

BREEDING AND HETEROSEXUAL PAIRING IN THE SNAPPING SHRIMP *ALPHEUS ESTUARIENSIS* (CARIDEA: ALPHEIDAE) IN A TROPICAL BAY IN NORTHEASTERN BRAZIL

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ABSTRACT

We investigated aspects of the breeding biology, including the reproductive period, egg production, and heterosexual pairing of the snapping shrimp *Alpheus estuariensis* Christoffersen, 1984 in Pontal Bay, municipality of Ilhéus, state of Bahia, northeastern Brazil. Samples were taken monthly during spring low tides from September 2011 to October 2012, on mud substrate in the intertidal zone. We obtained 305 females, of which 134 were ovigerous. The latter were observed in all months, with peaks in June and October 2012; this corresponded to months of higher rainfall indexes, suggesting continuous seasonal breeding. Seventy-five females had normal-appearing eggs and 59 had abnormal eggs (smaller mean size and whitish color). The abnormal eggs differed significantly in number and volume in relation to normal eggs in stage I. Eggs in three stages of embryonic development were observed, with a non-statistically significant reduction in mean fecundity between stages. Mean fecundity, calculated from females with normal eggs in stage I, was 154 ± 108.06 eggs. The mean volume of the eggs changed significantly during development, increasing 45% from stages I to III. A total of 86 male-female pairs were obtained. The sizes of paired males and females were positively correlated, although paired females were slightly larger than males. Formation of pairs begins early, when the females are smaller than the smallest ovigerous female. The mean size of male-female pairs with females carrying normal eggs was significantly larger than the size of male-female pairs with females carrying abnormal eggs. Based on the results provided here, the possible mating system of *A. estuariensis* is discussed.

KEY WORDS: abnormal eggs, Crustacea, Decapoda, estuarine fauna, reproductive biology

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INTRODUCTION

Alpheidae comprises a rich and diverse group of shrimp that inhabit a wide variety of microhabitats (Anker et al., 2006). These shrimps are usually found in shallow coastal environments of tropical and subtropical regions. The alpheids are among the most frequently encountered shrimps and are often dominant, in numbers of both individuals and species, compared to other marine decapods (with the exception of brachyuran crabs), on both soft and hard bottoms (Anker et al., 2006). Alpheids often live in mutualistic and commensal associations with other organisms such as sponges, anemones, corals, other decapods (including other alpheids), and fish of the family Gobiidae (Boltaña and Thiel, 2001; Bauer, 2004; Anker et al., 2006).

Another peculiarity of many species of this family is the formation of monogamous pairs, which share and maintain the same microhabitat (refuge or host) (Mathews, 2002a, b; Correa and Thiel, 2003). In this mating system, heterosexual pairs share a microhabitat for a period longer than their

reproductive cycles, and usually copulate only with this one partner (Correa and Thiel, 2003).

Within Alpheidae, the genus *Alpheus* Fabricius, 1798 is the most speciose with 296 described species and a species richness estimated as more than 400 (Anker et al., 2006; De Grave and Franssen, 2011; Soledade and Almeida, 2013). In contrast to the extensive knowledge of the taxonomy and diversity of *Alpheus*, studies focusing on reproductive aspects are few. The fecundity of *A. armillatus* H. Milne Edwards, 1837, *A. normanni* Kingsley, 1878, *A. heterochaelis* Say, 1818, and *A. websteri* Kingsley, 1880 (studied by Corey and Reid, 1991, as *A. ridleyi* Pocock, 1890, from Florida, USA). Fernández-Muñoz and García-Raso (1987) studied the distribution, abundance and reproductive biology of *A. dentipes* Guérin, 1832 from the southern coast of Spain; and Harikrishnan et al. (2010) studied some aspects of the population biology of *A. euphrosyne euphrosyne* de Man, 1887 from the Cochin River estuary, India. In Brazil, studies on reproductive biology have been conducted with only two species, both from the

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coast of São Paulo, southeastern Brazil. Mossolin et al. (2006) studied the population biology of *A. carlae* Anker, 2012 (as *A. armillatus*) including the sex ratio, larval release and recruitment periods, growth, and life span. Pavanelli et al. (2008, 2010) compared seasonal egg production in *A. carlae* (also as *A. armillatus*) and *A. nuttingi* (Schmitt, 1924), respectively.

Alpheus estuariensis Christoffersen, 1984 is a burrowing western Atlantic species, commonly found in estuarine environments, on mud, in burrows under rocks, in debris, among herbaceous vegetation and roots of *Rhizophora mangle*, and in rotting wood, from the intertidal zone to 22 m depth (Christoffersen, 1984; Almeida et al., 2012). The distribution of this shrimp ranges from the eastern coast of Florida to Santa Catarina, southern Brazil (Almeida and Mantelatto, 2013).

Although *A. estuariensis* is abundant in some areas, information on its biology and ecology is extremely sparse. The species has been treated in faunal surveys (e.g., Martínez-Iglesias et al., 1997; Almeida et al., 2012), and in studies of taxonomy and systematics (Christoffersen, 1984; McClure and Wicksten, 1997; Almeida and Mantelatto, 2013), genetics (Williams et al., 2001; Hurt et al., 2009) and morphology and development (Pires et al., 2008; Spence and Knowlton, 2008). *Alpheus estuariensis* is one of the most common species of *Alpheus* in estuarine mud substrates along the Brazilian coast. However, the only biological study in Brazil is that of Pires et al. (2008), who described the first four zoeal stages obtained from ovigerous females from the estuary of Bragança, Pará, and compared them with the same stages of congeneric species from other geographical regions.

Considering the continuous degradation of many estuaries caused by deforestation, pollution, uncontrolled urbanization along their shores, and overfishing of economically important species (Souza et al., 2009), ecological studies of the biota are needed to generate data that can assist in developing strategies for the preservation of these ecosystems.

In this study we analyzed some aspects of the breeding biology, including the reproductive period, egg production, and heterosexual pairing in a population of *A. estuariensis* in a tropical bay in Ilhéus, state of Bahia, northeastern Brazil. Current knowledge of population aspects of species of *Alpheus* from Brazil comes from studies carried out in the state of São Paulo (Mossolin et al., 2006; Pavanelli et al., 2008, 2010), which is farther south and consequently has a cooler climate than northeastern Brazil. Studies in other areas of the species' distribution will be useful for comparison of the influence of environmental factors on population dynamics.

MATERIALS AND METHODS

Study Area

Pontal Bay ($14^{\circ}48'31.1''\text{S}$, $39^{\circ}02'08.3''\text{W}$) is an estuarine system formed by the Cachoeira, Fundão and Santana rivers, bordered by the city of Ilhéus (Fig. 1). The estuary is formed by mud areas with mangroves and sandbanks on the lower part of the alluvial terraces (Nacif et al., 2003). The bay shores are densely urbanized, and their waters are impacted by domestic sewage discharge (Almeida et al., 2006; Souza et al., 2009). The city of Ilhéus has a tropical humid and semi-humid climate, mean annual temperatures varying from 22 to 25°C, and regular and abundant rainfall that can reach up to 2700 mm per year in coastal areas (Faria-Filho and Araújo, 2003).

Sampling and Laboratory Procedures

Samples were taken on a tidal mud flat. Samplings were carried out monthly from September 2011 to October 2012 during spring low tide periods, in

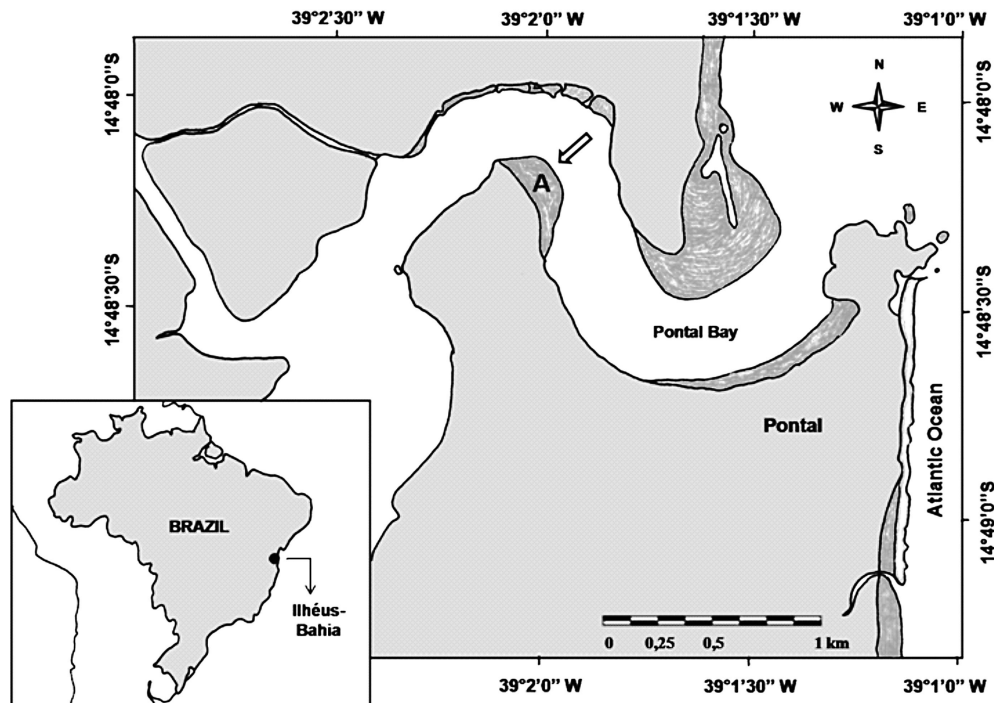


Fig. 1. *Alpheus estuariensis*. Location of the study area (A) in Pontal Bay, Ilhéus, state of Bahia, Brazil ($14^{\circ}48'31.1''\text{S}$, $39^{\circ}02'08.3''\text{W}$). Modified from Santos et al. (2010).

the intertidal zone. In October 2011 it was not possible to sample because of heavy rainfall during the spring-tide period.

In the study area, three transects 30 m long were demarcated (T1, T2 and T3), parallel to the shore and with approximately 24 m between T1 and T2 and 12 m between T2 and T3. On each transect, ten units of 1 m² were randomly selected for sampling, totaling 30 units sampled in each month.

Within the sampling units the specimens of *A. estuariensis* were captured either by hand, or by using a PVC pump 50 mm in diameter, since these shrimp live in the mud, in burrows with several openings (A. C. Costa-Souza and A. O. Almeida personal observation). The pump was used for taking cores in all visible burrow openings within the unit, taking care to separate specimens obtained from different burrows. The number of times that the pump was used on each burrow aperture was not standardized. After each core sample was taken, the sediment was sieved and the specimens obtained were placed in plastic flasks with water from the sampling site. Pairs of specimens obtained from the same burrow, presumably male-female pairs, were separated to avoid loss of information regarding paired specimens. All flasks were labeled and taken to the laboratory, where the shrimp were anesthetized on ice, fixed in 70% ethanol, and analyzed. Voucher specimens were deposited in the crustacean collection of the Universidade Estadual de Santa Cruz, Ilhéus, Bahia (UESC 1566).

Females were identified based on the absence of the *appendix masculina* on the second pleopods (vs. presence in males), or by the presence of eggs attached to the pleopods. Carapace length (CL) was measured from the tip of the rostrum to the posterior margin of the carapace to the nearest 0.01 mm, with the aid of a digital caliper and a stereomicroscope fitted with a camera lucida and ocular micrometer (used to measure specimens too small to be measured with the caliper).

Air-temperature data from Ilhéus were obtained from the web site of the Centro de Previsão de Tempo e Estudos Climáticos/Instituto Nacional de Pesquisas Espaciais – Cptec/Inpe (available online at <http://www.cptec.inpe.br/>). Rainfall data were obtained from the website of the Instituto do Meio Ambiente e Recursos Hídricos do Estado da Bahia – Inema-BA (available online at <http://monitoramento.inema.ba.gov.br/sistemas/planhas/plu/>). Salinity was measured using a portable refractometer.

Statistical Analyses

The reproductive period was determined from monthly observation of ovigerous and non-ovigerous females in the population. The distribution by size class was tested for normality by using the Kolmogorov-Smirnov test ($\alpha = 0.05$) (Zar, 1996).

The eggs of each ovigerous female were carefully removed with a brush, arranged in a Petri dish, counted, and classified in one of three stages of embryonic development, according to Mossolin et al. (2006): Early stage (I): no evidence of eyes and yolk occupying 75-100% of the egg volume; Intermediate stage (II): eyes vestigial and yolk occupying about 50-75% of the egg volume; Final stage (III): eyes well developed and yolk occupying 25-50% of the egg volume. Twenty eggs from each ovigerous female were separated, and the longest (d_1) and shortest (d_2) diameters of each eggs (both in mm) were measured with a stereomicroscope with a camera lucida, and used to calculate the mean egg volume v (in mm³): $v = (\pi/6) \times d_1^2 \times d_2$ (Bauer, 1991).

During egg staging, females were observed carrying abnormal-appearing eggs (shapeless and whitish), similar to those observed by Felder (1982) in *Synalpheus apioceros* Coutière, 1909. These eggs were also removed, counted, and measured (maximum 15 from each female) to calculate their volume. The fecundity and mean volume of these eggs were compared with those of normal eggs in stage I, using the Mann-Whitney-Wilcoxon U -test ($\alpha = 0.05$). This test was also used to compare the mean CL of females carrying abnormal eggs with those of paired females carrying normal eggs in stage I.

Spearman correlation analysis ($\alpha = 0.05$) was used to test the correlation of the size of females with fecundity and egg volume. For this analysis we used all ovigerous females with stage I eggs. The Analysis of Covariance Test (one-way ANCOVA) ($\alpha = 0.05$), with CL as co-variable, was used to assess the relationship between egg number and carapace length in each stage of embryonic development, and the Kruskal-Wallis Test and Mann-Whitney Test *a posteriori* ($\alpha = 0.05$) to compare the mean volume of eggs carried by females among the three stages. The Canonical Correspondence Analysis (CCA) was used to analyze the possible correlation between the monthly frequency of females (non-ovigerous, ovigerous, and ovigerous with abnormal eggs) and the environmental variables (rainfall, temperature, and salinity). The absolute

frequency of each female category was considered as the dependent variable, and the environmental variables were considered as independent variables. The Monte Carlo permutation test was used to evaluate the significance of correlations between the frequency distribution of the categories of females and the environmental variables.

Preliminary observations indicated that in this population, individuals of *A. estuariensis* live in male-female pairs, as observed in other populations of *Alpheus* (Mathews, 2002a, b). In order to confirm this observation, we calculated the proportion of specimens collected in pairs, i.e., extracted from the same burrow, in relation to the total population sampled. The monthly absolute frequency of pairs was also analyzed, as well as the size (CL) at which individuals begin to form pairs, if there was a correlation between size (CL) of paired males and females (Pearson's linear correlation; $\alpha = 0.05$) and if males and females differed regarding mean CL (Wilcoxon test; $\alpha = 0.05$). We also investigated if there was a difference in mean CL between pairs with a male plus ovigerous female with normal eggs, and a male plus ovigerous female with abnormal eggs (Mann-Whitney-Wilcoxon U -test, $\alpha = 0.05$), and analyzed the size-frequency distribution of these two types of pairs.

All statistical analyses were performed according to Zar (1996) and carried out with the use of Paleontological Statistics Windows software, version 2.16.

RESULTS

Environmental Conditions

The mean air temperature in Ilhéus during the sampling period was $25 \pm 2.8^\circ\text{C}$. The highest mean temperature was observed in January and February 2012 (both 27°C) and the lowest in September 2011 (22°C). The mean monthly precipitation ranged from 0.1 ± 0.2 mm in September 2012 to 13.9 ± 22.0 mm in August 2012, with well-distributed rainfall and no markedly dry periods. The mean salinity was 30.6 ± 2.3 , ranging from 24.5 in December 2011 to 34.3 in May 2012.

Breeding Biology

A total of 305 females of *A. estuariensis* (mean CL = 7.5 ± 1.4 mm, ranging from 5.9 to 13.0 mm) were collected during the sampling period. The total of 134 ovigerous females showed a mean CL = 9.0 ± 1.3 mm, ranging from 5.9 to 12.2 mm; 75 of these bore normal-appearing egg masses. The remaining 59 ovigerous females had only abnormal eggs, with no evidence of embryo development, and therefore they were not classified according to embryonic development stage. Figure 2 shows the appearance of the normal

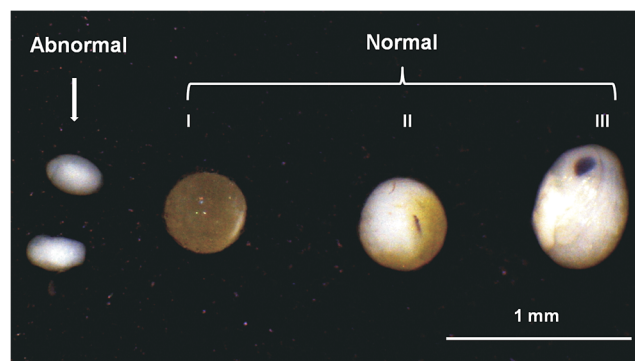


Fig. 2. *Alpheus estuariensis*. Eggs in stages I, II, and III of embryonic development and abnormal egg from ovigerous females obtained from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

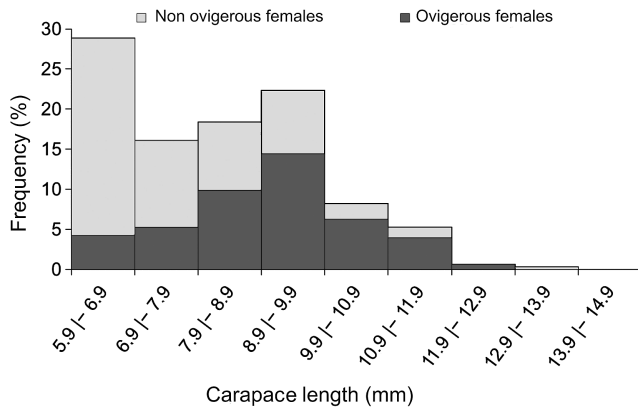


Fig. 3. *Alpheus estuariensis*. Frequency of non-ovigerous and ovigerous females ($n = 305$) by size-class from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil.

eggs in the three stages of development, and of the abnormal eggs. The frequency distribution by size class of the female population was non-normal (Kolmogorov-Smirnov $d = 0.10$; $P < 0.01$) (Fig. 3).

Ovigerous females were present in all samples (Fig. 4); their relative frequency (non-ovigerous/ovigerous females) in each month varied from 11% in September 2012 to 100% in June 2012. The proportion of ovigerous females exceeded 50% of total females in five months: September

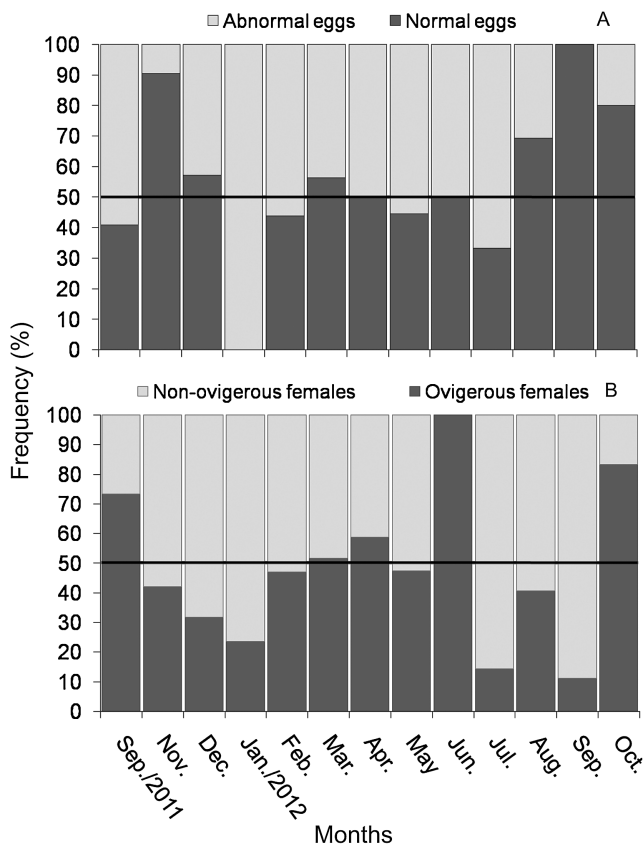


Fig. 4. *Alpheus estuariensis*. A, frequency of females with normal eggs relative to females with abnormal eggs; B, frequency of ovigerous females relative to non-ovigerous females obtained from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil.

2011 (approx. 73%), March 2012 (approx. 52%), April 2012 (approx. 59%), June 2012 (100%) and October 2012 (approx. 83%) (Fig. 4B). Females carrying abnormal eggs predominated in relation to females with normal eggs in September 2011 (approx. 59% of total ovigerous females) and in January, February, May and July 2012 (100, 56, 55 and 66% of total ovigerous females, respectively) (Fig. 4A).

The CCA indicated a positive correlation between the abundance of ovigerous females and the months with highest rainfall (June and October 2012) (Fig. 5). Non-ovigerous females were more abundant in months with the lowest rainfall and higher temperature and salinity (July and September 2012). However, the differences in mean abundance of ovigerous and non-ovigerous females were not significant ($P > 0.05$). The abundance of females carrying abnormal eggs was not correlated with any of the environmental variables.

Mean fecundity, based on ovigerous females with stage I eggs, was 154 ± 108.9 ($n = 48$), ranging from 33 (CL = 9.0 mm) to 443 (CL = 11.8 mm). The fecundity was positively correlated with female CL (Spearman correlation, $R_s = +0.67$; $P < 0.005$), i.e., the number of eggs increased proportionally with the size of the female (Fig. 6A). Females with eggs in stage I were more abundant (64%) than females carrying eggs in stages II (28%) and III (8%). The mean egg number in each stage of embryonic development was slightly different; however, this variation was not statistically significant (ANCOVA, I-II $F = 0.84$; II-III $F = 1.40$; I-III $F = 2.74$; $P = 0.14$), indicating no significant egg loss during the incubation period. The egg volume was negatively correlated with female CL (Spearman correlation, $R_s = -0.52$; $P < 0.005$) (Fig. 6B).

The mean volume of eggs was statistically different in all development stages (Kruskal-Wallis: $P < 0.005$), and also differed between stages (Mann-Whitney *a posteriori*: $P < 0.005$), increasing significantly from 0.11 mm^3 (stage I) to 0.21 mm^3 (stage III), indicating embryo development and growth (Table 1).

Females with abnormal eggs had significantly lower mean fecundity (Mann-Whitney-Wilcoxon U -test: $P < 0.001$) and egg volume (Mann-Whitney-Wilcoxon U -test: $P < 0.001$) compared to females with normal eggs in stage I. The difference in mean CL between single females carrying abnormal eggs and single females carrying normal eggs was statistically significant (Mann-Whitney-Wilcoxon U -test: $P < 0.001$).

Heterosexual Pairing

A total of 86 male-female pairs were obtained, totaling 172 specimens, which corresponded to 20% of the total sample of *A. estuariensis* (Costa-Souza et al., unpublished data). The highest frequency of sexual pairs was observed in November 2011 ($n = 14$ pairs), and August 2012 ($n = 12$ pairs), whereas in January 2012, no pairs were obtained (Fig. 7). The mean size of paired males and females was $8.2 \pm 1.3 \text{ mm}$ and $8.4 \pm 1.5 \text{ mm}$, respectively; these values were statistically different from each other (Wilcoxon test, $P = 0.034$). The CL of paired males and females was positively correlated (Pearson correlation $r = 0.81$; $P \leq 0.005$) (Fig. 8), indicating a tendency to pair formation between individuals of similar sizes (size-

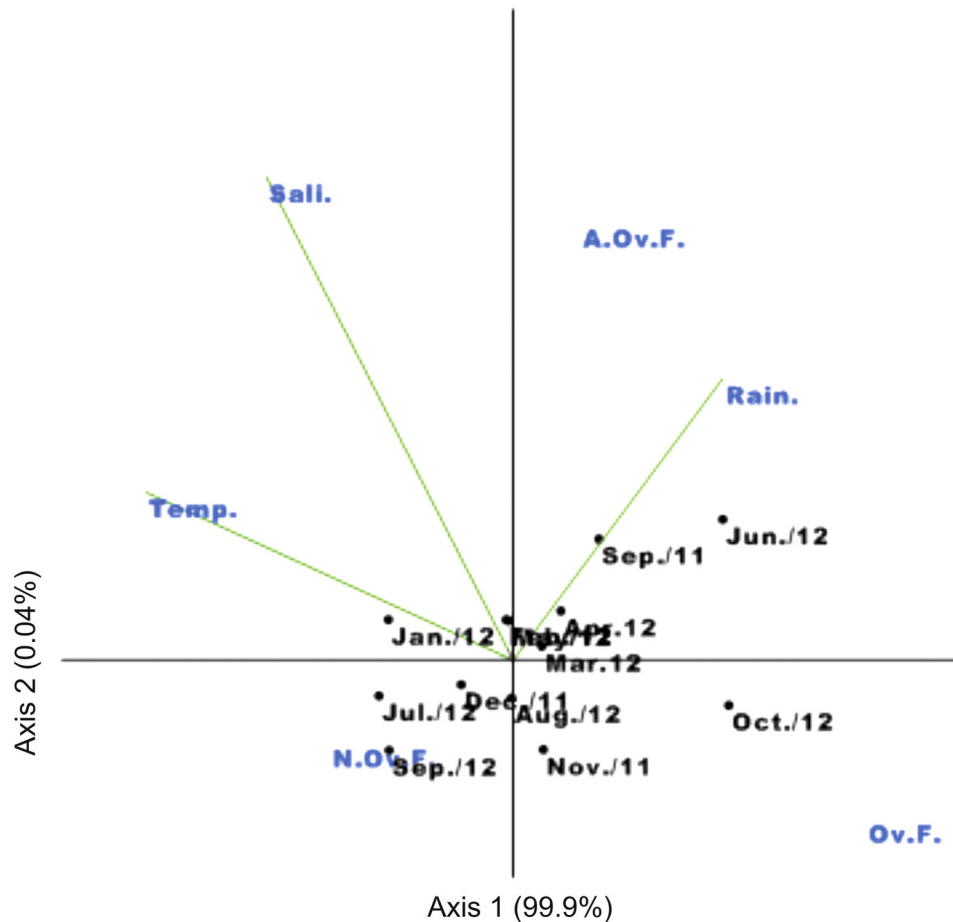


Fig. 5. *Alpheus estuariensis*. Canonical Correspondence Analysis (CCA). Abundance of ovigerous females (Ov.F.), non-ovigerous (N.Ov.F.) and ovigerous with abnormal eggs (A.Ov.F.). Environmental variables [rainfall (Rain), salinity (Salin.) and temperature (Temp.)] indicated by lines. Abundances of categories of females and environmental variables obtained from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

assortative pairing). The smallest male and female found in pairs measured 4.5 and 5.4 mm CL, respectively; and the smallest pair (mean CL) measured 4.5 mm (male) and 6.0 mm (female).

Of the 86 paired females, 45 were ovigerous (approx. 33.6% of the total of ovigerous females) and 41 non-ovigerous (approx. 13% of the total of females). The size-distribution frequency of pairs (male and female) is shown in Fig. 9. Of the total number of ovigerous females, 29 carried normal eggs and 16 abnormal eggs. The mean size of paired males and females with the female carrying normal eggs was 9.1 ± 0.8 mm (males) and 9.4 ± 1.0 mm (females). The mean size of paired males-females with the female carrying abnormal eggs was 7.9 ± 0.9 mm (males) and 8.0 ± 1.2 mm (females). Statistical analyses showed significant differences between the mean sizes of males (Mann-Whitney-Wilcoxon U -test: $P < 0.005$) and females (Mann-Whitney-Wilcoxon U -test: $P < 0.005$) in these two conditions.

DISCUSSION

Breeding Biology

Ovigerous females were observed in all sampling months. However, some monthly peaks of ovigerous females were

noted (Fig. 4B). In tropical and subtropical regions, temperature and photoperiod generally show little diurnal or annual variation and food resources may be constantly available (Sastry, 1983). These conditions enable crustaceans to reproduce continuously. Reproduction is termed continuous when the frequency of ovigerous females is similar throughout the year, and seasonal-continuous if there are monthly peaks of ovigerous females (Pinheiro and Fransozo, 2002; Terossi and Mantelatto, 2010). Thus, *A. estuariensis* in the study area showed seasonal continuous reproduction. The same type of reproduction was observed in the population of *A. nuttingi* from São Paulo, southeastern Brazil (Pavanelli et al., 2010), which is a transition zone between tropical and subtropical areas. On the other hand, in the same locality where the study of Pavanelli et al. (2010) took place, ovigerous females of *A. carlae* (as *A. armillatus*) showed a continuous reproductive pattern (Mossolin et al., 2006).

Monthly peaks of ovigerous females are, in general, related to changes in certain environmental variables such as rainfall and temperature (Sastry, 1983; Mossolin et al., 2006; Pavanelli et al., 2010; Harikrishnan et al., 2010). In the study area in northeastern Brazil, temperature variations are minimal with a humid and semi-humid climate and regular

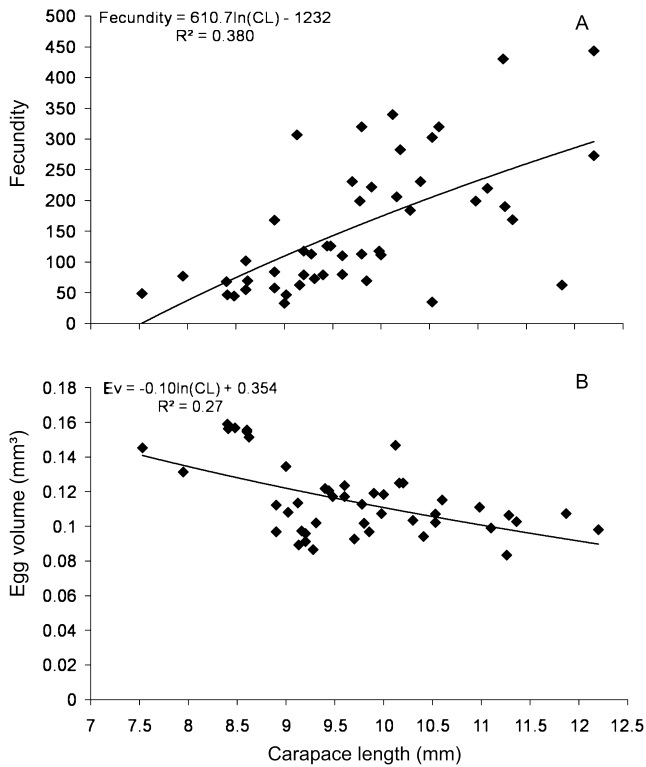


Fig. 6. *Alpheus estuariensis*. A, correlation between carapace length (CL mm) and fecundity of ovigerous females with eggs in stage I of embryonic development; B, correlation between carapace length (CL mm) and egg volume (mm^3) obtained from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil.

rainfall distribution throughout the year (Faria-Filho and Araújo, 2003). In the case of *A. estuariensis*, the existence of periods of higher frequency of ovigerous females was correlated only with variations in rainfall, mainly in June and October 2012 when the rainfall increased. The frequency of ovigerous females of *A. nuttingi* and *A. e. euphrosyne* from the Cochin River (India), was also influenced by rainfall (Pavanelli et al., 2010; Harikrishnan et al., 2010). Ovigerous females of *A. nuttingi* were more abundant in the rainy period in São Paulo (Pavanelli et al., 2010). On the other hand, in the population of *A. e. euphrosyne* the occurrence of ovigerous females was restricted to months before and after the monsoon rains, which directly influence the salinity, temperature and nutrient flow in estuaries where the species occurs (Hariskrishnan et al., 2010).

Fecundity varies widely among species of *Alpheus* that have been studied (see Table 2). In *A. estuariensis* the fecundity varied considerably (33–443 eggs). However, the mean fecundity (154.4 ± 108.9 eggs) and the mean size of ovigerous females (8.9 ± 1.3 mm CL) can be considered low compared to congeners such as *A. normanni* and *A. armillatus*, whose females had a smaller mean CL (5.99 and 7.98 mm, respectively) and higher mean fecundity (328.2 and 279.8 eggs, respectively) (Corey and Reid, 1991). Many extrinsic and intrinsic factors can influence egg production directly and indirectly, such as the latitudinal variation, temperature, salinity, amount of nutrients in the environment, pollution, incidence of parasites, and genetics (Sastry, 1983; Lardies and Werthmann, 2001; Lardies et al., 2008; Hernández et al., 2009; Pavanelli et al., 2010; Werthmann et al., 2011). In *A. estuariensis*, latitude apparently does not influence the fecundity, since at low latitudes a higher fecundity is expected (Lardies and Werthmann, 2001; Lardies et al., 2008). In tropical regions the energy investment in egg production tends to be lower, reducing the fecundity per spawning (Diaz, 1980; Jones and Simons, 1983). However, this might be counterbalanced by females reproducing throughout the year (as observed for *A. estuariensis*).

We observed a positive correlation between fecundity and size of females in *A. estuariensis*, as also observed in other populations of *Alpheus* (Fernández-Muñoz and García-Raso, 1987; Bauer, 1991; Corey and Reid, 1991; Pavanelli et al., 2008, 2010; Harikrishnan et al., 2010). Therefore, size is also an important factor influencing egg production (Corey and Reid, 1991; Bauer, 2004). In caridean shrimps, eggs are carried below the pleon in a cavity delimited laterally by the first to third pleura, which widens as the female increases in size (Bauer, 2004). The larger the female, the larger the space available and consequently the larger the number of eggs that can be carried (Corey and Reid, 1991; Clarke, 1993; Bauer, 2004).

In the course of embryonic development in *A. estuariensis*, we observed a slight decrease in the mean number of eggs. However, this difference was not statistically significant, similarly to the observations by Pavanelli et al. (2008, 2010) in populations of *A. carlae* (as *A. armillatus*) and *A. nuttingi*, respectively. These authors suggested that the smaller egg loss in *A. carlae* and *A. nuttingi* during embryonic development is possibly due to a larger pleonal space of the females of these species, to the cryptic habits of these species (sheltered under rocks, i.e., less exposed), and to het-

Table 1. *Alpheus estuariensis*. Mean fecundity, mean egg volume (mm^3) and increase in egg volume between three stages of egg development, and abnormal eggs from females obtained from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil. Letters a, b and c indicate significantly different mean values.

Stage	Fecundity		Egg volume (mm^3)		Increase (%)
	N	Mean \pm SD	N	Mean \pm SD	
Normal					
I	48	154.40 ± 108.96 a	960	0.11 ± 0.03 a	13.6 (I-II)
II	21	153.2 ± 75.52 a	420	0.14 ± 0.05 b	31.8 (II-III)
III	6	123.82 ± 81.32 a	120	0.21 ± 0.06 c	45.4 (I-III)
Abnormal	59	18.60 ± 14.93	571	0.0094 ± 0.0061	–

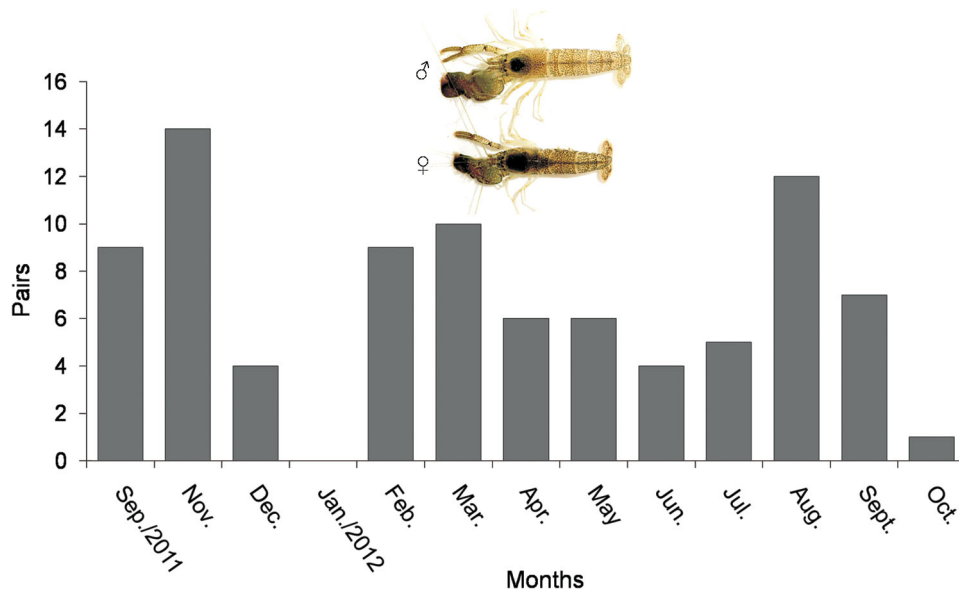


Fig. 7. *Alpheus estuariensis*. Monthly frequency of male-female pairs obtained from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

erosexual pairing (efficient protection of refuges and females by males).

We did not obtain data on the width of the pleonal pleura in *A. estuariensis*, and therefore cannot state that the female pleonal space is adequate for the number of eggs carried in all stages of embryo development. However, this species inhabits burrows in mud substrate (Christoffersen, 1984; Almeida et al., 2012), which reduces exposure and therefore can provide more protection to the ovigerous females. Some ovigerous females were observed in heterosexual pairings, and this behavior might have contributed to reducing egg loss between stages, as suggested by Pavanelli et al. (2008, 2010).

The mean egg volume in *A. estuariensis* increased considerably, about 45% from stages I to III, as observed in several caridean shrimps (Corey and Reid, 1991; Mossolin et al., 2006; Pavanelli et al., 2008, 2010; Terossi et al., 2010;

Tamburus et al., 2012). This increase is mainly due to incorporation of water by osmosis across the plasmatic membrane of the egg and to the lipid content (Wehrtmann and Graeve, 1998; Lardies and Wehrtmann, 2001). Pavanelli et al. (2008, 2010) observed an increase of 64.3% and 87.4% from stages I to III in *A. carlae* and *A. nuttingi*, respectively, and Harikrishnan et al. (2010) found an increase of 159% from stage I to V in *A. e. euphorysyne*. Despite the significant increase in egg volume observed in *A. estuariensis*, it is low compared to other species of *Alpheus*. In estuarine species such as *A. estuariensis*, the increase in volume was expected to be higher, due to the effect of salinity on osmolality (Giménez and Anger, 2001). However, there are no comparative studies on the effect of osmolality on egg production in marine or estuarine species of *Alpheus* that might help in understanding these differences between different populations of the same species and between species.

Many of the ovigerous females of *A. estuariensis* carried only abnormal-appearing eggs. This type of egg has been observed in other alpheids, and factors such as female infertility due to external parasites, female immaturity, and also adaptive adjustment of the species to the environment have been invoked to explain their production (Coutière, 1909; Chace, 1972; Felder, 1982; Sastry, 1983; Fernández-Muñoz and García-Raso, 1987). No ectoparasites were observed in the females of *A. estuariensis* analyzed. Females that were much larger than the smallest ovigerous females (5.9 mm) and females forming sexual pairs also produced this type of egg. However, as single females carrying abnormal eggs averaged significantly smaller than single females carrying normal eggs, they might be first-spawning females.

Comparing the mean fecundity of females carrying eggs in stage I with those carrying abnormal eggs, the latter had a significantly lower fecundity and mean egg volume (Table 1). Therefore these eggs may be infertile, since

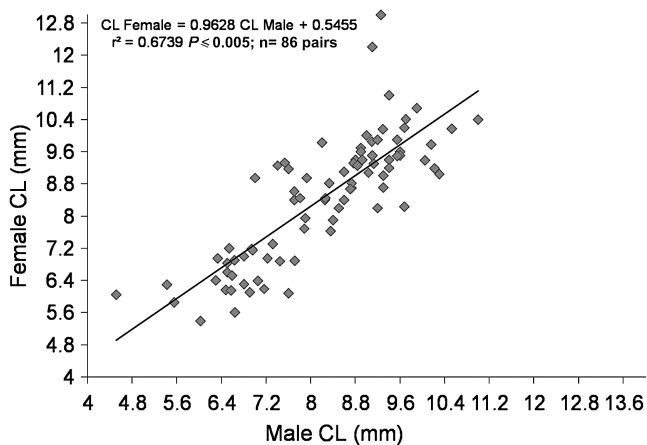


Fig. 8. *Alpheus estuariensis*. Correlation between carapace length (CL mm) of paired males and females obtained from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil.

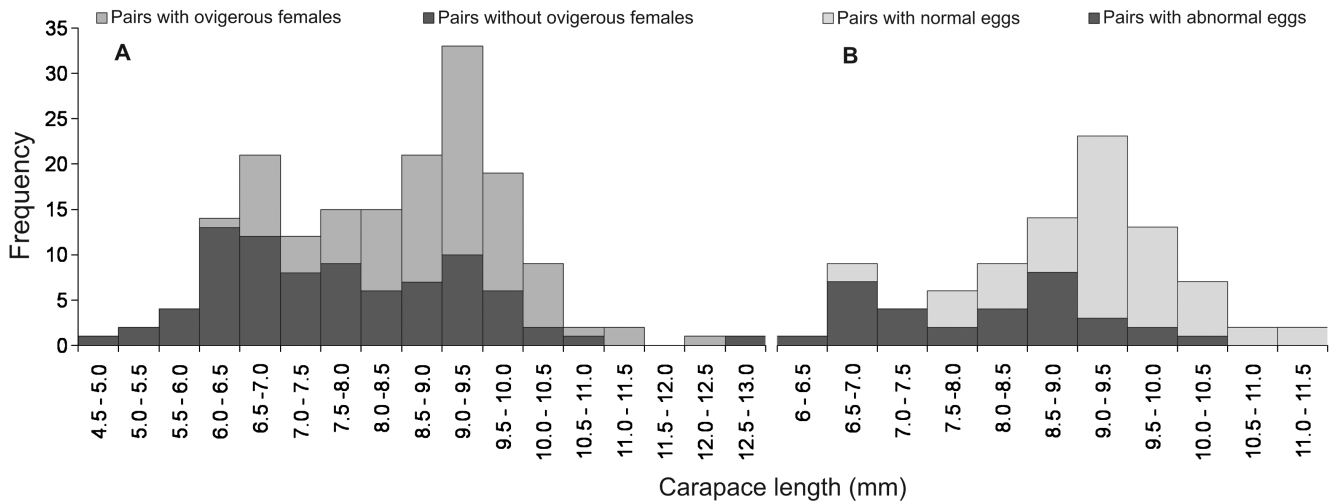


Fig. 9. *Alpheus estuariensis*. A, absolute frequency of pairs (male-female) with ovigerous females and non-ovigerous females by size-classes; B, absolute frequency of pairs (male-female) with females carrying abnormal eggs and pairs with females carrying normal eggs by size-classes obtained from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil.

normally developing eggs increase in volume (Felder, 1982; Sastry, 1983).

Heterosexual Pairing

Some specimens of *A. estuariensis* were found in male-female pairs, as observed in other species of *Alpheus* (Nolan and Salmon, 1970; Knowlton, 1980; Boltaña and Thiel, 2001; Mathews, 2002a, b; Correa and Thiel, 2003; Rahman et al., 2003; Mossolin et al., 2006; Harikrishnan et al., 2010). If individuals occur in their refuges or hosts as heterosexual pairs more frequently than expected by chance alone, that could indicate monogamy (Baeza, 1999; Baeza et al., 2011), a common mating system in Alpheidae (Mathews, 2002b; Correa and Thiel, 2003). However, paired individuals corresponded to only 20% of the total sample of *A. estuariensis* (Costa-Souza et al., unpublished data). This low percentage of paired specimens does not support the existence of monogamy in *A. estuariensis*.

Digging or using grabs and corers are the only methods for quantitatively sampling benthic invertebrates (Ausden

and Drake, 2006); the only viable method for sampling in the study area was taking cores with a suction pump. Large-sized members of the macrofauna may move rapidly deep into their burrows when they detect disturbances at the surface (Hines and Comtois, 1985; Ausden and Drake, 2006), affecting the sampling. This may explain why mostly single males or females were obtained. Alternatively, paired specimens in a single burrow system may locate in different parts of the burrows because they have different functions (Correa and Thiel, 2003; Bauer, 2004), resulting in the collection of only one specimen at the time of sampling.

The mean size of paired females of *A. estuariensis* was slightly larger than that of males. In male-female pairs of *A. inca* Wicksten and Méndez, 1981, *A. carlae* (as *A. armillatus*) and *A. normanni*, the size of the male was similar to or slightly smaller than the female (Nolan and Salmon, 1970; Boltaña and Thiel, 2001; Mossolin et al., 2006). For *A. heterochaelis*, Nolan and Salmon (1970) observed that males were slightly smaller than females, whereas Rahman et al. (2003) found females paired with similarly or larger-sized

Table 2. Size (CL), fecundity and egg volume of females of *Alpheus* (CL = carapace length in mm; FEC = Fecundity; EV = egg volume). An asterisk (*) indicates data obtained from eggs in early stage of development. Adapted from Pavanelli et al. (2008).

Species	N	CL		FEC		EV* (mm ³)	Locality	Reference
		Min.	Max.	Min.	Max.			
<i>Alpheus dentipes</i>	–	–	–	–	836	–	Málaga, Spain	Fernández-Muñoz and García-Raso (1987)
<i>Alpheus normanni</i>	7	4.1	7.4	68	584	0.09	Puerto Rico	Bauer (1991)
<i>Alpheus armillatus</i>	4	7.4	8.8	146	504	0.18	Florida, USA	Corey and Reid (1991)
<i>Alpheus heterochaelis</i>	5	10	13.4	133	336	0.91	Florida, USA	Corey and Reid (1991)
<i>Alpheus normanni</i>	5	10	17.4	–	–	–	Florida, USA	Corey and Reid (1991)
<i>Alpheus saxidomus</i>	35	–	–	–	–	0.03	Costa Rica, Pacific side	Wehrtmann and Graeve (1998)
<i>Alpheus carlae</i> (as <i>A. armillatus</i>)	31	7.7	14.1	42	1979	0.1	São Paulo, Brazil	Pavanelli et al. (2008)
<i>Alpheus nuttingi</i>	27	11	18.6	949	4222	0.09	São Paulo, Brazil	Pavanelli et al. (2010)
<i>Alpheus e. euphrosyne</i>	41	11	19.2	141	1553	0.004	Cochin, India	Harikrishnan et al. (2010)
<i>Alpheus estuariensis</i>	46	7.5	12.2	33	443	0.11	Bahia, Brazil	This study

males. Nolan and Salmon (1970) suggested that females form pairs with males of similar or slightly smaller size as a consequence of the agonistic behavior that occurs in the beginning of pairing behavior. Larger females remained until the end of the pairing interaction, whereas smaller females moved away at the beginning of the interaction to protect themselves. Rahman et al. (2003) observed that females that paired with larger males were expelled less frequently from the refuge and were more protected during conflicts between their paired male and an intruder male.

The existence of size-assortative pairing in *A. estuariensis* indicates the existence of monogamy (Baeza, 1999; Baeza et al., 2011, 2013). A similar trend was observed in monogamous populations of *A. armatus* from Jamaica, *A. inca* from Chile and *A. heterochaelis* from the USA (Nolan and Salmon, 1970; Knowlton, 1980; Boltaña and Thiel, 2001). Moreover, 52% of the paired females were ovigerous (carrying normal or abnormal eggs), most of them carrying eggs in stage I. This indicates that males might establish pairs with females, regardless of their reproductive state, i.e., brooding or non-brooding, which also suggests that this species has a monogamous mating system (Baeza, 1999; Baeza et al., 2011, 2013).

We observed pairs with both male and female slightly smaller than the smallest ovigerous females (5.9 mm) (Fig. 9A). In most crustaceans, including caridean shrimps, young females become receptive to males just before (pre-molt stage) or after the puberty molt, making them physiologically mature and morphologically able to carry the egg mass (Sastry, 1983; Bauer, 2004). Small, paired females of *A. estuariensis* might be close to the puberty molt, since their size is close to the smallest ovigerous female. On the other hand, the pairing behavior of small males might indicate that they are sexually mature (Knowlton, 1980).

Sixteen of the 86 paired females of *A. estuariensis* were carrying abnormal eggs. The mean size of these pairs (including males and females) was statistically lower than that of the pairs with females carrying normal eggs. Correa et al. (2000) analyzed the mating behavior and success in fertilizing females of three ontogenetic stages of males of the caridean *Rhynchocinetes typus* H. Milne Edwards, 1837. These authors observed that less-developed male morphotypes failed to fertilize females, but those in the last ontogenetic stage succeeded. Correa et al. (2000) argued that less-developed male morphotypes are less experienced in transferring the spermatophore, failing to release it at the proper time and positioning it incorrectly on the female pleon. As the spermatozoa within the spermatophores are instantly activated by contact with water, the release of spermatophores before or after the proper time may result in loss of sperm and consequently non-fertilization of eggs (Dupré and Schaaf, 1996). It is possible that the abnormal eggs in *A. estuariensis* were produced by “less experienced” male shrimp (based on their small size) paired with “young ovigerous females,” i.e., first-oviposition females, as in *A. dentipes* (cf. Fernández-Muñoz and García-Raso, 1987).

Finally, this study provided basic information that could be used for developing future research on alpheidids, particularly with respect to their reproductive biology and mating system. Little information is available on the population bi-

ology of decapod crustaceans in northern and northeastern Brazil, and this is the first study on the breeding biology of alpheidids in this area and the first on *A. estuariensis*. This contribution will provide the basis for future comparative studies with populations at other latitudes along the species' distribution.

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