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Populational Evidence Supports a Monogomous Mating System in Five Species of Snapping Shrimps of the Genus *Alpheus* (Caridea: Alpheidae)

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The objective of this study was to verify if populations of the snapping shrimps *Alpheus angulosus*, *A. bouvieri*, *A. carlae*, *A. estuariensis* and *A. nuttingi* from Pernambuco, northeastern Brazil, are monogamous based on population data. If these species are monogamous, then the populations must exhibit: 1) higher frequency of individuals living in pairs; 2) non-random population distribution, *i.e.*, pairs are found more often than expected by chance alone; 3) males paired with females regardless of their reproductive condition; 4) sexual dimorphism regarding body size and chelipeds weaponry little pronounced among paired individuals and 5) size-assortative pairing. Our samplings were carried out in August 2015, February and August 2016 and February 2017, in the intertidal zone, during low spring tides. We captured a total of 2,276 specimens: 300 of *A. angulosus*, 393 of *A. bouvieri*, 374 of *A. carlae*, 403 of *A. nuttingi* and 806 of *A. estuariensis*. The key population parameters (indicators 1, 2, 3, 4, 5 above) for the four species strongly suggest that all four undergo monogomous mating. Although our frequency distribution demonstrated a higher tendency to find solitary individuals in *A. nuttingi* and *A. estuariensis*, the other studied features agree with the occurrence of monogamy in those populations. Lastly, the sexual differences observed in the chelipeds and the existence of solitary egg-carrying females indicated that monogamy in the five species is not rigid, *i.e.*, heterosexual pairing may not last long, due to possible competition between males for females or refuge.

Key words: Crustacea, Decapoda, Mating system, Populational structure, Intertidal.

BACKGROUND

In crustaceans, monogamy (also referred to as social monogamy) is defined as a mating system wherein two adult individuals (gonochoristic or hermaphroditic) associate not only for reproduction, but to share and protect their refuge for an indefinite period exceeding one reproductive event (Correa and Thiel 2003; Baeza 2010). However, recognizing if a species/population is monogamous and estimating the longevity of the pairing may be difficult. The ideal would be observing the behavior of individuals *in situ* throughout the life cycle. In many cases, mainly in species of cryptic habits, this analysis is not feasible.

Some population studies on decapod crustaceans accepted/rejected the existence of monogamy based on populational data such as: observed frequency of individuals living solitarily, in pairs and or in aggregations; the sex of paired individuals; the frequency of pairs formed by breeding and non-breeding

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females in each stage of embryonic development; the existence of sexual dimorphism and the existence of association or symbiosis with other organisms (Baeza 2008 2010; Baeza et al. 2011 2016; Pescinelli et al. 2017; Barroso et al. 2018).

According to those studies, monogamous populations present higher frequency of individuals living in pairs; non-random population distribution (pairs are found more often than expected by chance alone); males paired with females regardless of their reproductive condition, *i.e.*, with non-breeding females and breeding at different stages of embryonic development; size-assortative pairing and sexual dimorphism regarding body size and cheliped weaponry absent or not pronounced (Baeza 2008; Baeza et al. 2011 2016). All these population characteristics may have been evolutionarily shaped in symbiotic species that reside almost all their lives inside the body of small and little abundant host species, and when these refuges are scarce and predation risk away from refuges is high (Thiel and Baeza 2001; Baeza and Thiel 2007; Baeza et al. 2016).

Monogamy is a widespread phenomenon in caridean shrimps (Correa and Thiel 2003; Chak et al. 2015; Pescinelli et al. 2017). Currently, monogamous or supposedly monogamous carideans are distributed among the families Hippolytidae, Lysmatidae, Palaemonidae (including Gnathophyliidae) and Alpheidae (Correa and Thiel 2003). A high number of alpheid populations have been reported to be monogamous or possibly monogamous, *e.g.*, *Alpheopsis chilensis* Coutière, 1896 (Chile), *Alpheus angulosus* McClure, 2002 (USA and Brazil), *A. armatus* Rathbun, 1901 (Jamaica), *A. bellulus* Miya & Miyake, 1969 (Japan), *A. brasileiro* Anker, 2012 (Brazil), *A. buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013 (Brazil), *A. carlae* Anker, 2012 (Brazil), *A. estuariensis* Christoffersen, 1984 (Brazil), *A. heterochaelis* Say, 1818 (USA), *A. idiocheles* Coutière, 1905 (Micronesia), *A. inca* Wicksten & Méndez, 1981 (Chile), *A. lobidens* De Haan, 1849 (Iran), *A. normanni* Kingsley, 1878 (USA) and *Synalpheus stimpsonii* (De Man, 1888) (Papua New Guinea) (Nolan and Salmon 1970; Knowlton 1980; Yanagisawa 1984; Kropp 1987; Boltaña and Thiel 2001; Mathews 2002a; Rahman et al. 2002 2003 2004; Atkinson et al. 2003; Costa-Souza et al. 2014; Dabbagh et al. 2012; Pescinelli et al. 2017; Soledade et al. 2018). However, few alpheid populations, mostly of the genus *Alpheus* Fabricius, 1798, have had their mating systems evaluated based on behavioral and/or populational studies.

Behavioral studies *ex-situ* with some species of *Alpheus*, including those considered monogamous, demonstrated that individuals naturally form pairs (male and female), protect their refuge from conspecific intruders and cooperate in refuge maintenance (Nolan and Salmon 1970; Yanagisawa 1984; Mathews 2002a; Dabbagh et al. 2012), indicating that pairing behavior does not only benefit reproduction. These behavioral aspects influence the population structure, making it possible to identify evidence of monogamy based on the analysis of the population characteristics (see Baeza 2008; Baeza et al. 2011 2016; Pescinelli et al. 2017).

With more than 300 described species, the snapping shrimps of the genus *Alpheus* are the most diverse of the family Alpheidae (De Grave and Fransen 2011; Almeida et al. 2014). These shrimps are mainly distributed in the intertidal and shallow subtidal zones in hard and soft bottoms of marine and estuarine areas, in tropical and subtropical regions (Soledade and Almeida 2013). Populations of some species are abundant, being easily observed and collected, enabling population studies to be performed. In spite of the genus wide diversity and abundance of some populations, few studies have investigated the mating system of *Alpheus* shrimps.

Based on an analysis of some aspects of the population structure, we tested the occurrence of monogamy in five species of *Alpheus* from northeastern Brazil: *A. angulosus*, *A. bouvieri*, A. Milne-Edwards, 1878, *A. carlae*, *A. estuariensis* and *A. nuttingi* (Schmitt, 1924). The target species are widely distributed in the Western Atlantic. The four former species are commonly found under rocks in the intertidal zone whereas *A. estuariensis* is found in burrows on muddy bottoms in estuarine environments (Christoffersen 1984; Anker et al. 2007 2009; Almeida and Mantelatto 2013; Almeida et al. 2012; Anker 2012). The main indicators of monogamy evaluated in those species were: (1) the frequency of individuals living solitarily, in pairs or in larger groups; (2) the pattern of population distribution (non-random or random); (3) the frequency of pairs with breeding and non-breeding females and the stage of embryonic development in paired breeding females; (4) the sexual dimorphism among paired individuals and (5) the existence of size assortative-pairing.

MATERIALS AND METHODS

Study area and Sampling design

Alpheus angulosus, *A. bouvieri*, *A. carlae* and *A. nuttingi* were collected at Praia do Paraíso (8°21'29.1"S 34°57'00.0"W), Municipality Cabo de Santo Agostinho, Pernambuco, northeastern Brazil. *Alpheus estuariensis* was collected in the estuary of the Paripe River, Municipality of Ilha de Itamaracá, Pernambuco

(7°48'38.0"S 34°51'22.1"W). Samplings were carried out in both localities in August 2015, February and August 2016, and February 2017.

Each study site was sampled during low tide for 4 hours per day, with four people collecting at the same time. Specimens of *A. angulosus*, *A. bouvieri*, *A. carlae* and *A. nuttingi* were collected from refuges (= spaces underneath boulder is a rock fragment with size larger than 25.6 cm) by hand or using small hand-fishing nets. Immediately after capture, all individuals collected were placed separately (solitaries, in pairs, trios, etc.) in the plastic bag filled with water from the locality and transported to the laboratory. In the laboratory, all shrimps were kept frozen for further analysis. *Alpheus estuariensis* were captured from within the burrows (= refuges) that they construct in mudflats using a yabby pump (diameter = 50 mm, length = 70 cm). Each burrow was pumped up a total of five times to ensure that all shrimps present in each burrow were captured and to standardize sampling effort per refuge. Pumped sediment from each burrow was sieved using a 1.8 mm fine mesh sieve and all shrimps separated from the sand grains were placed into individual plastic bags for transportation to the laboratory. For all species, the number of shrimps per burrow was recorded during sampling. The samplings complied with current applicable federal law of Brazil (Authorization ICMBio – SISBIO number 24408-1 to AOA).

Laboratory procedures

For each studied species, the sex of each shrimp was determined based on the presence (in males) or absence (in females) of *appendices masculina* on the endopod of the second pair of pleopods as well as the presence (in females) or absence (in males) of eggs underneath the pleon (Bauer 2004). Each shrimp was photographed under a stereomicroscope and the software ImageJ 1.45s (Rasband 2006) was used to measure (precision = 0.01 mm) the following body parts: carapace length (CL), propodus length (PL), height (PH), and width (PW) of the major cheliped, and sternite width (SW) and pleura width (PlW) of the second pleonal segment (Fig. 1).

In the case of breeding females, egg masses underneath the pleon were classified according to their embryo developmental stage following Wehrtmann (1990): Early stage (I) = embryos with no evidence of eyes and yolk occupying 75–100% of embryo volume; intermediate stage (II) = embryos with small and elongated eyes, and yolk occupying about 50–75% of embryo volume; late stage (III) = embryos with well-developed eyes and yolk occupying 25–50% of embryo volume. Some females carried apparently infertilized eggs (whitish, small in size), not classifiable, as described by Costa-Souza et al. (2014). Females carrying 1–10 eggs underneath the pleon were considered to have recently hatched their larvae.

Mating system evaluation

Frequency of individuals living solitarily, in pairs or in larger groups (Indicator 1) and the pattern of population distribution (Indicator 2)

We explored whether or not the different populations of *Alpheus* collected are monogamous. For this purpose, we first examined whether or not the distribution (*i.e.*, the frequency of occurrence of refuges with different numbers of shrimps) of the five species differed from a random distribution. We compared the observed distribution (*i.e.*, frequency of occurrence of refuges with one, two, three or more shrimps) with the Poisson distribution (Elliot 1983) using a Chi-square test of goodness of fit (Sokal and Rohlf 1981). The Poisson distribution describes random occurrences when the probability that an event will occur (*i.e.*, presence of a shrimp individual on a refuge) is low (as in this study). If significant differences between expected Poisson and observed distribution were observed, specific frequencies between the observed and expected distributions were compared by subdivision of the Chi-square test and using the sequential Bonferroni correction to adjust probability (p) values, avoiding erros when conducting multiple statistical tests (Zar 1999).

To determine whether the sexes were randomly distributed, the observed distribution was compared with a random distribution of the sexes, the observed distribution was compared with the binomial calculated based on the proportion of males and females recorded in the population for each studied species of shrimp. A Chi-square test of goodness of fit was used to inspect for significant differences between observed and expected (binomial) distributions (Sokal and Rohlf 1981).

Female reproductive condition (Indicator 3)

We observed the frequency of breeding and non-breeding females among solitary and paired individuals. A Chi-square test of goodness of fit was used to inspect for significant differences. Additionally, the frequency of paired breeding females carrying eggs in stage I, II and III was analyzed. The differences were verified using Chi-square Test of Independence.

Sexual dimorphism among paired individuals (Indicator 4)

We tested whether or not the different studied species of shrimps exhibited sexual dimorphism in CL, PL, PH, PW, SW and PlW. The mean values of each variable were compared using Student's paired *t*-Test. Assumptions of normality and homogeneity of variances were evaluated using the Kolmogorov–Smirnov and Levene tests, respectively, and found to be satisfactory before conducting the *t*-test. We explored the relationship between PL and body size of shrimps (CL) using the allometric model $y = ax^b$ (Hartnoll 1978 1982). The slope b of the log-log least-squares linear regression represents the rate of exponential increase $(b > 1)$ or decrease $(b < 1)$ of the claw with a unit of increase in body size of shrimps. To determine if the relationship deviates from linearity, a *t*-test was used to test if the estimated slope b deviates from the expected slope of unity (Sokal and Rohlf 1981). If, *e.g.*, the cheliped grows more or less than proportionally with a unit increase in body size of shrimps, then the slope should be greater or smaller than the unity, respectively (Hartnoll 1978). Lastly, differences in the size and growth rate (slope b) of the major cheliped between the sexes were determined using an analysis of covariance (ANCOVA).

Existence of size assortative-pairing (Indicator 5)

Finally, the existence of a correlation (CL) for evaluating the occurrence of size-assortative pairing between males and females was verified using Pearson's linear correlation.

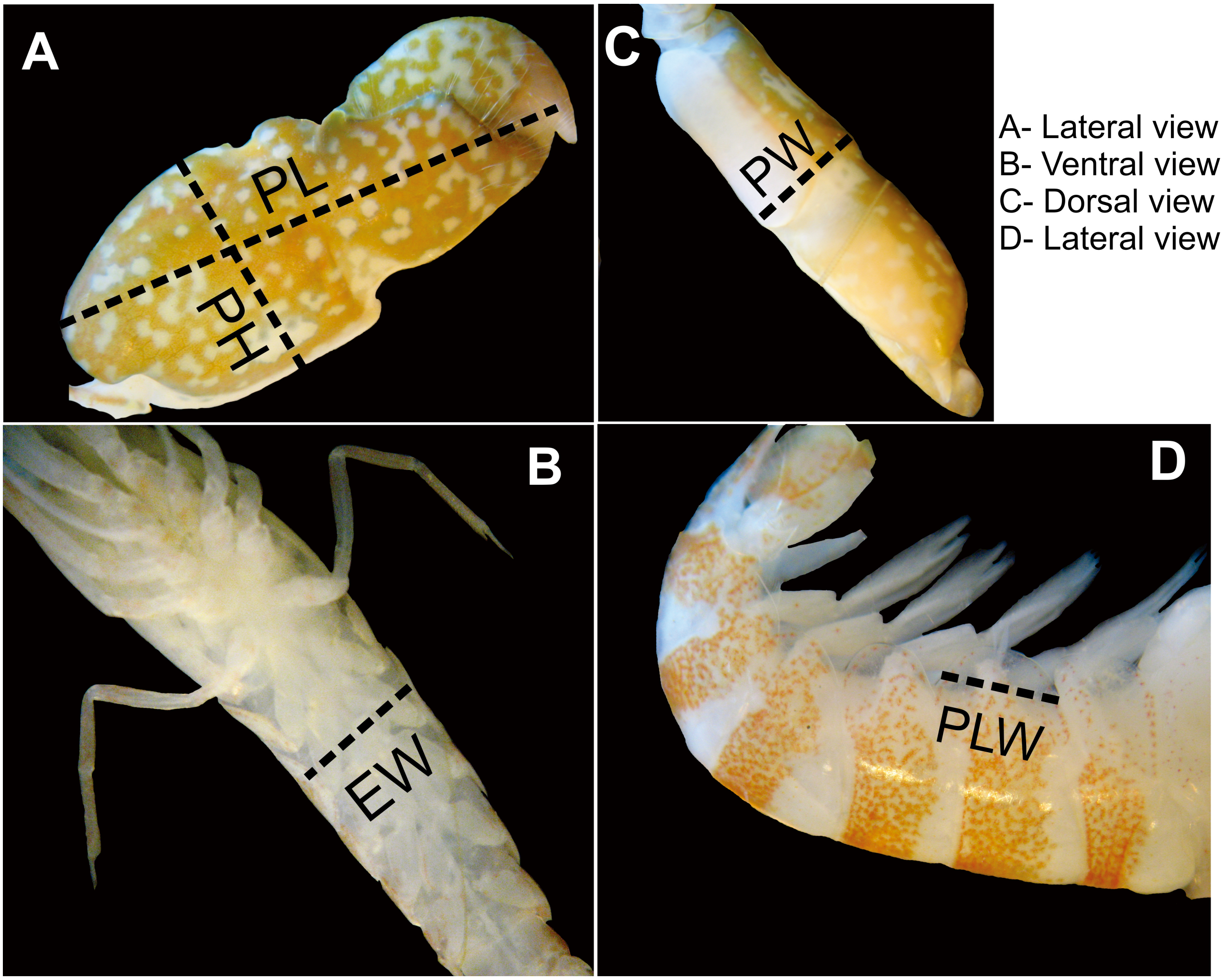

Fig. 1. Morphometrics obtained from each shrimp of the five species of *Alpheus* Fabricius, 1798. Carapace Length (CL), Propodus Length (PL), Propodus Height (PH); Propodus Width (PW), Pleura Width (PLW) and Esternite Width (EW). Specimen of *A. carlae* represented.

RESULTS

Frequency of individuals living solitarily, in pairs or in larger groups (Indicator 1) and the pattern of population distribution (Indicator 2)

We captured a total of 2,276 specimens: 300 of *A. angulosus*, 393 of *A. bouvieri*, 374 of *A. carlae*, 403 of *A. nuttingi* and 806 of *A. estuariensis*. The total sex ratio (M:F) was unbiased in *A. angulosus* (147:153; $\chi^2 = 0.12$, *d.f.* = 1, *p* = 0.7728), *A. bouvieri* (182:211; $\chi^2 = 2.14$, *d.f.* = 1, *p* = 0.1578), *A. carlae* (174:200; $\chi^2 = 1.807$, *d.f.* = 1, *p* = 0.1961) and *A. nuttingi* (204:199; $\chi^2 = 0.62$, *d.f.* = 1, *p* = 0.8421), and females biased in *A. estuariensis* (391:415; $\chi^2 = 12.55$, *d.f.* = 1, *p* = 0.0005).

The number of shrimps per host refuge varied between 1 and 2 (mean ± s.d. = 1.65 ± 0.5 shrimps/refuge-1) in *A. angulosus*, 1 and 3 (1.61 ± 0.5 shrimps/refuge-1) in *A. bouvieri*, 1 and 2 (1.59 ± 0.49 shrimps/refuge-1) in *A. carlae*, 1 and 6 (1.41 ± 0.48 shrimps/refuge-1) in *A. estuariensis*, and 1 and 6 (1.41 ± 0.55 shrimps/refuge-1) in *A. nuttingi*. The population distribution of the five species differed significantly from a Poisson random distribution (Chi-square test of goodness of fit: *A. angulosus*: $\chi^2 = 110.34$, *d.f.* = 6, *p* < 0.0001; *A. bouvieri*: $\chi^2 = 130.37$, *d.f.* = 6, *p* < 0.0001; *A. carlae*: $\chi^2 = 130.13$, *d.f.* = 6, *p* < 0.0001; *A. estuariensis*: $\chi^2 = 149.32$, *d.f.* = 6, *p* < 0.0001; *A. nuttingi*: $\chi^2 = 148.17$, *d.f.* = 6, *p* < 0.0001).

In *A. angulosus*, *A. bouvieri* and *A. carlae* the disparity between observed and expected distributions was explained by the relatively large number of refuges used by shrimp pairs and relatively small number of refuges hosting solitary shrimps compared to the numbers expected by chance alone. In *A. estuariensis* and *A. nuttingi* the number of refuges harboring solitary was relatively large compared to paired individuals, and both were higher than expected by chance alone (Fig. 2). In *A. angulosus* we observed 66 solitary shrimps (25 males and 31 females), 122 paired shrimps distributed in 120 heterosexual pairs and 2 homosexual (Table 1); in *A. bouvieri* we observed 97 solitary shrimps (36 males and 61 females), 145 paired shrimps distributed in 141 heterosexual and 4 homosexual pairs; in *A. carlae* we observed 93 solitary shrimps (31 males and 62 females), 139 paired shrimps distributed in 138 heterosexual pairs, and 1 homosexual pair; in *A. estuariensis* we observed 363 solitary shrimps (151 males and 212 females), 209 paired shrimps distributed in 190 heterosexual pairs, and 19 homosexual pairs. Finally, in *A. nuttingi* a total of 173 solitary shrimps (92 males and 81 females), 113 paired shrimps distributed in 108 shrimps heterosexual pairs, and 5 homosexual pairs were observed. Among pairs, there was a predominance of heterosexual pairs in the five species (Chi-square test of goodness of fit: *A. angulosus*: $\chi^2 = 112.20$, *d.f.* = 1, *p* < 0.0001; *A. bouvieri*: $\chi^2 = 127.59$, *d.f.* = 1, *p* < 0.0001; *A. carlae*: $\chi^2 = 133.05$, *d.f.* = 1, *p* < 0.0001; *A. estuariensis*: $\chi^2 = 138.27$, *d.f.* = 1, *p* < 0.0001; *A. nuttingi*: $\chi^2 = 92.07$, *d.f.* = 1, *p* < 0.0001).

The values of the carapace length obtained for paired and solitary females and males of the five species are in table 1. In *A. angulosus*, *A. bouvieri*, *A. carlae* and *A. estuariensis*, solitary and paired individuals were more frequent in intermediate size-classes (Fig. 3). In *A. nuttingi*, paired individuals predominated in the intermediate size-classes and the solitary ones were most common in smaller classes (CL), meaning a displacement of the frequencies between these groups (Fig. 3).

Female reproductive condition (Indicator 3)

Non-breeding individuals were more frequent among solitary females of *A. angulosus*, *A. carlae*, *A. nuttingi* and *A. estuariensis*. On the other hand, most of the solitary females of *A. bouvieri* were carrying eggs (Table 2). Among the paired individuals, breeding females were more frequent in *A. angulosus*, *A. bouvieri* and *A. estuariensis*. In *A. carlae* and *A. nuttingi*, there was no significant difference between the frequencies of paired breeding and non breeding females (Table 2).

Table 1. Refuges hosting shrimps and number of male (M) and female (F) shrimps of the five species of *Alpheus* Fabricius, 1798 living solitarily in pairs, trios, quartets, quintets and sextets

Species	Refuges with shrimps (*n*: number of individuals)					
	1	2	3	4	5	6
	(*n*)	(*n*)	(*n*)	(*n*)	(*n*)	(*n*)
A. angulosus	(25 - M) (31 - F)	(120 - MF) (1 - FF) (1 - MM)	0	0	0	0
A. bouvieri	(36 - M) (61 - F)	(141 - MF) (3 - FF) (1 - MM)	(1 - MMM) (1 - FFF)	0	0	0
A. carlae	(31 - M) (62 - F)	(138 - MF) (1- MM)	0	0	0	0
A. estuariensis	(151 - M) (212 - F)	(190 - MF) (6 - FF) (13- MM)	(1 - MMM) (1 - MMF) (5 - MFF)	(1 - MMMF) (1 - MMFF)	(1 - MMMMF)	(1 - MMMFFF)
A. nuttingi	(92 - M) (81 - F)	(108 - MF) (2 - FF) (3 - MM)	0	0	0	(1 - FFFFFF)

Among the paired breeding females, females with eggs in stage I of development predominated in *A. angulosus*, *A. carlae*, *A. nuttingi* and *A. estuariensis*. However, in *A. bouvieri*, females with eggs in the final stage predominated (Table 3).

Sexual dimorphism among the pairs (Indicator 4)

There was no significant difference between the mean CL of paired males and females (*t*-test paired = 0.408; $p = 0.683$) of *A. angulosus* and *A. carlae* (*t*-test paired = -0.316; $p = 0.752$). In *A. bouvieri* (*t*-test paired = 2.65; $p < 0.005$) and *A. estuariensis* (*t*-test paired = 4.47; $p < 0.005$), females were larger than males. In *A. nuttingi* (*t*-test paired = 2.65; $p < 0.005$), males were larger than females. Major cheliped PL, PH and PW were larger in males of *A. angulosus*, *A. carlae*, *A. nuttingi* and *A. estuariensis* (Table 4), demonstrating the existence of sexual dimorphism relative to the size and robustness of this appendage. On the other hand, in *A. bouvieri* there was no significant difference, demonstrating the absence of dimorphism in the chelipeds. The pleonal measures (PlW and SW) were statistically larger in the females of the five species (Table 4).

The relation PL vs CL demonstrated positive allometric growth in males of the five species, with the cheliped developing in larger proportions than the carapace (Fig. 5) (Table 5). The females' regressions of *A. angulosus*, *A. bouvieri*, *A. carlae* and *A. estuariensis* also showed positive allometry; however, females of *A. nuttingi* showed negative allometry in PL vs CL relationship (Fig. 4). The ANCOVA one-way analyses revealed a significant difference between the slopes of the regression (PL vs. CL) in both sexes of all species, indicating higher absolute growth in proportion of the PL in males of *A. angulosus*, *A. bouvieri*, *A. carlae*, *A. nuttingi*, and *A. estuariensis* (Table 5).

Existence of size assortative-pairing (Indicator 5)

Strong positive correlations were observed between the CL of the paired individuals (Fig. 4), showing the existence of size assortative-pairing in the five species.

DISCUSSION

The quantity of shrimps observed in the refuges did not exceed two individuals per refuge, indicating that these populations do not live in aggregations. Populations of *A. angulosus*, *A. bouvieri* and *A. carlae* presented higher frequencies of paired individuals. Moreover, a non-random distribution of individuals was observed, indicating that paired individuals are

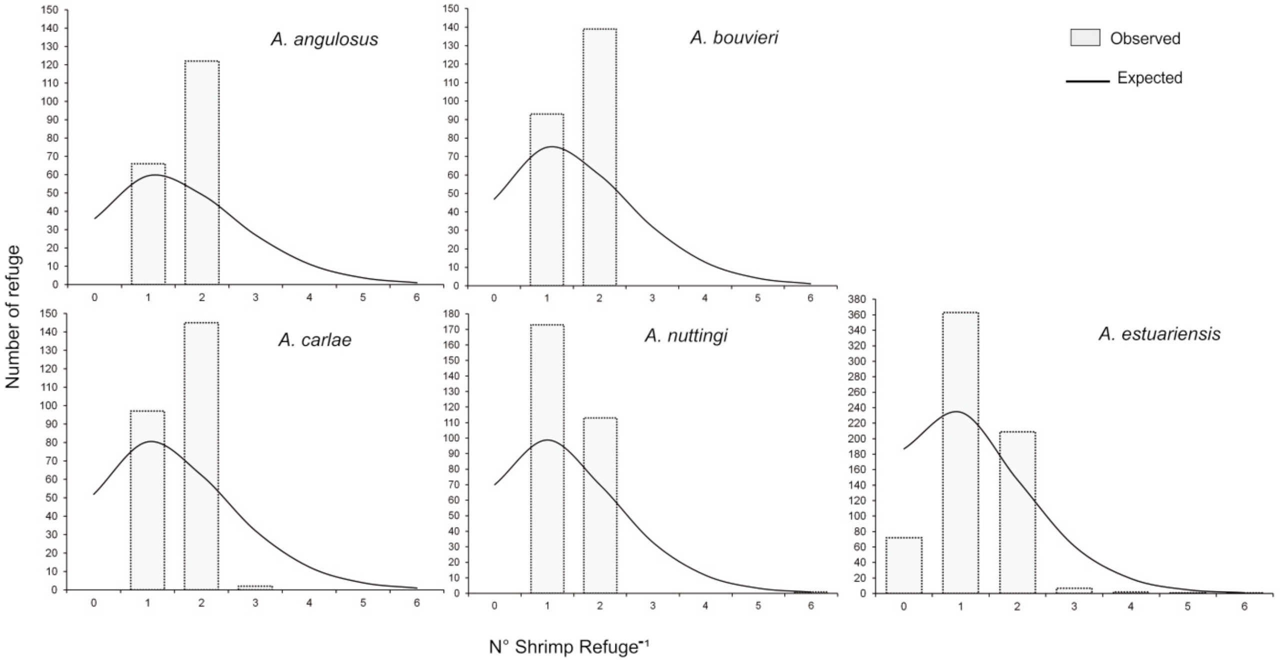

Fig. 2. Population distribution of the five species of *Alpheus* Fabricius, 1798. Observed frequency of shrimps on hosts differed significantly from an expected Poisson random distribution.

more common than expected by chance alone. Thus, our data regarding the frequency of paired individuals and distribution pattern supports the existence of monogamy in such species, as observed in other decapod populations (Baeza 2008; Baeza et al. 2011 2016; Pfaller et al. 2014; Pescinelli et al. 2017).

On the other hand, solitary shrimp were a little more frequent in *A. nuttingi* and much more numerous in *A. estuariensis*; the non-random distribution of individuals indicated a higher probability of finding

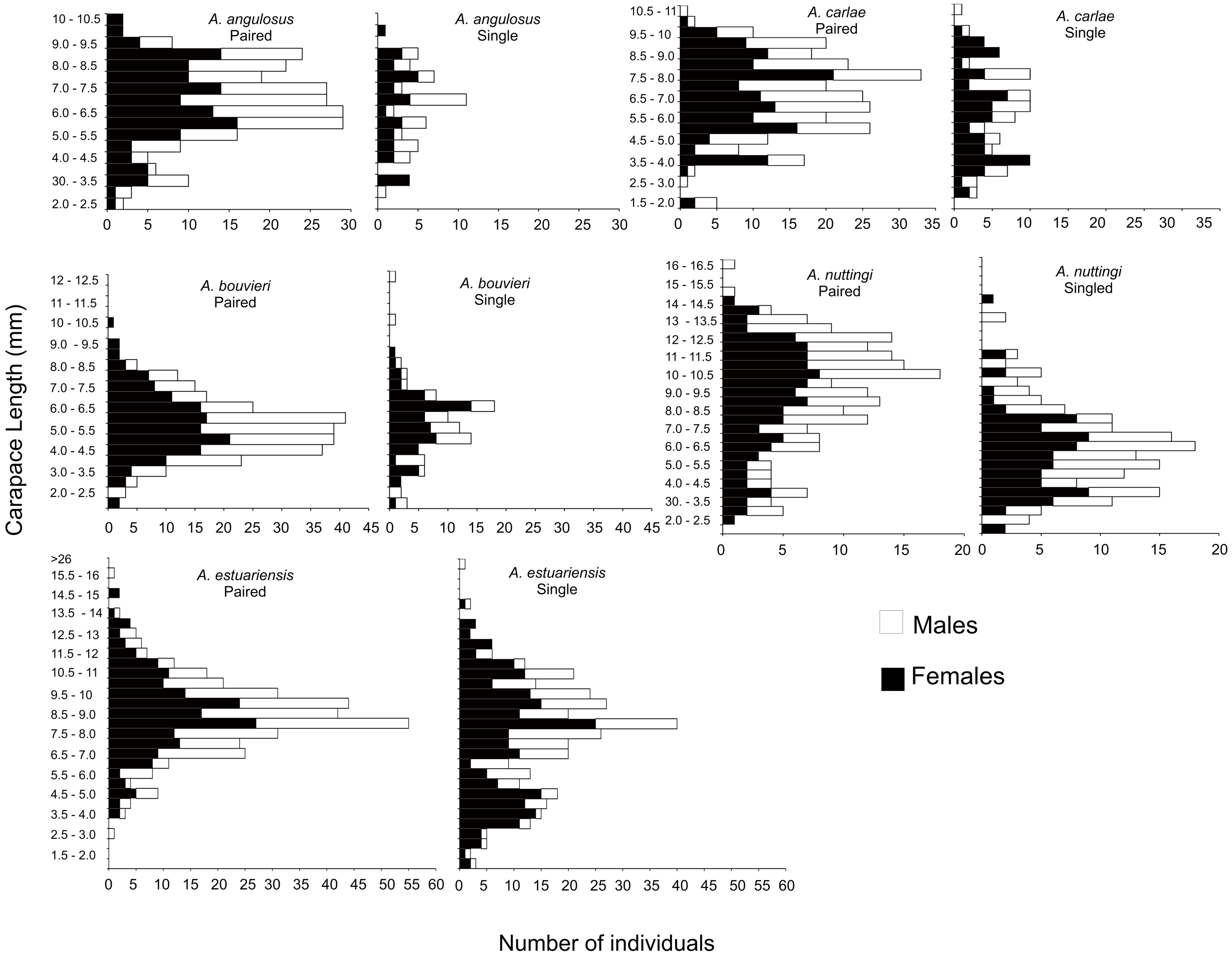

Fig. 3. Frequency distributions in CL classes of solitary and paired individuals (males and females) of the five species of *Alpheus* Fabricius, 1798. White bars represent the males and black bars the females.

Table 2. Number of breeding and non-breeding females among shrimps living solitarily and in pairs in five species of *Alpheus* Fabricius, 1798. Chi-square test of female reproductive condition, *d.f.* (degrees of freedom) = 1; s: $p < 0.05$ significant; ns: $p > 0.05$ not significant

Species	Solitary		Chi-Square	Paired		Chi-Square
	Non-breeding	Breeding	χ^2 value	Non-breeding	Breeding	χ^2 value
Alpheus angulosus	22	9	4.6 s	41	79	11.4 s
Alpheus bouvieri	13	46	17.3 s	48	96	15.3 s
Alpheus carlae	41	21	5.8 s	65	73	0.3 ns
Alpheus nuttingi	76	3	65.6 s	55	53	0.009 ns
Alpheus estuariensis	109	82	3.5 s	52	138	38 s

solitary individuals. In *A. nuttingi*, the majority of solitary individuals was observed in the smallest CL size classes (Fig. 4). The mean CL of these individuals was smaller than that of the paired shrimps (Table 6). These results may be explained by two hypotheses: 1) smaller individuals do not form pairs because they are not sexually mature or 2) they are not able to stay paired and/or stay in the refuge, making them more susceptible to being evicted from the refuge by a more able conspecific, as observed in behavioral studies with *A. angulosus* and *A. heterochaelis* (Mathews 2002b; Rahman et al. 2003). These results do not exclude the existence of monogamy in *A. nuttingi*; monogamous behavior may take place among sexual mature individuals or in individuals near puberty as observed in other populations (Costa-Souza et al. 2014).

On the other hand, solitary individuals of *A. estuariensis* in the smaller size class were less frequent, which suggests that the species does not favor monogomy. Our results agree with those obtained in two other populations from Sergipe, northeastern Brazil (Barroso et al. 2018). In this study, although the number of heterosexual pairs was a higher than expected by chance alone, the distribution of the individuals did not differ from a random distribution, and the data fitted with the pure-search mating system (when males

Table 3. Stages of embryo development of paired breeding females of five species of *Alpheus* Fabricius, 1798. * I, II and III: embryo stages; LH: females in final phase of larval hatching; IN: Infertile eggs

Species	Embryo stage					Chi-Square test		
	I	II	III	IN	LH	χ^2 value	*d.f.*	p value
Alpheus angulosus	48	12	8	6	5	86.8	4	< 0.001
Alpheus bouvieri	27	18	44	1	6	61.6	4	< 0.001
Alpheus carlae	41	10	7	7	8	60.1	4	< 0.001
Alpheus nuttingi	23	10	15	2	3	28.8	4	< 0.001
Alpheus estuariensis	50	19	26	16	27	25.8	4	< 0.001

Table 4. Morfometric variables of the major chelipeds [propodus length (PL), height (PH) and width (PW)], and pleurae of second pleonal segment [width (PlW) and esternite width (EW)] in males and females and tests statistic values for each species of *Alpheus* Fabricius, 1798 (Min = minimum; Max = maximum; M = mean; SD = standard deviation; all measurements in millimeters)

Species	PL (Min-Max/ M ± SD)	PH (Min-Max/ M ± SD)	PW (Min-Max/ M ± SD)	PlW (Min-Max/ M ± SD)	EW (Min-Max/ M ± SD)
Alpheus angulosus					
Males	2.5–14.7 (9.2 ± 3.3)	1.0–6.0 (3.9 ± 1.3)	0.6–4.0 (2.3 ± 0.9)	0.5–3.0 (1.6 ± 0.4)	0.7–5.4 (3.0 ± 0.8)
Females	2.5–12.3 (7.2 ± 2.9)	1.0–4.8 (3.0 ± 1.2)	0.6–3.1 (1.7 ± 0.7)	0.7–5.2 (2.7 ± 1.0)	1.1–5.8 (3.3 ± 1.1)
t-Test (p-value)	7.49 ($p < 0.001$)	8.38 ($p < 0.001$)	9.06 ($p < 0.001$)	15.14 ($p < 0.001$)	4.70 ($p < 0.001$)
Alpheus bouvieri					
Males	3.0–12.7 (6.6 ± 3.2)	1.2–5.4 (2.7 ± 1.3)	0.7–3.3 (1.6 ± 0.8)	0.4–2.6 (1.3 ± 0.4)	0.7–3.8 (2.1 ± 0.6)
Females	2.4–12.5 (6.8 ± 3.1)	0.4–5.3 (2.8 ± 1.3)	0.6–3.5 (1.6 ± 0.8)	0.6–4.6 (2.1 ± 0.7)	0.8–4.7 (2.6 ± 0.9)
t-Test (p-value)	0.45 ($p = 0.653$)	0.54 ($p = 0.583$)	0.36 ($p = 0.719$)	13.10 ($p < 0.001$)	6.19 ($p < 0.001$)
Alpheus carlae					
Males	2.0–16.5 (9.0 ± 3.6)	1.7–6.5 (3.9 ± 1.5)	0.5–4.4 (2.3 ± 1.0)	0.6–3.2 (1.8 ± 0.6)	1.1–5.3 (3.1 ± 0.9)
Females	2.0–13.7 (7.1 ± 3.0)	1.3–6.0 (3.1 ± 1.3)	0.5–3.7 (1.8 ± 0.8)	0.6–4.7 (2.7 ± 1.0)	0.7–6.2 (3.4 ± 1.3)
t-Test (p-value)	6.54 ($p < 0.001$)	6.49 ($p < 0.001$)	7 ($p < 0.001$)	14.53 ($p < 0.001$)	4.39 ($p < 0.001$)
Alpheus nuttingi					
Males	3.0–19.2 (11.4 ± 5.2)	1.2–8.2 (5.0 ± 2.3)	0.7–6.3 (3.2 ± 1.6)	0.5–4.0 (2.3 ± 0.8)	0.9–6.3 (4.0 ± 1.4)
Females	2.4–15.0 (8.3 ± 4.4)	1.0–8.0 (3.6 ± 0.2)	0.6–4.7 (2.3 ± 1.2)	0.5–6.8 (3.3 ± 1.6)	1.0–10.5 (4.3 ± 2.0)
t-Test (p-value)	6.27 ($p < 0.001$)	5.92 ($p < 0.001$)	6.49 ($p < 0.001$)	9.96 ($p < 0.001$)	3.33 ($p < 0.001$)
Alpheus estuariensis					
Males	3.5–21.6 (12.2 ± 2.8)	1.2–9.0 (5.2 ± 1.2)	0.9–7.8 (3.2 ± 0.8)	0.5–5.0 (2.1 ± 0.6)	1.2–7.1 (4.3 ± 1.0)
Females	3.9–18.8 (11.4 ± 2.6)	1.2–8.2 (4.8 ± 1.1)	0.9–5.8 (2.9 ± 0.8)	0.8–6.8 (3.4 ± 1.2)	1.6–10 (4.7 ± 1.4)
t-Test (p-value)	9.40 ($p < 0.001$)	9.61 ($p < 0.001$)	5.74 ($p < 0.001$)	20.35 ($p < 0.001$)	7.18 ($p < 0.001$)

search for nearby females to mate with). In our view, the predominance of solitary individuals may be a result of the species' habitat—complex burrows in mudflats (also observed by Barroso et al. 2018)—and the sampling method. However, although pumping is the most viable sampling method in this type of habitat, the complexity of burrows (with several openings and internal channels) helps shrimps escape when they feel the disturbance in the sediment caused by pumping (Costa-Souza et al. 2014).

Males of all species paired both with breeding and non-breeding females carried egg masses in initial, intermediate and final stages of embryonic development. Moreover, pairs formed by males and

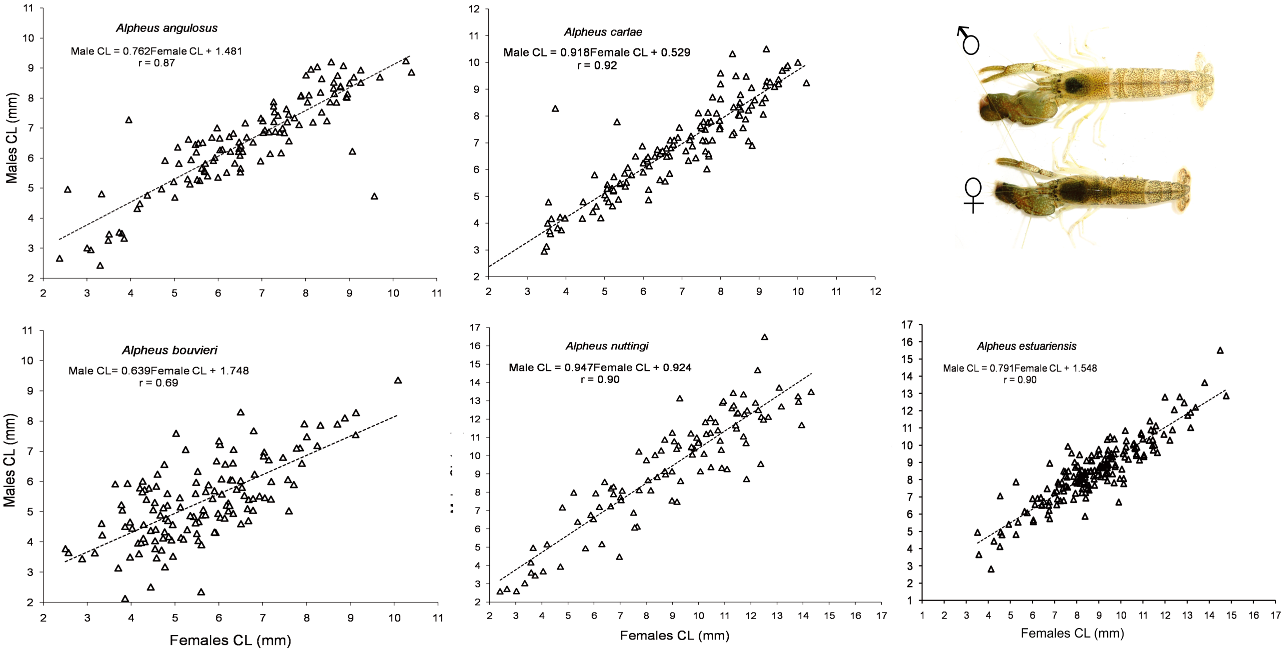

Fig. 4. Relation between the carapace length (CL, mm) of males and females paired of the five species of *Alpheus* Fabricius, 1798.

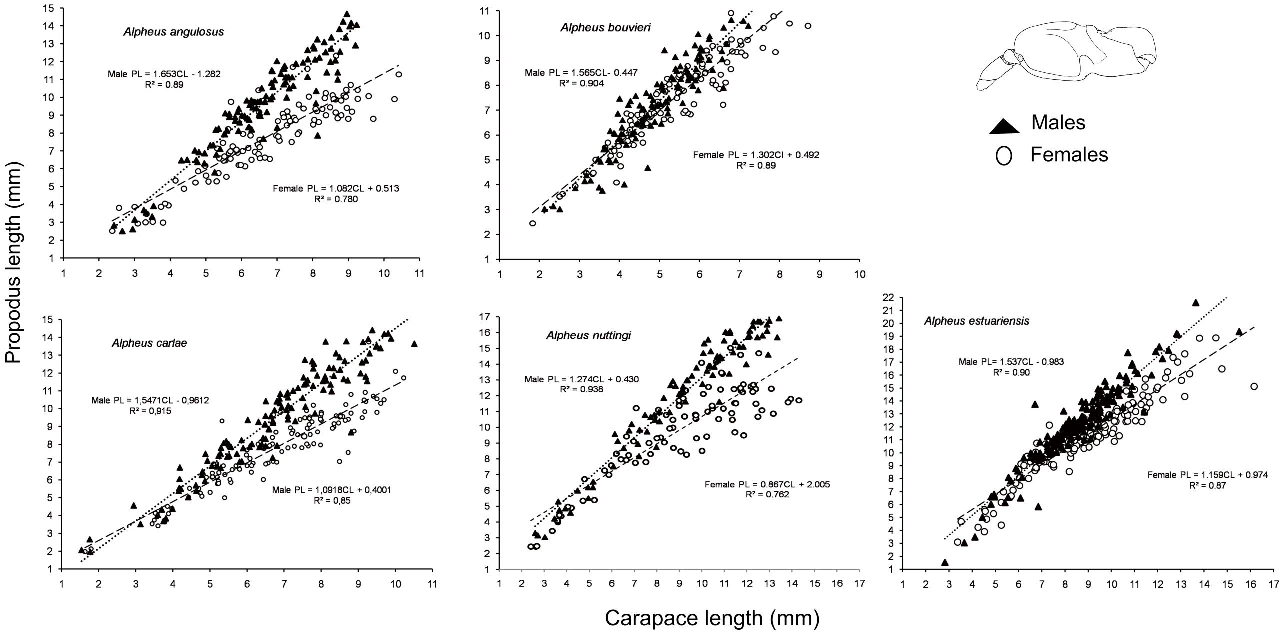

Fig. 5. Relative growth of the Propodus Length (PL) in function of Carapace Length (CL) in males and females of the five species of *Alpheus* Fabricius, 1798.

females apparently carrying unfertilized eggs (possibly newly released, see Costa-Souza et al. 2014) and others in the final phase of larval hatching were also observed. These population traits are strong indicators that males remain with females throughout the incubation period (Baeza 2008; Baeza et al. 2016; Pescinelli et al. 2017), perhaps remaining until the next reproductive event (Rahman et al. 2002; Correa and Thiel 2003).

The time of embryonic development until larval hatching in some species of *Alpheus* is estimated to be 3 to 4 weeks (Knowlton 1973; Tracey et al. 2013). If males pair only for mating, then the frequency of pairs formed by males and females carrying eggs in all stages of developed is expected to be very low. Other evidence that males remain is that populations of tropical crustaceans present a continuous reproductive cycle observed in other populations of *A. estuariensis*, *A. carlae*, *A. nuttingi* and *A. dentipes* (Fernández-Muñoz and García-Raso 1987; Mossolin et al. 2006; Pavanelli et al. 2010; Costa-Souza et al. 2014), and the females become sexually receptive soon after larval hatching (Mathews 2003; Bauer 2004; Chack et al. 2015), ensuring that males have the possibility of reproducing with the same female. Futhermore, the male genetic contribution may influence "paternal care" and the staying of the male next to the offspring, which was observed in an experimental study with *A. angulosus* (Mathews 2007). In populations with "search and attend" mating system (Correa and Thiel 2003), in which males are found with females only for mating purposes, only the occurrence of pairs with non-breeding females (close to starting the reproductive moult) or with unfertilized eggs is observed (Diesel 1986; Van der Meeren 1994; Baeza et al. 2016), which is not the case of *A. angulosus*, *A. bouvieri*, *A. carlae*, *A. nuttingi* and *A. estuariensis*.

Table 5. Relative growth between propodus (PL) and carapace length (CL) of paired males and females of the five species of *Alpheus* Fabricius, 1798

Species	Y	X	Equation regression	R^2	t	Type of allometry	ANCOVA between regressions	Sexual dimorphism
A. angulosus								
Males	PL	CL	y = 1.563x - 1.282	0.89	29.79^s	+	F = 151.1*; $d.f.$ = 1	M > F
Females	PL	CL	y = 1.082x - 0.513	0.78	19.42^s	+	F = 37.16**	
A. bouvieri								
Males	PL	CL	y = 1.565x - 0.492	0.9	33.36^s	+	F = 24.9; $d.f.$ = 1	M > F
Females	PL	CL	y = 1.302x + 0.492	0.89	32.09^s	+	F = 17.9	
A. carlae								
Males	PL	CL	y = 1.547x - 0.9612	0.91	36.53^s	+	F = 202.5; $d.f.$ = 1	M > F
Females	PL	CL	y = 1.091x + 0.4001	0.85	26.94^s	+	F = 59.7	
A. nuttingi								
Males	PL	CL	y = 1.274x + 0.430	0.93	37.78^s	+	F = 117.9; $d.f.$ = 1	M > F
Females	PL	CL	y = 0.867x + 2.005	0.76	16.72^s	-	F = 44.8	
A. estuariensis								
Males	PL	CL	y = 1.537x - 0.983	0.9	40.95^s	+	F = 159; $d.f.$ = 1	M > F
Females	PL	CL	y = 1.1596x + 0.974	0.87	36.07^s	+	F = 58.2	

Dependent variable (Y), independent variable (X), determination coefficient (R^2 ajusted), t (t-test value), (s): $p < 0.0001$. *Between regressions; ** Slope of the line.

Table 6. Minimum (Min) and maximum (Max) size, mean (M) and standard deviation (SD) of carapace length (CL) of solitary and paired males and females of the five species of *Alpheus* Fabricius, 1798. Measurements in millimeters

Species	Solitaries				Paired			
	Males		Females		Males		Females	
	CL (Min. - Max.)	CL (M. ± SD)	CL (Min. - Max.)	CL (M. ± SD)	CL (Min. - Max.)	CL (M. ± SD)	CL (Min. - Max.)	CL (M. ± SD)
A. angulosus	2.9–8.7	6.3 ± 1.5	3.0–9.7	6.3 ± 1.9	2.4–9.2	6.6 ± 1.6	2.4–10.4	6.7 ± 1.8
A. bouvieri	1.8–12.1	5.3 ± 2.1	2.0–8.5	5.4 ± 1.4	2.1–8.3	5.1 ± 1.2	1.8–10.1	5.5 ± 1.5
A. carlae	2.3–10.6	6.0 ± 2.0	2.4–9.7	5.9 ± 2.1	1.5–10.5	6.7 ± 1.9	1.6–10.2	6.7 ± 1.9
A. estuariensis	2.0–26.5	8.0 ± 2.6	2.0–14.0	7.4 ± 2.9	2.8–15.5	8.5 ± 1.8	3.5–14.7	8.8 ± 2.1
A. nuttingi	2.2–13.4	6.3 ± 2.4	1.9–14.2	5.8 ± 2.3	2.6–16.5	9.4 ± 3.0	2.4–14.3	9.0 ± 2.9

However, we observed some solitary breeding females in all species, although the largest of them were non-breeding (see Table 3). The presence of breeding solitary females is characteristic of promiscuous and free-living species (Thiel and Baeza 2001; Baeza et al. 2016). On the other hand, in many species of monogamous crustaceans, fidelity between sexual partners is not rigid; there may be abandonment or exchange of partners when environmental factors are favorable, or even when there is some connection between the refuges (Knowlton 1980; Boltaña and Thiel 2001; Mathews 2002a; Baeza 2008; Baeza et al. 2013 2016). The presence of these females in the studied populations may be explained by two hypotheses: (1) the same paired individuals do not stay through the entire reproductive life and/or (2) males paired with these females were recently predated, since breeding females have a lower activity (Hughes et al. 2014), getting more protected in the refuge. Thus, the occurrence of solitary females carrying eggs does not exclude monogamy in those species.

The mean CL of paired males and females of *A. angulosus* and *A. carlae* was similar. In *A. bouvieri* and *A. estuariensis* females were slightly larger than males and in *A. nuttingi* males were slightly larger than females. In several species of *Alpheus* differences in size between the sexes are absent or very small (Mossolin et al. 2006; Pavanelli et al. 2008 2010; Harikrishnan et al. 2010; Costa-Souza et al. 2014 2019; Pescinelli et al. 2017; Soledade et al. 2018).

Males of *A. angulosus*, *A. carlae*, *A. nuttingi* and *A. estuariensis* presented larger/more robust chelipeds than females, whereas in *A. bouvieri* differences in cheliped size between the sexes were not observed. In male/female pairs of *A. angulosus*, *A. buckupi* and *A. carlae* from Bahia, Brazil, males also had larger cheliped than females (Soledade et al. 2018). These differences may indicate some degree of competition, mainly between males for females and refuges, and that the pairing behavior may not last for a lifetime, there being exchange of partners when appropriate, similar to that observed in other monogamous populations where males have larger chelipeds (Knowlton 1980; Baeza 2008; Baeza et al. 2011; Pfaller et al. 2014).

The analysis of relative growth showed that in males and females of *A. angulosus*, *A. bouvieri*, *A. carlae* and *A. estuariensis*, and in males of *A. nuttingi*, the cheliped develops in larger proportions than the carapace. However, the major cheliped developed in a smaller proportion in females of *A. nuttingi*. However, the proportion of increase in growth of this appendage in relation to the body was higher in males in the five species, confirming the existence of differences in the development of this appendage among the sexes.

The cheliped in *Alpheus* is a fundamental structure for survival, used in defense against predators, in prey capture, defense of the sexual partner and in the construction and protection of the refuges, presenting similar function in males and females (Versluis et al. 2000; Anker et al. 2006; Hughes et al. 2014). Behavioral studies with *A. heterochaelis* and *A. angulosus* revealed a contrast between the sexual dimorphism of the major cheliped and the level of aggression between the sexes, where the females aggressively defend their territory, although they present smaller chelipeds, and that the aggressiveness of the females may contribute to the maintenance of the pairing (Hughes et al. 2014). However, it is still not clear how the level of aggressiveness is decisive for the maintenance of monogamy. In addition, there are indications that energy expenditure on egg production may decrease the energetic allocation to the cheliped in females after maturity (Costa-Souza, unpublished data; Hughes et al. 2014).

On the other hand, the pleonal features of females of *A. angulosus*, *A. bouvieri*, *A. carlae*, *A. estuariensis* and *A. nuttingi* were larger than in males, evidencing sexual dimorphism in those structures, as observed in other carideans (Pescinelli et al. 2017; Barroso et al. 2018). The sexual dimorphism was observed in the chelipeds and pleonal structures; however, it may be explained by other factors than mating system. Differences in cheliped size may indicate that males compete for females and change pairs throughout the lifetime, and males pair for a short time before mating (Knowlton 1980; Baeza 2008; Baeza et al. 2011). The differences observed in pleonal features are related to pleonal egg incubation by caridean females until larval hatching (Saito 2002; Bauer 2004; Sganga et al. 2016).

Finally, the existence of size-assortative paring was observed in all populations studied, *i.e.*, shrimps always paired with conspecifics of a very similar size, which supports the hypothesis that such populations exhibit monogomy. In *A. angulosus*, *A. carlae*, *A. estuariensis* and *A. nuttingi* the male body explained more than 75% of the variation in female body size (Fig. 4). This tendency has been observed in other species of monogamous crustaceans (Baeza 1999 2008; Boltaña and Thiel 2001; Rahman et al. 2002; Costa-Souza et al. 2014; Pescinelli et al. 2017).

CONCLUSIONS

The frequency of paired individuals vs. single or in groups (trios, quartets, etc.), the frequency of pairs formed by males and breeding and non-breeding females, the females' reproductive condition and the existence of size-assortative pairing in the populations of *A. angulosus*, *A. bouvieri* and *A. carlae* indicate that these three species are monogamous. Although results from the frequency distribution demonstrated a higher tendency for finding solitary individuals in *A. nuttingi* and *A. estuariensis*, other studied features agree with the occurrence of monogamy in those populations. Lastly, the sexual differences in the chelipeds and the existence of solitary egg-carrying females indicated that monogamy in the five species is not rigid, *i.e.*, that heterosexual pairing may not last long, due to possible competition between males for females or refuge.

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