embryonic stages, respectively. The increment in size during embryonic development was significant for the major ($t = 7.67$; $p < 0.001$) and minor ($t = 3.56$; $p < 0.001$) axes. Mean egg volume was 1.78 ± 0.35 mm^3 (early eggs) and 2.18 ± 0.38 mm^3 (late eggs), thus occurring significant increment in egg volume during embryonic development ($t = 5.46$; $p < 0.001$).

DISCUSSION

The sex ratio found in this study was similar to that reported by other authors who have studied populations of *M. jelskii* at different locations. Gamba (1997) and Barros-Alves *et al.* (2012) found female biased sex ratios in populations from Venezuela, and from state of Minas Gerais, Brazil, respectively. On the other hand, Lima *et al.* (2013) and Mossolin *et al.* (2013) found no statistical difference in the sex ratio of populations from eastern Amazonia and from São Paulo State, respectively. Finally, Soares *et al.* (2015), studying a population from the São Francisco River, found a female biased sex ratio in lentic environments and the opposite condition in lotic ones. However, these last authors concluded that the male biased sex ratio in lotic environment occurred because females seek shelter among marginal vegetation, which was abundant downstream the Três Marias Dam. Therefore, most available information on *M. jelskii* populations show that a female biased sex ratio is the most frequent condition (Gamba, 1997; Barros-Alves *et al.*, 2012; Soares *et al.*, 2015; this study).

The reversal pattern of sex ratio results from the fact that adult males are markedly concentrated in smaller size classes, while adult females are predominantly found in larger classes, with narrow superposition area between these two groups (Fig. 3A, B). A similar size distribution pattern has been reported for the adult population of *M. jelskii* from Grande River, state of Minas Gerais (Barros-Alves *et al.*, 2012). This pattern has often been attributed to the occurrence of hermaphroditism in caridean shrimps (Wenner, 1972; Bauer, 2000; 2004; Correa and Thiel, 2003). However, several studies focusing on histology and gonadal development found no evidence of hermaphroditism in species of *Macrobrachium* (Carvalho and Pereira, 1981; Damrongphol *et al.*, 1991; Chaves and Magalhães, 1993; Mossolin and Bueno, 2002; Silva *et al.*, 2009; Revathi *et al.*, 2012). By ruling out hermaphroditism, variations in the sex ratio of populations of *Macrobrachium* spp. might be explained by other factors, for instance: differences in migration rates, mortality, longevity and growth between the sexes (Wenner, 1972; Souza and Fontoura, 1996; Mantel and Dudgeon, 2005; Mattos and Oshiro, 2009), and different reproductive strategies (Mossolin and Bueno, 2002; Hayd and Anger, 2013; Rocha *et al.*, 2015).

According to Anger (2013) and Vogt (2013), there has been strong selective pressure on decapods colonizing freshwater environments (such as *M. jelskii*) towards reducing the number of eggs and increasing their sizes, lecithotrophy and reduction of larval stages. Furthermore, it is well-established that fecundity in caridean shrimps is directly proportional to the size of females (see Corey and Reid, 1991 for review). Therefore, the large size of *M. jelskii* females (which are naturally less fertile due to the abbreviated development of the species) would be advantageous because it would allow them to carry a higher number of eggs per brood (Hartnoll, 1985; Guerao *et al.*, 1994; Mossolin and Bueno, 2002; Mossolin *et al.*, 2013). This strategy can be found in various populations of *M. jelskii*, since the majority of studies conducted to date (Gamba, 1997; Barros-Alves *et al.*, 2012; Mossolin *et al.*, 2013; present study) have found that females are larger than males.

In addition, other patterns observed in the population structure of *M. jelskii* from Laranjeiras pond might also be correlated to its reproductive strategy. The predominance of females and the smaller size of males are strong indications that the mating system in this case is "pure search" (*sensu* Correa and Thiel, 2003). This reproductive pattern was also observed in populations of *Macrobrachium amazonicum* (Heller, 1862) that inhabit lentic environments (Pantaleão *et al.*, 2012; Rocha *et al.*, 2015).

In this mating system, population densities are high, males are smaller than females, do not develop large cheliped weapons, and do not display agonistic behaviors or guard their females during mating (Correa and Thiel, 2003; Bauer, 2004). Therefore, males are not territorial, are highly mobile (Bauer, 2004), and their reproductive success depends on their ability to fertilize the highest number of females, with whom they interact quickly and without an elaborate pre-copulatory behavior (Correa and Thiel, 2003). In this context, a female biased sex ratio would also be advantageous, since males would have a higher amount of potentially receptive females available for mating, which would increase the reproductive output of the population.

Based on the presence of females with maturing or mature ovaries and ovigerous females throughout the sampling period, and reproductive peak in March we concluded that the reproductive pattern of the studied population is continuous-seasonal (*sensu* Pinheiro and Fransozo, 2002). Populations of *M. jelskii* from the states of São Paulo (Mossolin *et al.*, 2013) and Minas Gerais (Barros-Alves *et al.*, 2012; Soares *et al.*, 2015) also showed continuous-seasonal reproductive pattern. On the other hand, populations from Ceará (Paiva and Barreto, 1960), Venezuela (Gamba, 1997) and Amapá (Lima *et al.*, 2013) showed a seasonal reproductive period. Therefore, the reproductive pattern of *M. jelskii* populations do not support the paradigm that the reproductive activity of decapod crustaceans varies with latitude (Tab. 1), being continuous in lower latitudes and seasonal in higher latitudes (Bauer, 1992; 2004; Defeo and Cardoso, 2002).

Specifically in the case of *M. jelskii*, rainfall and water temperature play key roles in establishing the reproductive period, as several authors have noted the intensification of the reproductive activity during the warmer and humid months (Gamba, 1997; Lima *et al.*, 2013; Mossolin *et al.*, 2013; Soares *et al.*, 2015; present study).

Palaemonid shrimps synchronize their reproduction with the warmer and rainy seasons, when there is higher availability of food for the larvae (Takino *et al.*, 1989), since higher levels of rainfall increase the supply of nutrients in lentic environments, increasing primary productivity (Henry *et al.*, 1998; Calijuri *et al.*, 2002). This increased nutrient input could also contribute to the further development of macrophytes, which provide shelter for ovigerous females and serve as nursery habitat (Montoya, 2003; Paschoal *et al.*, 2013). Moreover, higher temperatures also stimulate gonadal development and shorten post-embryonic development (Bond-Buckup and Buckup, 1982; Magalhães and Walker, 1988; Rao, 1991; Pinheiro *et al.*, 1994).

The size of the smallest ovigerous female is usually taken as the smallest size at which individual maturity is recorded (Soares *et al.*, 2015). Thus, we reported the earliest sexual maturity among all populations of *M. jelskii* studied to date (Tab. 1). Furthermore, in our data, the values of the smallest ovigerous female and the average size at the onset of functional maturity (L50%) were very similar. On the other hand, Soares *et al.* (2015) estimated a much higher value (between 39.23 and 41.73 mm TL) for the functional maturity of a population from Minas Gerais. However, the criterion used by Soares *et al.* (2015) was only the presence / absence of eggs on the pleopods of females, while we also considered the macroscopic gonadal development.

The mean fecundity and the minimum and maximum number of eggs per female of *M. jelskii* from Laranjeiras pond were similar to those found in other Brazilian populations (*e. g.*, São Paulo), and Venezuela, while in populations from other localities females had higher fecundity (Tab. 1). The number of eggs produced by a female can be genetically determined, but it may vary depending on environmental factors (*e. g.*, temperature and food availability), size and age of the female (Sastry, 1983; Oh and Hartnoll, 1999; Ammar *et al.*, 2001). Therefore, differences in fecundity among populations of *M. jelskii* (as described in Tab. 1) may be related to different sizes of the ovigerous females sampled from different locations, since the number of eggs is directly proportional to the body size of the female in this species (Gamba, 1997; Nery *et al.*, 2015; Soares *et al.*, 2015; present study), as well as in several other caridean shrimps (see Anger and Moreira, 1998 for review).

Moreover, we sampled females with a very low fecundity (Tab. 1; Fig. 7) (*e. g.*, n ≤ 5). Antunes and Oshiro (2004) and Soares *et al.* (2015) also reported "ovigerous" females of *Macrobrachium potiuna* (Müller, 1880) and *M. jelskii*, respectively, with very few eggs or even with an empty brood chamber. This condition may occur as the result of accidental egg loss, incomplete fertilization or diseases (Parsons and Tucker, 1986). These same factors might also be responsible for the variation in fecundity within the same size class (Lobão *et al.*, 1985; Negreiros-Fransozo *et al.*, 1992), as reported in this study (Fig. 7).

The color of the early eggs of *M. jelskii* varies from orange (Paiva and Barreto, 1960; Mossolin *et al.*, 2013) to green (Gamba, 1997; present study). This variation in color may correspond to differences in the composition of the vitellum, as observed in hermit crabs (Turra and Leite, 2007). Furthermore, all studies conducted to date have reported that the late eggs of *M. jelskii* become whitish. According to Habashy *et al.* (2012), in *Macrobrachium rosenbergii* (De Man, 1879), the change in egg color during embryonic development corresponds to biochemical changes, particularly in the concentrations of proteins, lipids and carbohydrates.

In general, eggs of *M. jelskii* from different localities are elliptical, and very similar in size, with the exception of eggs from a population from Ceará (Paiva and Barreto, 1960), which are notably smaller (Tab. 2). In addition, all studies conducted to date reported a significant increase in egg size during embryonic development, particularly along the major axis (see Tab. 2 for references). This egg growth pattern is common in Malacostracans (Müller *et al.*, 2004; Sudhakar *et al.*, 2014). It is associated with an increase in the water content of the egg (Yao *et al.*, 2006; Habashy *et al.*, 2012), and with an increase in the size of the developing embryo (Anderson, 1982; Lourdes and Cuvin-Aralar, 2014).

Table 1. Reproductive pattern, size of ovigerous females and fecundity of *Macrobrachium jelskii* populations.

Locality/Latitude	Reproductive pattern	TL (CL) of ovigerous females (mm)	Fecundity	Reference
Pueblo de Mantecal, Venezuela (07º33’30” N)	Seasonal	34.50 – 45.3	10 – 56	Gamba (1997)
Índios Lagoon, Macapá, Amapá (0º01’50.8” N)	Seasonal	39.90 – 47.5 Mean = 43.3	29 – 97	Lima *et al.* (2013)
Alagadiço Grande Creek, Ceará (03º44’S)	Seasonal	31.15 – 44.00	16 – 107	Paiva and Barreto (1960)
Laranjeiras pond, Cruz das Almas, Bahia (12°39’59.54” S)	Seasonal-continuous	28.10 (5.96) – 43.06 (10.80) Mean = 37.40 (8,52)	5 – 56 (Mean = 25.2)	Present study
São Francisco River, downstream Três Marias Reservoir, Minas Gerais (18º12’49” S)	Seasonal-continuous	35.24 – 48.72	5 – 69 (Mean = 35)	Soares *et al.* (2015)
São Francisco River, upstream Três Marias Reservoir, Minas Gerais (18º21’49”S)	Seasonal-continuous	30.32 – 50.64	5 – 78 (Mean = 37)	Soares *et al.* (2015)
Grande River, Planura, Minas Gerais (20º09’S)	Seasonal-continuous	(6.50) – (11.2) Mean = 9.21	No data	Barros-Alves *et al.* (2012)
Anhumas River, São Paulo (21º42’17”S)	Seasonal-continuous	(7.85) – (10.70)	1 – 56 (Mean = 23.95)	Mossolin *et al.* (2013)

Table 2. Egg size in populations of *Macrobrachium jelskii.*

Egg stage	Mean (± S.D.) egg size (mm)		References
	Minor axis	Major axis	
Early	1.03	1.53	Paiva and Barreto (1960)
Late	1.17	1.73	
Early	1.42 ± 0.07	1.91 ± 0.05	Gamba (1997)
Late	1.54 ± 0.04	2.27 ± 0.04	
Early	1.59 ± 0.06	2.17 ± 0.11	Soares *et al.* (2015) (downstream)
Late	1.68 ± 0.11	2.39 ± 0.16	
Early	1.54 ± 0.07	2.07 ± 0.12	Soares *et al.* (2015) (upstream)
Late	1.62 ± 0.08	2.32 ± 0.19	
Early	1.36 ± 0.11	1.83 ± 0.12	Present study
Late	1.43 ± 0.10	2.02 ± 0.13	

The present study contributes to the knowledge of the biology of *M. jelskii* and reports a correlation between aspects of the population structure, reproductive strategies, and environmental factors. In addition, our study demonstrated that the population was stable in its environment, although Laranjeiras pond suffered from anthropogenic impacts because our results were similar to that reported by other authors who have studied populations of *M. jelskii* at natural environments. However, given the wide geographic distribution of this species, we recommend additional studies on populations from different regions to understand better the patterns of the life cycle of this Palaemonidae.

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