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Research Article

Fecundity, egg volume and reproductive output of *Macrobrachium tenellum* (Crustacea: Palaemonidae) from the northern coast of Jalisco, Mexico

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ABSTRACT. Our knowledge of the reproductive biology of palaemonid shrimps is an important tool to assess potential candidates for aquaculture as well as being useful to develop adequate strategies for the conservation of the biodiversity. Here we analyzed the fecundity, volume and water content of the eggs, and the reproductive output (RO) of *Macrobrachium tenellum* in the Ameca River, Jalisco-Nayarit, Mexico. The total length of the females ranged from 26.6 to 67.0 mm (average 44.2 ± 8.8 mm) and fecundity (considering all stages) fluctuated between 253 and 10,384 eggs (average 2,418 ± 2,089 eggs). Females lost on average 26% of the initially produced eggs. The average egg length increased from 0.55 (recently produced eggs) to 0.66 mm (eggs close to hatching). The water content of eggs increased significantly during embryogenesis by 11.4%. The RO was not related to female length and fluctuated between 4.1 and 16.0%, which are values within the range reported for other decapods. The results of the current research contribute to laying the foundations for future studies that help to define strategies for the conservation and sustainable use of this crustacean.

Keywords: egg production, embryogenesis, freshwater shrimp, reproductive biology, egg loss, water content, Ameca River.

INTRODUCTION

Aquaculture is an economic activity with great potential for food production under a sustainable scheme. A species with high potential for aquaculture should combine the following features: fast-growing, easy reproduction in captivity, high fecundity, low aggressiveness, and diseases resistance (Da Silva *et al*., 2004). One of such species combining these characteristics is *Macrobrachium tenellum*, locally known in Mexico as "manopalito", "chacal", "brazo largo", "popotillo," "langostino", among other names, depending on the region. This shrimp is of economic importance, and is target of the artisanal fishery in coastal cities and lagoons of Mexico, El Salvador and Guatemala (Cabrera-Peña, 1983). Information of the reproductive biology of palaemonid shrimps is an important tool to identify potential candidates for aquaculture; moreover, such information is required for the development of adequate management strategies of these decapods (Mossolin & Bueno, 2002). Therefore, fecundity studies are fundamental to assess the capacity of the use of (freshwater) shrimps as a sustainable living resource. Fecundity refers to the number of eggs produced in each spawning (Bertini & Baeza, 2014) or to the number of eggs carried by the female under the abdomen (Bond & Buckup, 1982; Valenti *et al*., 1989). Information about egg production permits not only to recognize the potential of each species to be cultivated on a commercial scale, but also allows to estimate the minimum number of adults needed to maintain wild populations (Valenti *et al*., 1989; Barros-Alves *et al*., 2012; Aya-Baquero & Velasco-Santamaría, 2013).

The estimation of the egg volume is important to understand the mechanisms of adaptation to the environment used by the different species (Hernáez & Palma, 2003). *Macrobrachium* species have different adaptations to the freshwater environment (Lara & Wehrtmann, 2009; Bauer, 2013): some species complete their entire life cycle in freshwater, producing a small number of eggs but of relatively large volume (Melo & Brossi-Garcia, 1999). Other species are dependent on brackish water and larvae require coastal waters to complete their life cycle (Gamba, 1982; Bauer, 2013). These species produce smaller eggs but in large quantity (Jalihal *et al*., 1993; Pereira & Garcia, 1995). The energy that the females allocated for reproduction can be estimated through the reproductive output (RO) (Hines, 1988, 1991, 1992). The common formula to measure reproductive output is: dry weight of the ovigerous mass divided by the dry weight of the female without eggs (López *et al*., 1997). In crustaceans, the energy investment made by the female may be affected by the loss of eggs during incubation caused by ecological, allometric and/or mechanical factors (Kuris, 1991; Oh & Hartnoll, 1999; Oyarzún *et al*., 2010).

In Mexico, the egg production of *M. tenellum* has been studied by Román-Contreras (1979) and Guzmán-Arroyo (1987); however, these studies did not assess the female energy investment per egg clutch. Therefore, the objective of the present investigation was to analyze aspects of the reproductive biology previous not studied (fecundity, egg volume, reproductive output) in *M. tenellum* in the Ameca River, Jalisco-Nayarit, Mexico.

MATERIALS AND METHODS

Shrimps were captured between February 2015 and January 2016 in four different collecting sites in the Ameca River: Boca, Las Juntas and San Juan (Fig. 1). Boca and Las Juntas sites are located closer to the river mouth (0 and 3 km from the river mouth, respectively), San Juan are situated upstream (23 km from the coast) (Fig. 1). In each locality, shrimps were collected on the riverbank, between the vegetation and roots of trees using an electrofishing equipment (Samus 725G) for 30 min. at each sampling point. After the sampling, organisms were placed individually in plastic bags and kept at a temperature of 0-5°C during the transportation to the Laboratory of Water Quality and Experimental Aquaculture (LACUIC) located in the University Centre of the Coast of the Guadalajara University. Once in the laboratory, the organisms were kept frozen until further analysis.

Collected organisms were identified according to Holthuis (1952) and Hendrickx (1995). Ovigerous females were selected and the following parameters were measured: 1) female overall length (from the posterior margin of the eye orbit until the distal extreme of the telson: TL; mm) with a digital vernier caliper (±0.01 mm), 2) female total weight (TW; g) using a digital balance Ohaus® (0.001 g), 3) total number of eggs present on the pleopods, 4) size, volume, water content of the egg, and 5) the reproductive output (RO).

To determine fecundity, the total egg mass of the female was detached carefully with the aid of dissection tweezers. Three subsamples (between 250 to 1000 eggs each) were taken, and eggs were counted in each of the subsamples with a stereomicroscope (AmScope®). The three subsamples along with the remaining eggs were dried in an oven at 60°C for 48 h. A digital balance (Ohaus®, 0.001g) was used to estimate dry weight. The average weight of each egg, and fecundity were calculated according to the following equations proposed by Hernáez & Wehrtmann (2011): (1) $E = S/100$ and (2) $NE = WEM/E$ where E = egg weight, S = average weight of the subsamples; NE = total number of eggs; WEM = weight of the total egg mass. In this case, an adaptation was made since the utilized number of eggs was different. Thus the following formula was applied: $E = S/N$ in which S = sample weight and N = number of eggs in the sample, in agreement with I. Wehrtmann (*pers. comm.*).

The developmental stage of the egg was determined according to the criteria proposed by Wehrtmann (1990): Stage I: rounded egg, uniform yolk and without visible eye pigments; Stage II: ovoid egg, elongated and barely visible eye pigment; and Stage III: ovoid egg, well-developed and intensely pigmented eyes; embryo with free abdomen. An analysis of covariance was applied (ANCOVA, $P < 0.05$) to the relationship between the number of eggs and the total length in Stage I and Stage III to rule out the possible influence of the stage of development in the number of eggs carried by female. Subsequently, a regression analysis was used to analyze the relationship between the number of eggs, TL and TW.

To determine the egg size, 20 eggs of each female were separated and digital photographs were taken; the length and width was measured with the software Image Tool version 3.0 (University of Texas, Health Science Center, San Antonio, Texas (http://compdent.uthscsa.edu/dig/itdesc.html). The egg volume was calculated with the formula $V = 1/6\ (a \times b \times \pi)$ proposed by Corey & Reid (1991), where a is the length and b the egg width in mm; $\pi = 3.14$. Average volume and standard deviation was calculated for each of the three stages. An ANOVA was applied ($P < 0.05$) to determine possible differences between stages. A linear regression model was used to represent the relationship

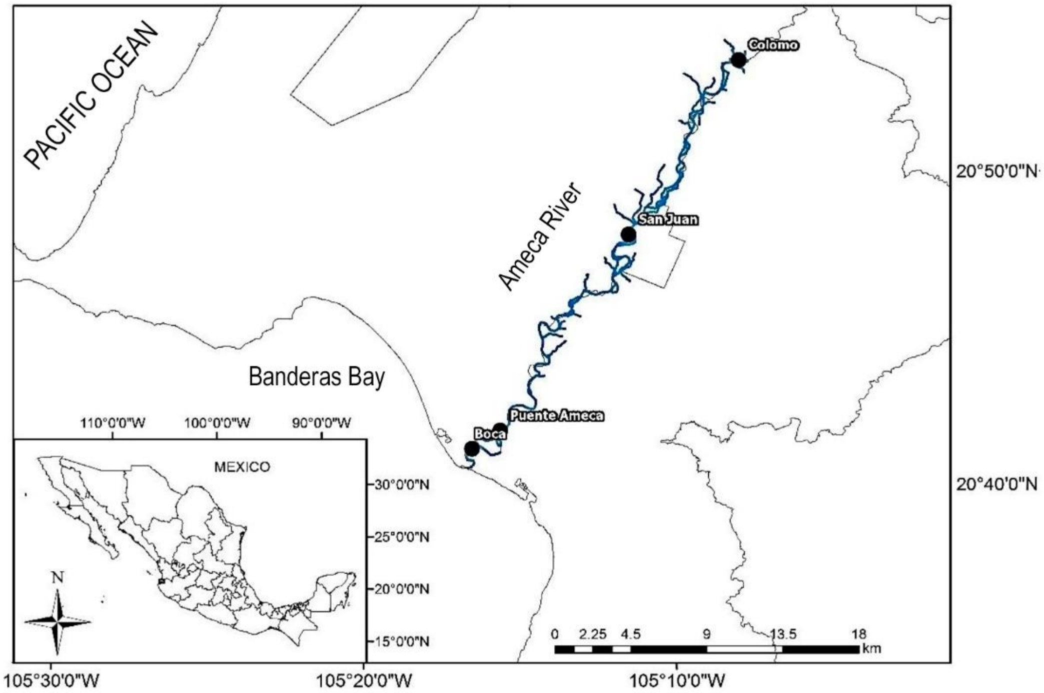

Figure 1. Location of the Ameca River sampling sites. The kilometer values refer to the distance from the river mouth.

between fecundity and female size (TL) for Stage I and III.

The estimation of the egg water content was obtained from the difference between wet and dry weight of the ovigerous mass. An ANOVA ($P < 0.05$) was applied to analyze differences between developmental stages. The RO was obtained by dividing the dry weight of the ovigerous mass by the dry weight of the female without eggs (López *et al*., 1997), taking into account all development stages. A linear regression was performed to determine the relationship between the RO and TL of the females.

RESULTS

A total of 92 *M. tenellum* ovigerous females were selected from the Ameca River (San Juan [18], Las Juntas [39] and Boca [35]) for the fecundity analysis. Taking into account all the localities, the size of females varied between 26.6 and 67.0 mm TL with an average of 44.2 ± 8.8 mm TL (Boca 42.0 ± 3.8 mm, Puente 41.7 ± 7.4, San Juan 48.8 ± 10.2 mm). The average weight was 2.1 ± 1.6 g and fluctuated between 0.4 and 6.5 g. The ANCOVA analysis showed no significant effect of the locality over the fecundity (F = 2.7, d.f. = 2, number of eggs P = 0.07) (Fig. 2); however, fecundity increased significantly with female TL (F = 101.2, d.f. = 1, $P = < 0.0001$). Considering all the localities, fecundity ranged from 253 to 10,384 eggs with an average of 2,418 ± 2,089 eggs.

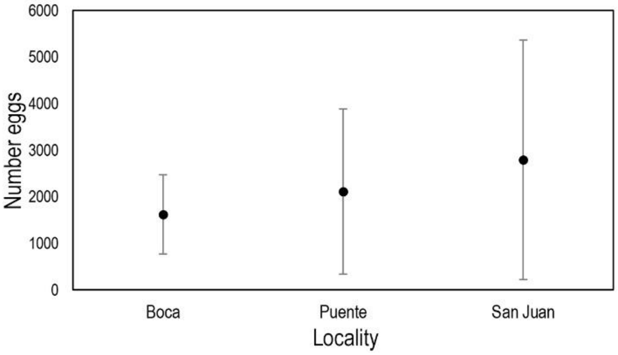

Figure 2. Average fecundity (with standard deviation) of *Macrobrachium tenellum* between different sampling locations in the Ameca River, Jalisco-Nayarit, Mexico.

The relationship between fecundity and female size showed a linear positive relationship in Stage I and II (Fig. 3). The number of eggs per ovigerous female decreased significantly with egg stage (ANCOVA, F = 7.63, d.f. = 1, $P = 0.007$). The Stage I and Stage III slopes were not significantly different (F = 0.24, d.f. = 1, $P > 0.6$). Calculations of estimated egg numbers in early and late stage of development suggest that the percentage of egg loss in *M. tenellum* is 26%.

The average egg length increased during the incubation period from of 0.55 (Stage I) to 0.66 mm (Stage

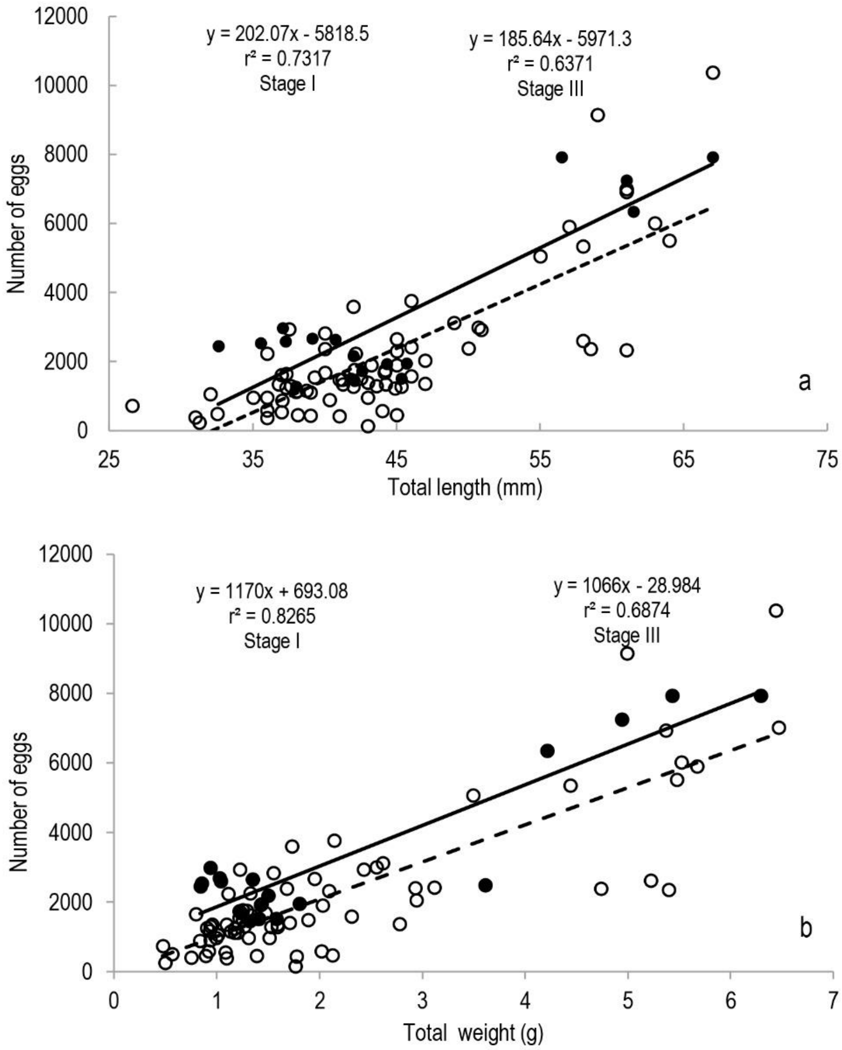

Figure 3. *Macrobrachium tenellum*: relationship between a) total length and b) total weight *versus* number of eggs (black circles indicate Stage I and white circles refer to Stage III).

Table 1. *Macrobrachium tenellum*: water content percentage, volume and size of the different egg development stages (average, maximum and minimum as well as standard deviation values).

Stage	n	Average ± SD	Maximum	Minimum
		Water content %		
I	6	78.1 ± 5.1	86.7	71.9
II	12	78.7 ± 3.7	83.8	70.5
III	35	82.8 ± 3.6	92.0	73.0
		Volume (mm^3)		
I	18	0.054 ± 0.010	0.059	0.037
II	39	0.059 ± 0.009	0.068	0.049
III	35	0.074 ± 0.012	0.087	0.056
		Length (mm)		
I	18	0.553 ± 0.034	0.585	0.500
II	39	0.590 ± 0.033	0.640	0.531
III	35	0.667 ± 0.050	0.707	0.610

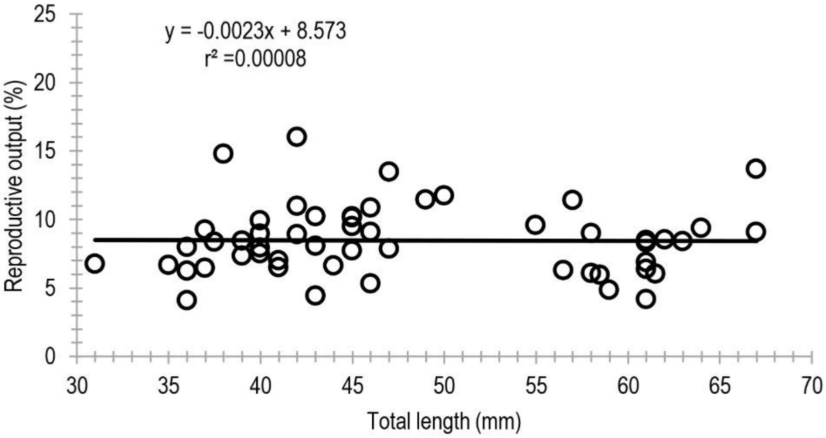

Figure 4. Relationship between total length (mm) and females reproductive outputs of *Macrobrachium tenellum*, considering all stages of development.

III). Similarly, the egg volume showed significant differences (F = 4.04, d.f. = 2, *P* = 0.04) during embryonic development: 0.054 (Stage I) to 0.074 mm^3 (Stage III), which represents a total increase of 37.9%. The water content of eggs (Table 1) increased significantly by 11.4% during embryogenesis (F = 7.66, d.f. = 2, *P* = 0.001). The RO was not related to female length (R = 0.00008). Females invested on average 8.5 ± 2.5% of their body weight in egg production, and this value varied between 4.1 and 16% (Fig. 4).

DISCUSSION

Numerous studies revealed that fecundity in decapods is closely related to female size (*e.g*., Antezana *et al*., 1965; Corey & Reid, 1991; Echeverría-Sáenz & Wehrtmann, 2011). This pattern is related to the fact that large-sized females have larger ovaries than smaller individuals of the same species, which allows them to produce and carry more eggs. Our results are in accordance with this general trend: larger and heavier *M. tenellum* females produced significantly more eggs than smaller ones (Fig. 2). Similar results have been obtained from other *Macrobrachium* species: *M. acanthurus* (Anger & Moreira, 1998; Tamburus *et al*., 2012), *M. amazonicum* (Da Silva *et al*., 2004; Parra-Medina *et al*., 2008; Aya-Baquero & Velasco-Santamaría, 2013), *M. carcinus* (Graziani *et al*., 1993; Lara & Wehrtmann, 2009), *M. heterochirus* (Ching & Velez, 1985) and *M. olfersii* (Anger & Moreira, 1998).

The relationship between female size and fecundity has been described usually by linear regressions, although in some cases an exponential or potential function was used to describe this relationship (Sutcliffe, 1993; Hernáez & Palma, 2003). In the present study, *M. tenellum* fecundity increased linearly with female size, corroborating similar results reported by Gutiérrez-Jara (2010) for the same species. Similarly, such a positive linear relationship has been described also for *M. acanthurus* (Valenti *et al*., 1989; Albertoni *et al*., 2002; Tamburus *et al*., 2012), *M. amazonicum* (Da Silva *et al*., 2004; Aya-Baquero & Velasco-Santamaría, 2013; Lima *et al*., 2014), *M. carcinus* (Lobão *et al*., 1985; Lara & Wehrtmann, 2009), *M. heterochirus* (Ching & Velez, 1985), and *M. olfersii* (Ammar *et al*., 2001; Mossolin & Bueno, 2002). However, an exponential model was used to describe the relationship between the number of eggs and females size of the following *Macrobrachium* species: *M. rosenbergii* (Rajyalakshmi, 1961), *M. carcinus* (Pérez & Segura, 1981; Mejía-Ortiz *et al*., 2001), *M. acanthurus* (Pérez & Segura, 1981; Mejía-Ortiz *et al*., 2001), and *M. heterochirus* (Mejía-Ortiz *et al*., 2001). Finally, other authors mentioned that a potential model provided the best fit for this relation in *M. acanthurus* (Anger & Moreira, 1998), *M. amazonicum* (Hayd & Anger, 2013), and *M. olfersii* (Anger & Moreira, 1998). According to Lara & Wehrtmann (2009), the relationship between fecundity and female size in species of the genus *Macrobrachium* should be analyzed and described separately for each species to assess which model described best this relation.

The fecundity range estimated in this study for *M. tenellum* is comparable to that reported for the same species by Román-Contreras (1979) and Guzmán-Arroyo (1987) (Table 2). Nevertheless, the range of fecundity in the present study were higher than those mentioned by Signoret & Brailovsky (2002) for *M. tenellum* collected in the Coyuca de Benitez Lagoon in Guerrero, Mexico. Moreover, Gutiérrez-Jara (2010) reported a higher fecundity of *M. tenellum* in Costa Rica compared to the present data; this difference may be due to the fact that the study by Gutiérrez-Jara (2010)

Table 2. Fecundity (number of eggs per female) of different *Macrobrachium* species (n: number of females, TL: total length; maximum and minimum values are indicated in parenthesis). *Carapace length.

Species	n	TL mm Mean (max-min)	Fecundity Mean (max-min)	Reference
M. acanthurus	87	(60.0 - 135.9)	8,929 (740 - 17,769)	Valenti *et al.* (1989)
	29	10.7 - 53.5)	(440 - 3042)	Anger & Moreira (1998)
	36	71.1 (42.9 - 110.4)	1,886 (113 - 5568)	Mejía-Ortiz *et al.* (2001)
M. amazonicum	46	(38 - 67)	(178 - 1344)	Lobão *et al.* (1986)
	32	(7 - 21)*	(150 - 2165)	Odinetz Collart (1991)
	60	(50 - 100)	(480 - 2128)	Da Silva *et al.* (2004)
	246	(7.6 - 19.5)*	211 (16 - 1630)	Hattori *et al.* (2009)
	19	17.2*	2,237 (1341 - 2956)	Meireles *et al.* (2013)
M. americanum		34.1 (33.9 - 60.8)*	76,900 (17942 - 124057)	Gutiérrez-Jara (2010)
M. carcinus	41	(100 - 220)	53,764 (6350 - 194,350)	Lobão *et al.* (1985)
	16	90.9 (46.4 - 127.7)	7,892 (502 - 23,852)	Mejía-Ortiz *et al.* (2001)
	35	161.2 (120.0 - 190.0)	98,749 (14,420 - 242,437)	Lara & Wehrtmann (2009)
M. heterochirus	34	71.8 (51.7 - 153.1)	3659 (293 - 28,512)	Mejía-Ortiz *et al.* (2001)
	50	(18 - 61)	1788 (184 - 5031)	Ching & Velez (1985)
M. rosenbergii	20		25,083	Graziani *et al.* (2003)
M. tenellum		(68 - 7)	(2,288 - 11,102)	Guzmán-Arroyo (1987)
	43	(56 - 101)	(900 - 10,800)	Román-Contreras (1979)
		38.0 (67 - 80)	984 (900 - 1,200)	Signoret & Brailovsky (2002)
	15	32*	15,315	Gutiérrez-Jara (2010)
	92	44.2 (26.6 - 67.0)	2,418 (253 - 10,384)	Present study

included larger females when compared to our study. The number of eggs obtained in the present study for *M. tenellum* was lower than in other larger species of the same genus, such as *M. americanum* (Smitherman *et al.*, 1974; Gutiérrez-Jara, 2010), *M. carcinus* (Lara & Wehrtmann, 2009), or *M. rosenbergii* (Habashy, 2010) (Table 2). These results reveal that fecundity in *Macrobrachium* species is highly variable and strongly related to female size.

Inter- and intraspecific differences in the egg production of decapods are not only influenced by size differences (Ching & Velez, 1985; Da Silva *et al.*, 2004), but also by temperature, quality and quantity of food, which may vary within the latitudinal range of the species´ distribution (Odinetz-Collart & Rabelo, 1996; Fransozo *et al.*, 2004). Similarly, Mashiko (1990, 1992) indicated that the egg number could vary within a river system with the distance from the coast.

Some studies estimated the production of eggs, considering all embryonic stages (*e.g.*, Walker & Ferreira, 1985; Mejía-Ortiz *et al.*, 2001; Albertoni *et al.*, 2002; Antunes & Oshiro, 2004). Other studies reported only the number of recently extruded eggs to exclude possible egg loss during embryonic development, caused by infections, parasites, poor water quality, predation or constant friction with the bottom (*e.g.*, Lara & Wehrtmann, 2009; Tamburus *et al.*, 2012; Meireles *et al.*, 2013; Bertini & Baeza, 2014). Our results revealed an egg loss of 26% during the embryogenesis of *M. tenellum*, which is within the range reported for other *Macrobrachium* species (10-46%): *M. rosenbergii* 30% (Wickins & Beard, 1974), *M. nobilii* 46% (Balasundaram & Pandian, 1982), *M. acanthurus* 23% (Anger & Moreira, 1998; Bertini & Baeza, 2014), and *M. lanchesteri* 20% (Phone *et al.*, 2005). Egg loss in *M. tenellum* may be explained by the egg volume increase during the incubation period (Bertini & Baeza, 2014), thus probably outgrowing the available physical space of the abdominal chamber. The increase of the egg volume is a common pattern in crustaceans (Zhao *et al.*, 2007) and is the result of a gradual water intake during the incubation period (Lardies & Wehrtmann, 1997; Müller *et al.*, 2004) and/or the retention of metabolic water product of respiration (Anger *et al.*, 2002). In the present study, the eggs of *M. tenellum* showed an average egg volume increase of 37.0% during embryogenesis, similar to the results of Gutiérrez-Jara (2010) working with the same species. Likewise, similar results have been reported for other species of the same genus (Table 3). The increase in the egg volume in the *Macrobrachium* species seems to be independent to the size of the females (Lara & Wehrtmann, 2009; Tamburus *et al.*, 2012).

Table 3. Increase egg volume and reproductive output (RO) of different *Macrobrachium* species.

Species	Increase egg volume (%)	RO (%) mean (min-max)	Reference
M. acanthurus	38.0		Tamburus *et al*. (2012)
		19.0 (14.0 - 30.0)	Anger & Moreira (1998)
M. amazonicum	33.4		Odinetz-Collart & Rabelo (1996)
		11.7 (4.8 - 21.8)	Lima *et al*. (2014)
M. carcinus	35.4	12.0 (4.0 - 21.0)	Lara & Wehrtmann (2009)
M. hainananse		10.0 (4.0 - 17.0)	Mantel & Dudgeon (2005)
M. olfersii	30.7		Mossolin & Bueno (2002)
		22.0 (7.0 - 38.0)	Anger & Moreira (1998)
M. potiuna	28.0		Nazari *et al*. (2003)
M. vollenhovenii	58.5		Oben *et al*. (2015)
M. surinamicum		4.3 - 35.5	Lima *et al*. (2015)
	36.0	18.5 (3.1 - 49.4)	Gutiérrez-Jara (2010)
M. tenellum	37.0	8.5 (4.1 - 16)	Present study

The size (length) of the egg in *M. tenellum* increased from 0.55 to 0.66 (Table 1), and these values are in the range reported for other *Macrobrachium* species, which require estuarine environments to complete its reproductive cycle (*M. carcinus, M. olfersii, M acanthurus,* and *M. ohione* (Lara & Wehrtmann, 2009).

The water content of *M. tenellum* eggs increased during the embryogenesis on average by 11.4% (from 78.1% in Stage I to 82.8% in Stage III), a value similar to that reported by Lara & Wehrtmann (2009) for *M. carcinus* (15.8%). According to Pandian (1970), the egg water content of marine benthic decapods with planktonic larval development increases from 50-60% in recently extruded eggs to 70-80% at the end of the incubation period (Pandian, 1970). Lara & Wehrtmann (2009), studying *M. carcinus*, suggested that the pattern proposed by Pandian (1970) might be also valid for freshwater shrimps with planktonic larval development. This assumption is further supported by similar values of water content in eggs of *Atya scabra* (60.0-82.6%; Herrera-Correal *et al*., 2013).

The energy that females invest in reproductive processes is one of the most interesting factors on the reproductive biology of crustaceans (Hernáez & Palma, 2003). Females of *M. tenellum* allocate between 4.1 to 16% (average 8.5 ± 2.5%) of the body weight in egg production. For the same species, Gutiérrez-Jara (2010) mentioned values ranging from 3.1 to 49.4% (average 18.5%). These results are in the range reported for other species of the same genus (Table 3). Just as in other *Macrobrachium* species (*e.g.*, Mantel & Dudgeon, 2005; Lara & Wehrtmann, 2009; Lima *et al.*, 2014, 2015), the RO of *M. tenellum* was not size-related.

The results of the current research contribute to laying the foundations for future studies that help to define strategies for the conservation and sustainable use of this crustacean with ecological as well as economic and social importance.

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