SEXUAL MATURITY, FECUNDITY, AND EMBRYO LOSS IN THE PONTONIINE SHRIMP *CUAPETES AMERICANUS* (KINGSLEY, 1878) (DECAPODA: PALAEMONIDAE) IN BAHÍA DE LA ASCENSIÓN, QUINTANA ROO, MEXICO

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A B S T R A C T

Cuapetes americanus (Kingsley, 1878) is distributed along the Atlantic coast of the Americas, from North Carolina and Bermuda to São Paulo, Brazil and the West Indies. The present goal was to conduct a comparative study of reproductive aspects of *C. americanus*: size at sexual maturity, fecundity, and embryo loss. Specimens were obtained from Bahía de la Ascensión, Quintana Roo, Mexico in November 2000 ($n = 345$) and November 2001 ($n = 156$). Samples were collected with a marsh net on *Thalassia testudinum*-meadows. The average size of the specimens was significantly different between the two dates, with larger females in 2001 (2.46 ± 0.47 mm CL) than in 2000 (2.20 ± 0.23 mm CL). The size at which females reached sexual maturity was 2.01 ± 0.24 mm CL in 2000, and 2.39 ± 0.51 mm CL in 2001. The embryos were categorized in three embryonic stages. Average fecundity at the first stage of development was higher in specimens collected in 2001 (74 ± 57) than in 2000 (47 ± 21). On both sampling dates, fecundity increased with female size but also varied among females of the same size group. Embryos were significantly larger in 2000 than in 2001 (0.034 mm^3 and 0.028 mm^3, respectively). The maximum increase of embryo volume (78.5%) and brood loss (27.5%) with developmental stage was seen in 2001. The differences between the sampling dates and from others populations of this species from different localities suggested an apparent plasticity of the reproductive traits of *C. americanus*.

KEY WORDS: *Cuapetes americanus*, embryo loss, fecundity, Mexican Caribbean, Palaemonidae

INTRODUCTION

Reproduction is an essential aspect of the ecology and life cycle of organisms (Anger and Moreira, 1998) but its intensity and duration can vary even in populations of the same species, depending on environmental and endogenous factors (Sastry, 1983). In caridean shrimp, the breeding season is assessed by the presence of berried females (Béguer et al., 2010). Shrimp of tropical waters experience a continuous reproduction whereas those inhabiting temperate or cold water regions show a seasonal reproduction restricted to periods of higher water temperature (Bauer, 1989; Kim and Hong, 2004).

The carideans also exhibit a great variety of reproductive strategies and variations in several reproductive traits that are reflected in the diversity of their life-history patterns, necessary for the success of their reproduction (Bauer, 2004; Mortari et al., 2009). Therefore, knowledge of these strategies is important if the ecology and life cycles of the species are to be understood.

Fecundity is generally defined as the number of embryos produced by a female in a particular spawning period (Ramirez Llodra, 2002). This important parameter allows the reproductive potential and stock size of a species or population to be estimated (Mantelatto and Garcia, 1999), although the reproductive potential often varies as a function of female body size (Corey and Reid, 1991) but also can be influenced by biological and environmental factors (Sastry, 1983).

In crustaceans, brood loss during embryogenesis is a common feature that reduces their reproductive potential (Oh and Hartnoll, 1999). Embryo loss may have several causes including mechanical stress, increased embryo volume during development, embryo predation and parasitism, and physical damage of the abdomen and/or pleopods (Kuris, 1991; Pandian, 1994). Embryo loss is frequently estimated by comparing fecundity in the early and late stages of development. Since it may regulate the stock density, it should be considered in fecundity-per recruit models (Morizur et al., 1981; Oh and Hartnoll, 1999).

Size at sexual maturity is also central for understanding the reproductive strategy of a species, and it is important in establishing management regulations such as fixing minimum legal size in commercial fisheries (Anala et al., 1980; Béguer et al., 2010). In decapods the size at sexual maturity is usually studied in females, since many indicators are easier to identify in them than in the males; they include the presence of embryos under the pleon and gonadal development stages (Anala et al., 1980; Lizárraga-Cubedo et al., 2008).

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The present study concerns *Cuapetes americanus* (Kingsley, 1878), which ranges from Beaufort, North Carolina to São Paulo, Brazil and the West Indies (Holthuis, 1951, as *Periclimenes* (*Harpilius*) *americanus*; Coelho and Ramos, 1972, as *Periclimenes americanus*; Román-Contreras and Martínez-Mayén, 2010).

Cuapetes americanus is an important component of the invertebrate community associated with submerged vegetation. Together with other species, *C. americanus* plays a key role in the transfer of primary production to higher trophic levels in these ecosystems (Bauer, 1985). However, despite its ecological importance and wide distribution, most of the published information on this species has focused on its taxonomy (Holthuis, 1951; Bruce, 2004, as *Kemponia americanus*; Okuno, 2009; De Grave and Fransen, 2011), distribution (Chace, 1972, as *P. americanus*; Coelho and Ramos, 1972; Román-Contreras and Martínez-Mayén, 2010; Santos et al., 2012), and morphology and general ecology (Gurney, 1943, as *P. americanus*; Fausto-Filho, 1969, as *P. (Harpilius) americanus*). Information on the reproductive biology of *C. americanus* (as *P. americanus*) is limited to studies in Puerto Rico (Bauer, 1989, 1991) and Florida (Corey and Reid, 1991).

In populations with an established breeding period, whether continuous or not, a concentrated effort to capture females during a reduced time period is an adequate method for obtaining representative data on some reproductive aspects (Litulo et al., 2005; Penha-Lopes et al., 2007; Torres et al., 2007; Wehrtmann et al., 2012), this study adopts this strategy. The purpose is to provide new data concerning the reproduction of *C. americanus*, such as size at sexual maturity, number of embryos (realized fecundity), and volume and loss of embryos in a locality of the Mexican Caribbean, as well as to compare the results in two different sampling dates with data available for the same species from other regions. The results may encourage other comparative studies, mainly in areas where urban and tourist activities alter and severely degrade the habitat of this and other shrimp species.

MATERIALS AND METHODS

Bahía de la Ascensión is on the Mexican Caribbean coast (19°47.00′-19°30.03′N, 87°44.03′-87°07.30′W), on the eastern Yucatán Peninsula. It is a shallow bay (2.7-3.5 m depth) with a total surface area of 740 km^2, bordered by well-developed mangroves. A discontinuous line of coral banks that lies roughly parallel to the coastline at the mouth of the bay reduces wave surge within the bay (Briones-Fourzán and Gutiérrez-Carbonell, 1992; Suárez-Morales and Gasca, 1996). Average salinity in the bay is 32 and the water temperature varies from 21°C to 32°C through the year (Suárez-Morales and Gasca, 1996). The substratum is sandy mixed with calcareous material and rocks; marine vegetation consists predominantly of *Thalassia testudinum* Banks and Solander ex König and *Syringodium filiforme* Kützing. Additional information on the flora and environmental parameters of the study area is provided by Briones-Fourzán and Gutiérrez-Carbonell (1992).

Ovigerous females of *C. americanus* were collected at different points of the bay on 15 November 2000 and 20 November 2001 (for sampling localities see Martínez-Mayén and Román-Contreras, 2009) in a depth of approx. 1 m by two 5-min trawls with a marsh net over seagrass beds of *T. testudinum*. Samples were immediately preserved in 10% neutralized formalin and transferred in 70% ethanol in the laboratory. Average water temperature during collections was 30°C in November 2000 and 27.5°C in November 2001.

Carapace length (CL) of each female was measured from the postorbital margin to the mid-posterior end of the carapace; the data were grouped into 0.29 mm CL size classes and analyzed with respect to their frequency distribution. Size at sexual maturity (CL$_{50}$) of the ovigerous females in both sampled dates was calculated with the logistical equation $P = 1/(1 + \exp[-(a + b\text{CL})])$ that relates the proportion of females (P) in each size class with carapace length (CL), where a and b are the parameters resulting from the correlation between P and CL after linearization; thus, the size at which 50% of the females reach sexual maturity was obtained from the negative ratio between the parameters a and b: CL$_{50} = -(a/b)$ (Penha-Lopes et al., 2007; Torres et al., 2007; Martínez-Mayén and Román-Contreras, 2009).

All embryos were carefully detached from the pleopods with fine forceps under a dissecting microscope, and three stages of embryonic development, modified from Martínez-Mayén and Román-Contreras (2009, 2013), were considered: Stage I, embryos with evenly distributed yolk; Stage II, with pigmented ocular line defined and scarcely developed appendages; Stage III, eyespot fully defined, embryo well developed with pleon folded on the ventral side of the carapace.

For each date, embryo sizes were obtained from ten ovigerous females for each developmental stage (Martínez-Mayén and Román-Contreras, 2013; Rocha et al., 2013). Ten embryos per individual were arbitrarily separated and the minor (d_1) and major (d_2) diameters of the embryos were measured under a microscope equipped with a calibrated ocular micrometer. The embryos were treated as oblate spheroids and their volume was calculated with the formula $V = \pi(d_1)^2 \times (d_2)/6$ (Turner and Lawrence, 1979).

The embryos of all females were counted directly, but the realized fecundity was estimated only in females with recently produced embryos (Stage I) to avoid underestimation related to the embryo loss during embryogenesis (Kuris, 1991; Wehrtmann et al., 2012). Data from females with embryos in Stages II and III were used to estimate the average increase (%) in embryo volume between each stage; the possible brood loss was calculated by comparing the difference in average embryo number between successive embryonic stages, assuming that the females with embryos in Stage I did not suffer embryo loss prior to the counts (Wehrtmann et al., 2012).

The Kolgomorov-Smirnov test was applied to test the normality of size frequency distributions (Terossi et al., 2010; Grabowski et al., 2013). Analysis of variance (ANOVA) compared the sizes of ovigerous females between the two years; the same analysis was applied to test differences in fecundity per same size group, embryo volume between the developmental stages, and embryo loss in the early and late stages of embryonic development (Lardies and Castilla, 2001; Terossi et al., 2010; Wehrtmann et al., 2012). Prior to ANOVA, assumptions of ANOVA were examined with Barlett's test (Zar, 2010). Linear regressions of log-transformed data were carried out for number of embryos versus carapace length and the possible differences of fecundity (Stage I) between the two sampling periods were evaluated with an analysis of covariance (ANCOVA) applied to the slopes of these regressions (Terossi et al., 2010; Zar, 2010; Wehrtmann et al., 2012). In all comparisons differences were considered significant at 95% ($P < 0.05$) confidence level.

RESULTS

The samples taken in 2000 and 2001 included 345 and 156 ovigerous females, respectively. In 2000, the average size of ovigerous females was 2.20 ± 0.23 mm CL (range 1.55-3.22 mm), although most females (77.4%) were in the size range 1.80-2.39 mm CL (Fig. 1).

In 2001 the average size of ovigerous females was 2.46 ± 0.47 mm CL (range 1.72-4.58 mm); 65.4% measured 2.10-2.69 mm CL (Fig. 1). The average size of specimens differed significantly between the two years ($F_{(1,499)} = 63.50$, $P < 0.05$), and size frequency distributions showed non-normal distribution (K-S $d = 0.24$, $P < 0.05$).

The relationship between the proportion of ovigerous females and CL was expressed as $P = 1/(1 + \exp(11.64 - 5.78\text{CL}))$ in the year 2000, and as $P = 1/(1 + \exp(6.35 - 2.65\text{CL}))$ in 2001. The estimated size at 50% sexual maturity (CL ± 95% confidence interval) was 2.01 ± 0.24 mm CL and 2.39 ± 0.51 mm CL for the years 2000 and 2001, respectively.
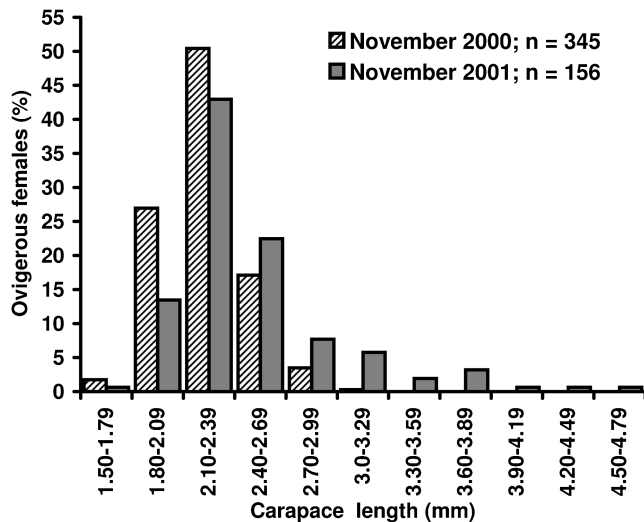
Fig. 1. Carapace length frequency distributions of ovigerous females of *Cuapetes americanus* on two sampling dates.
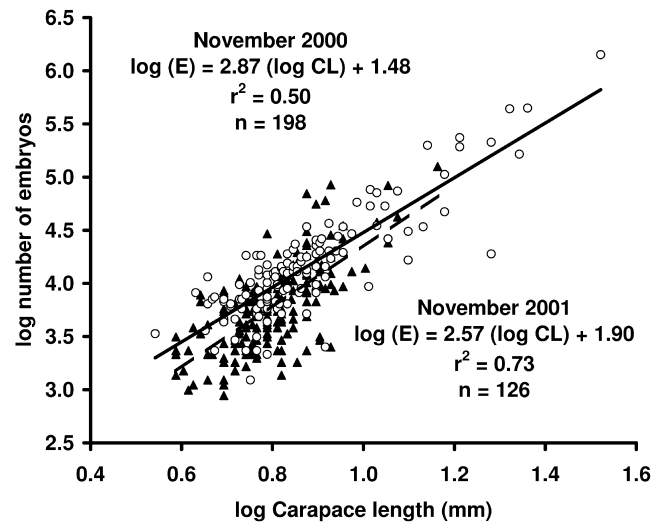

Fig. 2. Relationships between log-transformed data of carapace length (CL) versus log-transformed number of embryos (E) for Stage I of *Cuapetes americanus* in 2000 (triangles, dashed lines) and in 2001 (circles, continuous line).

Fecundity (Stage I) of *C. americanus* fluctuated between 19 and 164 embryos in 2000, and between 22 and 469 in 2001 (Table 1). Linear regression revealed that embryo number increased with female size in both years (Fig. 2). The slopes of the regression lines of embryo number did not differ significantly between the years (ANCOVA, $F_{(1,320)} = 1.38$, $P > 0.05$); significant differences were found between the two intercepts (ANCOVA, $F_{(1,321)} = 29.63$, $P < 0.05$), indicating that females collected in 2001 carried more embryos than those in 2000. Likewise, females were significantly more fecund in 2001 than those of the same size group in 2000 ($F_{(9,5)} = 89.07$, $P < 0.05$).

The embryos of the females collected in 2000 had a greater volume in all embryonic stages than those collected in 2001 (Fig. 3), with significant differences between the same stages for the two years ($F_{(5,594)} = 395.05$, $P < 0.05$).

The average increase in embryo volume was highest between Stages I and III, with 73.5% (from 0.034 mm³ to 0.059 mm³) in 2000 and 78.5% (from 0.028 mm³ to 0.050 mm³) in 2001; it was lowest between Stages II and III (Table 2).

Embryo loss was detected in both years but it was more pronounced between Stages I and III during which, 21.5% were lost in 2000 and 27.5% in 2001, while the lowest loss occurred between Stages I-II in each year (Table 2).

DISCUSSION

The reproductive aspects treated in the present study differed conspicuously between the two years and also from others

populations of the same species from different localities (Table 3); this may reflect adaptations to possible variations in the environmental conditions as well as an apparent plasticity of reproductive traits of *C. americanus*, as has been documented in other palaemonids (Ituarte et al., 2007; Mortari et al., 2009; Béguer et al., 2010; Meireles et al., 2013; Puspitasari et al., 2013).

The difference in sizes of ovigerous females between the two sampling dates may be related to differences in environmental conditions and ecological requirements of individuals, such as water temperature, depth, feeding, food availability, predation pressure, abundance of vegetation (Mantelatto and Barbosa, 2005; Terossi and Mantelatto, 2010), and possible genetic intra-specific characteristics (Mortari et al., 2009); or may be natural variation in the population.
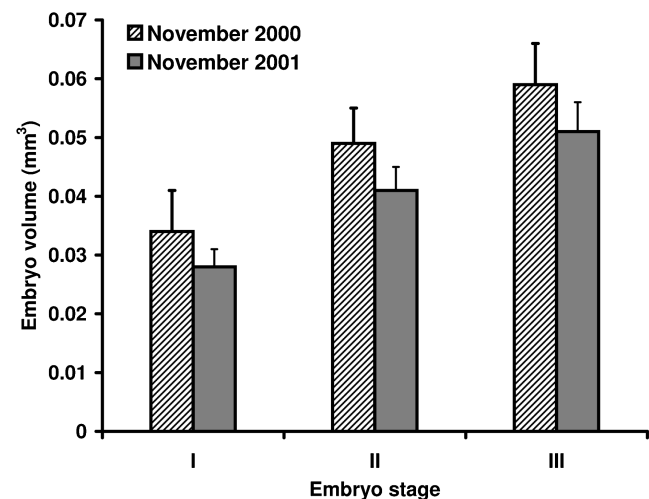

Fig. 3. Changes in average volume of the embryos of *Cuapetes americanus* in the different stages of development in two sampling dates (vertical bar: standard deviation).

Table 1. Number of embryos of *Cuapetes americanus* in two sampling dates (SD, standard deviation).

Stage	November 2000			November 2001		
	n	Range	Average ± SD	n	Range	Average ± SD
I	198	19-164	47 ± 21	126	22-469	74 ± 57
II	54	13-117	43 ± 22	15	16-193	66 ± 48
III	93	11-129	37 ± 21	15	22-104	53 ± 25

Table 2. Embryo volume increase and embryo loss between the stages of development of *Cuapetes americanus* in two sampling dates. * Significant difference, ANOVA test, $P < 0.05$.

Stages	Embryo volume increase (%)		Embryo loss (%)	
	November 2000	November 2001	November 2000	November 2001
I-II	44.1*	46.4*	8.7	10.5
II-III	20.4*	21.9*	13.9*	18.9*
I-III	73.5*	78.5*	21.5*	27.5*

Bauer (1989) defined the size of sexual maturity for *C. americanus* as the smallest ovigerous female observed (1.6 mm CL). In the present study, the minimum size of ovigerous females was similar (1.55 mm CL); however, the size for 50% sexual maturity was 2.01 mm CL in 2000 and 2.39 mm CL in 2001, respectively.

The difference in size at sexual maturity of ovigerous females between the two dates may be attributable to the water temperature (Penha-Lopes et al., 2007; Torres et al., 2007; Ahamed and Ohtomi, 2011). During the sampling in 2001 it was lower (27.5°C) than in 2000 (30°C). This result was consistent with the fact that high temperatures stimulate gonadal development and promote the rapid sexual maturation of the organisms (Annala et al., 1980; Kim and Hong, 2004; Béguer et al., 2010; Wehrtmann et al., 2012) and their reproduction (Bauer, 1989). Another possible factor that may partially explain the size difference between the sampled dates is female nutritional condition since in crustaceans this factor directly influences maturity (Harrison, 1990; Meireles et al., 2013).

On each date was a positive relationship between the number of embryos and the size of female. This has also been observed for other pontoniines including *C. americanus* by Corey and Reid (1991) and Bauer (1991); in

Phycomenes siankaanensis (Martínez-Mayén and Román-Contreras, 2006) by Martínez-Mayén and Román-Contreras (2009) (as *Periclimenes siankaanensis*); and in *Periclimenes ornatus* Bruce, 1969 (Omori et al., 1994). Specimens collected in 2001 were more fecund than those of 2000; this may have been the result of differences in female body size between the two dates, since larger females carry more embryos than smaller ones owing to the greater physical space available in the pleopods (Corey and Reid, 1991). These dissimilarities also could be related to the embryo size (Bauer, 1991; Ramirez Llodra, 2002; Pavanelli et al., 2008); in this respect, the larger embryo size in 2000 would explain the lower fecundity of the females in this period.

The average fecundity of *C. americanus* calculated in this study differs substantially from values reported by Corey and Reid (1991) for the same species, but is close to the value recorded by Bauer (1991) in a Puerto Rican population (Table 3). It is also close to those of other pontoniine species, except for *P. ornatus* and *Periclimenes thermohydrophilus* Hayashi and Ohtomi, 2001 (Table 3), species of a larger size than *C. americanus* (see Omori et al., 1994 and Hayashi and Ohtomi, 2001).

Variation in fecundity of populations of the same species in different localities seems to be the result of genetic

Table 3. Comparative fecundity (Stage I) of some pontoniine shrimps. *Calculated from original source; numbers in parentheses indicates range. Cited as: [a] *Periclimenes siankaanensis*, [b] *Periclimenes longicaudatus*, [c, d] *Periclimenes americanus*.

Species	Average carapace length (mm)	Average fecundity	Average embryo volume (mm³)	Locality	Reference
Periclimenes ornatus Bruce, 1969	(3-6)	(10-1000)	(0.38-0.49)	Murote, Shikoku Island, Japan	Omori et al., 1994
Periclimenes pandionis Holthuis, 1951	3.53 (2.84-4.0)	171 (67-259)	0.050	Indian River, FL, USA	Corey and Reid, 1991
Periclimenes thermohydrophilus Hayashi and Ohtomi, 2001	(6.1-7.0)	(260-510)	0.048*	Kagoshima Bay, Japan	Hayashi and Ohtomi, 2001
Phycomenes siankaanensis[a] (Martínez-Mayén and Román-Contreras, 2006)	(1.91-3.2)	53 (23-141)	0.056	Bahía de la Ascensión, Quintana Roo, Mexico	Martínez-Mayén and Román-Contreras, 2009
Urocaris longicaudata[b] Stimpson, 1860	2.51 (2.16-3.04)	92.75 (49-149)	0.049	Florida Middle Ground, USA	Corey and Reid, 1991
Cuapetes americanus[c] (Kingsley, 1878)	2.1	56	0.013	Dorado, north coast of Puerto Rico	Bauer, 1991
Cuapetes americanus[d]	3.06 (2.28-3.88)	247 (76-519)	0.034	Seahorse Key, FL, USA	Corey and Reid, 1991
Cuapetes americanus	2.23 (1.8-3.2)	47 (19-164)	0.034	Bahía de la Ascensión, Quintana Roo, Mexico	Present study; November 2000
	2.42 (1.72-4.58)	74 (22-469)	0.028	Bahía de la Ascensión, Quintana Roo, Mexico	November 2001

Table 4.   Values of embryo loss for some American Palaemonidae. Cited as: [a] *Palaemonetes argentinus*, [b] *Periclimenes longicaudatus*.

Species	Embryo loss (%)	Reference
Macrobrachium acanthurus (Wiegmann, 1836)	23	Anger and Moreira, 1998
Macrobrachium olfersii (Wiegmann, 1836)	25.2	Nazari et al., 2003
Macrobrachium potiuna (Müller, 1880)	24.6	Nazari et al., 2003
Palaemon pandaliformis (Stimpson, 1871)	23	Anger and Moreira, 1998
Palaemon argentinus[a] (Nobili, 1901)	8-47	Ituarte et al., 2007
Urocaris longicaudata[b] Stimpson, 1860	14.5	Corey and Reid, 1991
Cuapetes americanus (Kingsley, 1878)	21.5-27.5	Present study

characteristics specific to a particular population, and of the number of specimens and the methods of calculation (Pavanelli et al., 2008; Hoffmann and Negreiros-Fransozo, 2010; Martínez-Mayén and Román-Contreras, 2013); but it may also be attributable to the local conditions of temperature and salinity (Sastry, 1983; Lardies and Castilla, 2001; Ramirez Llodra, 2002; Pavanelli et al., 2008). However, the intraspecific variations in fecundity reported for *C. americanus* by Bauer (1991), Corey and Reid (1991), and in the present study are difficult to explain in terms of these factors, since the values of temperature and salinity in Puerto Rico, Florida, and Bahía de la Ascensión are similar (see Bauer, 1985; Mason and Zengel, 1996). Therefore, it is possible that food supply varies along the latitudinal range of distribution of the species and partially determines the number of embryos produced by the females (Sastry, 1983; Anger and Moreira, 1998; Ramirez Llodra, 2002; Kim and Hong, 2004).

The average volume of recently extruded embryos agrees with values reported for other pontoniine species with the exception of *P. ornatus*, which produces larger embryos (Table 3). The data of embryo volume of *C. americanus* for the year 2000 are identical to those reported by Corey and Reid (1991) for the same species, but the value recorded by Bauer (1991) is substantially smaller (Table 3). The short life spans of many seagrass shrimp combined with an intense predation pressure, may explain the production of extremely small embryos by females of *C. americanus* (Terossi et al., 2010), although the embryo volume may also be genetically determined (Pavanelli et al., 2008; Lara and Wehrtmann, 2009; Martínez-Mayén and Román-Contreras, 2009).

The observed difference in size of newly extruded embryos of *C. americanus* between the two sampled dates, is probably due to differences in energy invested per embryo (Clarke, 1993), or could represent an intrapopulational variability among females (see Anger et al., 2002); however, it also may suggest that the embryos could contain a greater proportion of water rather than of organic matter (Pandian, 1994; Wehrtmann and Kattner, 1998; Wehrtmann et al., 2012; Meireles et al., 2013).

The increase in volume calculated for embryos of *C. americanus* in each year (73.5% and 78.5%) was less than that for *Palaemon gravieri* (Yu, 1930) (161%) (Kim and Hong, 2004), and for *P. siankaanensis* (82.75%) (Martínez-Mayén and Román-Contreras, 2009), but similar to that for *Palaemon schmitti* (Holthuis, 1950) (75.7%) (Wehrtmann and Graeve, 1998, as *Palaemonetes schmitti*) and *Palaemon paucidens* De Haan, 1844 (75.6%) (Puspitasari et al., 2013).

The data obtained in this study agree with those for crustaceans in general (20-180%) (Oh and Hartnoll, 1999), and Palaemonidae (3.9-155.9%) (Corey and Reid, 1991). The increase in embryo volume during the incubation period is a general feature in crustaceans (Wehrtmann and Kattner, 1998), that usually is associated with gradual water uptake by the embryo, and changes in biochemical composition during embryonic development (Wehrtmann and Graeve, 1998) as well as with growth of the embryo (Pavanelli et al., 2008).

Owing to the increases in embryo volume through the incubation period, a brood loss could be expected. In the present study the increase in the sample from 2001 was greater and consequently a greater embryo loss also occurred (27.5%). Reports in the literature on embryo loss in Pontoniinae are scarce (Calado, 2008), although brood loss calculated in this study is within the percentages reported in other American palaemonids (Table 4).

The data herein presented showed that the embryo loss in *C. americanus* was more intense in a late stage of development than in others (Table 2). The embryo loss in crustaceans may be relatively evenly distributed over any stage of embryogenesis, although the highest losses have been reported in the latter phases of development (Kuris, 1991; Lardies and Wehrtmann, 1996); this is probably caused by the larger size of late-stage embryos, which would make them vulnerable to the weakness of their attachment structures and consequently more liable to be detached from the female pleon (Oh and Hartnoll, 1999).

Parasites and micropredators of the embryos can also be an important factor of brood loss for decapod crustaceans (Kuris, 1991; Pandian, 1994), but these were not detected in the brood mass of *C. americanus*. Another possible reason for embryo loss is that the mass is exposed to the environment and may be abraded when females moves over the substratum, or may be detached when it is ventilated by the female pleopods (Balasundaram and Pandian, 1982; Pandian, 1994); however, the increase in embryo volume during incubation appears to be the major reason for the reduction in fecundity in *C. americanus*.

The information herein contributes to knowledge of the reproductive aspects of *C. americanus*. In future studies, samples should be collected monthly for at least a year. Additional information regarding larval development and ecology, breeding season and genetic variation along the geographic distribution is required, in order to elucidate the possible reproductive differences among populations of *C. americanus*.

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