

Embryo Production of Two Sympatric Snapping Shrimps of the Genus *Alpheus* (Caridea: Alpheidae) from Northeastern Brazil: a Comparative Approach

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Abstract In spite of the high number of species (~ 300) and their wide geographic distribution, studies on reproductive biology have only been conducted with a few species of the genus *Alpheus* Fabricius 1798. The objective of this study was to compare the characteristics of embryo production of two sympatric species of shrimps, *Alpheus buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, Zootaxa 3652:437–452, 2013a and *A. carlae* Anker, Zootaxa 3386:1–109, 2012. Brooding females were collected in two sites on the coast of Bahia, northeastern Brazil, between July 2012 and May 2013. Female's carapace length (CL) was measured and their embryos were classified according to stage of development. A total of 47 females of *A. buckupi* (mean CL 9.4 ± 1.0 mm) and 36 of *A. carlae* (mean CL 8.6 ± 1.3 mm³) were sampled. Fecundity was positively correlated with CL in both species. Fecundity was higher (117 ± 80) in *A. buckupi*, which also produced smaller embryos (0.10 ± 0.03 mm³) than *A. carlae* (0.13 ± 0.03 mm³; fecundity: 50 ± 58). The reproductive output (RO) of *A. buckupi* and *A. carlae* was similar, 0.05 ± 0.06

and 0.04 ± 0.02 , respectively. The fecundity and reproductive output of both species were lower than those reported for other alpheids. Our results indicated that sympatric lineages differ regarding reproductive features, suggesting that different selective forces influenced fecundity in these snapping shrimps. This study provides the first insights on the embryo production of *A. buckupi* in the Western Atlantic and of *A. carlae* in northeastern Brazil.

Keywords Crustacea · Reproduction · Maternal output · Embryo volume

Introduction

Reproductive strategies vary widely among crustaceans (Hartnoll 1985) and are controlled by the interaction of intrinsic (phylogenetic component) and extrinsic (environmental component) factors. Factors such as mode of larval development, body size, periodicity of spawning throughout the year and food availability may determine reproductive traits such as embryo size and fecundity (Sastry 1983; Hartnoll 1985).

The caridean shrimps of the family Alpheidae Rafinesque 1815 show a high morphological, ecological, and behavioral heterogeneity. They are widely distributed in the Indo-West Pacific, East Pacific and across the Atlantic, with estimates of about 600 species (Chace 1988; Anker et al. 2006). Alpheids occur from the intertidal zone to the deep sea of tropical and subtropical, inhabiting various marine and estuarine ecosystems (e. g., mangroves, coral reefs, stygobitic habitats), and few are adapted to oligohaline and freshwater habitats (Anker et al. 2006). Despite the large information available on this family, studies on their reproductive biology have focused in a few species of the genera *Alpheus* Fabricius 1798, *Betaeus* Dana 1852 and *Synalpheus* Spence Bate 1888 (e. g.,

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Fernández-Muñoz and Garcia-Raso 1987; Corey and Reid 1991; Lardies and Wehrmann 1997, 2001; Mossolin et al. 2006; Lardies et al. 2008; Pavanelli et al. 2008, 2010; Harikrishnan et al. 2010; Costa-Souza et al. 2014; Rebolledo et al. 2014; Pescinelli et al. 2017).

The western Atlantic snapping shrimp *A. carlae* is a common representative of the *A. armillatus* H. Milne Edwards, 1937 [in H. Milne Edwards 1834–1840] species complex found along the Brazilian coast. *Alpheus buckupi* Almeida, Terossi, Araújo-Silva & Mantelatto, 2013a is an amphiatlantic species and its distribution in the western Atlantic overlaps with that of *A. carlae* Anker 2012 (see Anker 2012; Almeida et al. 2013a). Although *A. buckupi* shares some morphological similarities with species of the *A. armillatus* complex, it belongs to the *A. lobidens* de Haan 1850 complex (see Almeida et al. 2013a).

In northeastern Brazil, these two snapping shrimps are frequently observed co-existing in the field, living under rocks in the intertidal (e. g., Almeida et al. 2013b). There is evidence from southeastern Brazil that sympatric species may adopt distinct reproductive strategies [Pavanelli et al. 2008, *A. carlae*; Pavanelli et al. 2010, *A. nuttingi* (Schmitt 1924)]. On the other hand, there is a lack of studies with populations of the northeast coast. Some biological aspects of *A. carlae* have been studied (Pavanelli et al. 2008; Mossolin et al. 2006, as *A. armillatus*), however, knowledge on its biology is still very scarce. *Alpheus buckupi* was recently described and little is known about it. The sympatric distribution of such frequently co-existing shrimps raises an interesting question: do these lineages differ regarding reproductive features related to embryo production (fecundity, embryo volume, and reproductive output)? Thus, the objective of this study was to investigate, by means of a comparative approach, the characteristics of embryo production of two species of *Alpheus* found along the coast of Bahia, northeastern Brazil, and to contribute to the knowledge of these species' biology and to the reproductive biology of alpheids in general.

Materials and Methods

Sampling was conducted on four occasions between July 2012 and May 2013 at two locations on the coast of Bahia, northeastern Brazil [Moreré, Cairu (August 2012 and May 2013) and Itacaré (July 2012 and March 2013)] (Fig. 1). Specimens of *A. buckupi* and *A. carlae* were collected at Praia de Moreré, Boipeba Island, municipality of Cairu (13°36'49.5"S 38°54'16.2"W). Additional samples of *A. carlae* were taken at Praia da Concha, municipality of Itacaré (14°16'31.4"S 38°59'14.5"W).

Brooding females were collected by hand or with the use of small hand nets in tide pools, under rocks on soft bottoms, during low tides. The individuals were separated and placed in

plastic bags containing water from the collection site. The species were separated based on their color pattern, and later the identification was confirmed by morphology (Anker 2012; Almeida et al. 2013b). The shrimps were anesthetized on ice and kept frozen until the analyses.

In the laboratory, the embryos of each female were carefully removed from the pleopods using a thin brush and tweezers. The embryos were classified according to their stage of embryonic development, following the classification of Mossolin et al. (2006): initial (I – embryos without visible eyes; yolk occupying more than 75% of the embryo volume), intermediate (II – embryos with small and elongated eyes; yolk occupying 50–75% of the embryo volume) and final (III – embryos with well-developed eyes and yolk occupying 25–50% of the embryo volume). Only normal (apparently viable) embryos were observed. Embryos with abnormal features such as those previously observed in *A. estuariensis* Christoffersen 1984 (see Costa-Souza et al. 2014) were not observed. Females and embryos were photographed under a stereoscopic microscope with an image capture system. The photos and the software ImageJ (1.45 s) were used to calculate the carapace length (CL), and the longest and shortest embryo diameters (Rasband 2006). The CL was measured from the tip of the rostrum to the posterior edge of the carapace. Females with embryos in stage I were oven-dried at 50 °C until constant weight was reached. The same procedure was adopted for the embryo masses (about 48 h for females and 24 h for embryo masses). The dried material was then weighed on an analytical balance with a precision of four decimal places (Mantelatto et al. 2002).

Fecundity was obtained based on the mean number of embryos. Mean embryo volume was based on 10 embryos from each female and calculated using the formula [$v = \frac{1}{6} \times \pi \times (d1)^2 \times d2$] where d1 and d2 correspond to the longest and shortest diameters, respectively (Bauer 1991). Due to the low number of females with embryos in stages II and III, a larger number of embryos (25 maximum) per female were measured in these cases. The reproductive output (RO) was calculated as the ratio of the dry weight of the embryo mass to the dry weight of the female (Clarke et al. 1991). Only embryos in the initial stage of development (Stage I) were used to calculate fecundity and RO. Possible differences in embryo number and volume during embryonic development were accessed by comparing embryo mean number and volume between the three stages; such methodology was adopted in previous studies of *Alpheus* spp. (e. g., Pavanelli et al. 2008, 2010; Costa-Souza et al. 2014; Pescinelli et al. 2017).

All data were tested for normality using the Shapiro-Wilk test. Nonparametric procedures were adopted. The 95% significance level was adopted for all analyses. Samples of different collections were grouped due to the lack of statistical differences between them (after comparisons with the Kruskal-Wallis test). The differences between species

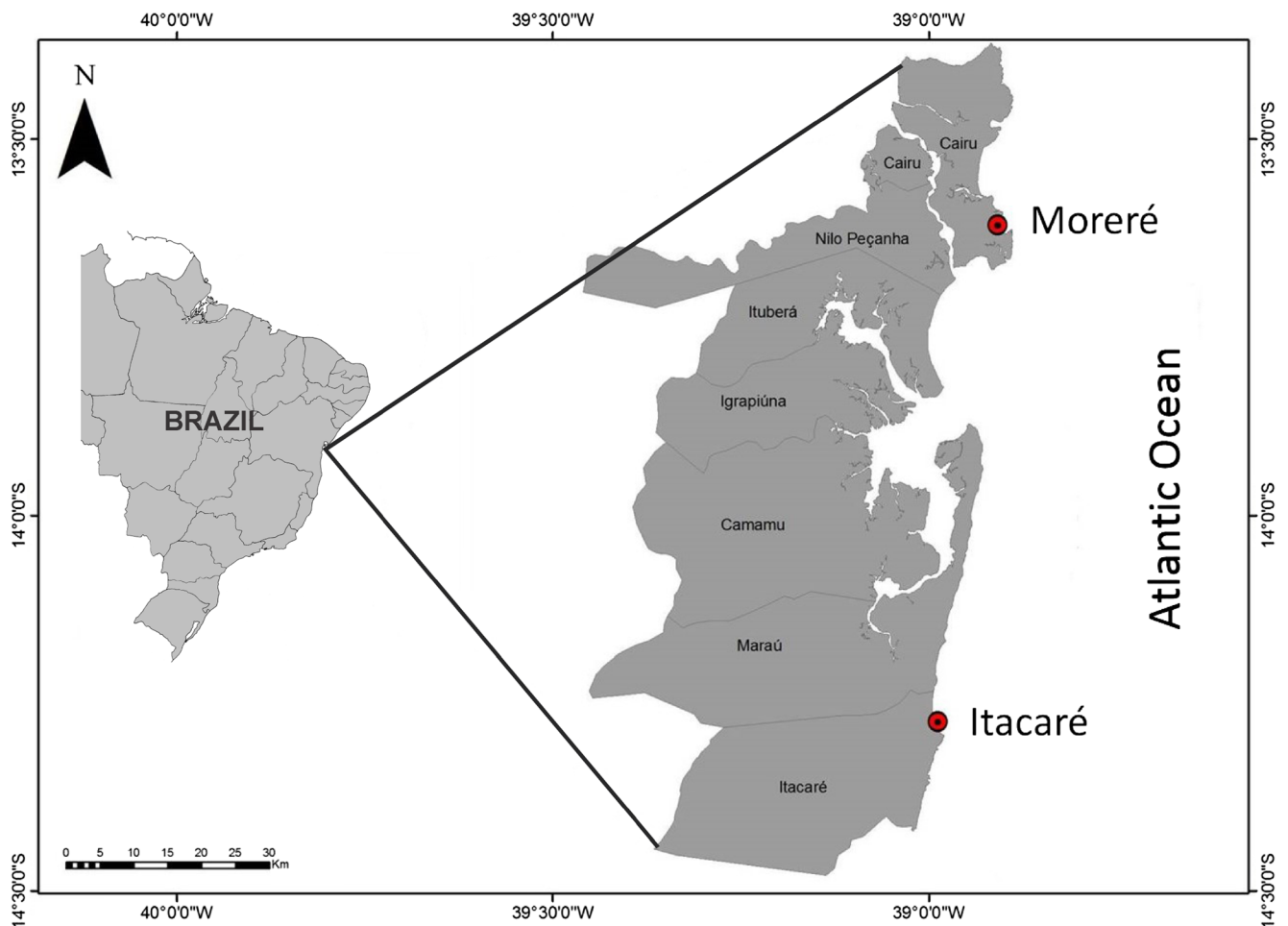


Fig. 1 Location of sampling sites (Moréré and Itacaré) of *Alpheus buckupi* Almeida et al. 2013a and *Alpheus carlae* Anker 2012 on the coast of Bahia, northeastern Brazil

regarding CL, fecundity, embryo volume, and RO were also tested using the Kruskal-Wallis test. Differences in fecundity and embryo volume were tested with an analysis of covariance (ANCOVA). The relationship between CL and fecundity was examined using the Spearman correlation coefficient. The CL was used as the independent variable in all analyses (Zar 1996). Statistical procedures were carried out using PAST (Paleontological Statistics 2.16).

Voucher specimens of both species were preserved in ethanol 70% and deposited in the carcinological collection of the Museum of Oceanography Professor Petrônio Alves Coelho, Universidade Federal de Pernambuco, Recife, Brazil (*A. buckupi* MOUFPE 15774; *A. carlae* MOUFPE 15875).

Results

A total of 47 *A. buckupi* and 36 *A. carlae* females carrying embryos were obtained. The CL was significantly larger in females of *A. buckupi* (9.4 ± 1.0 mm, range: 6.8–12.0 mm)

than *A. carlae* (8.6 ± 1.3 mm; range: 6.7–12.1 mm) (Kruskal-Wallis, $p < 0.05$).

Both fecundity and embryo volume differ significantly between both species (ANCOVA, $p < 0.05$). The females of *A. carlae* had a lower fecundity (50 ± 58) and larger embryo volume (0.13 ± 0.03 mm³) than *A. buckupi*, whose mean fecundity was 117 ± 80 and embryo volume was 0.10 ± 0.03 mm³ (see Table 1). Overall, fecundity was correlated with female size in both *A. buckupi* and *A. carlae* ($r > 0.5$; $p < 0.05$), (Fig. 2).

The number of embryos in developmental stages II and III in *A. buckupi* were lower than in stage I (Table 1). However, these differences were not significant (Kruskal-Wallis, $p > 0.05$). On the other hand, embryos in stages II and III were significantly larger than embryos in stage I (Kruskal-Wallis, $p < 0.05$) (see Table 1). Comparisons between stages were not possible in *A. carlae* due to the low number of embryos in stages II and III. The mean RO did not differ significantly between *A. buckupi* and *A. carlae* (0.05 ± 0.06 and 0.04 ± 0.02 , respectively; Kruskal-Wallis, $p > 0.05$) (Table 1).

Table 1 Mean fecundity (number of embryos), embryo volume and reproductive output (RO) in *Alpheus buckupi* Almeida et al. 2013a and *Alpheus carlae* Anker 2012, from the coast of Bahia, northeastern Brazil, July 2012–May 2013

	Number of embryos			Embryo volume (mm ³)			RO
	Stage of development			Stage of development			
	I	II	III	I	II	III	
<i>A. buckupi</i>	117 ± 80 [32] a	114 ± 69 [4] a	113 ± 95 [11] a	0.10 ± 0.03 [287] a	0.13 ± 0.03 [30] b	0.13 ± 0.05 [100] b	0.05 ± 0.06 [19] a
<i>A. carlae</i>	50 ± 58 [34] b	64 [1]	20 [1]	0.13 ± 0.03 [100] b	-	-	0.04 ± 0.02 [8] a

Different letters (a or b) = significant statistical difference; N = [].

Discussion

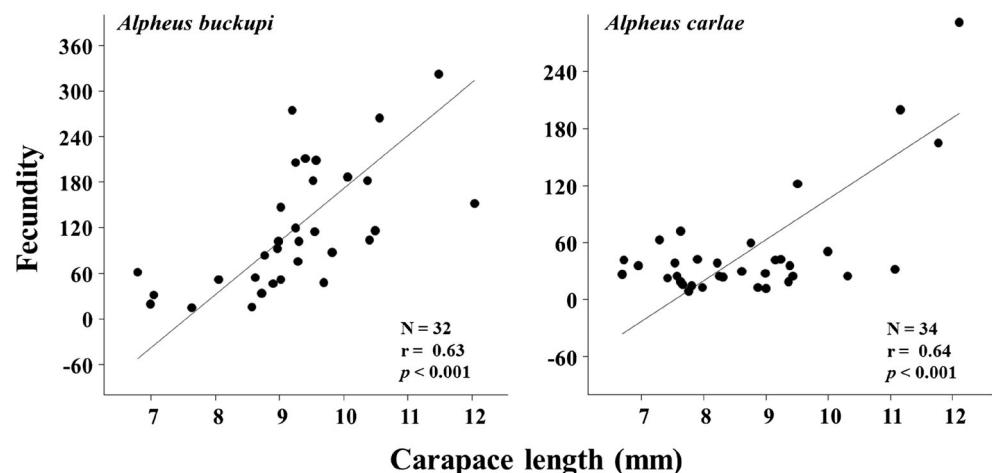
The inverse relationship between fecundity and embryo size observed in the species analyzed is the pattern commonly observed in alpheid shrimps (e. g., Pavanelli et al. 2008, 2010; Harikrishnan et al. 2010), as well as in other caridean shrimps (e. g., Clarke et al. 1991; Bauer 1991; Clarke 1993). Here, *A. buckupi* showed a higher investment in embryo production whereas brooding females of *A. carlae* produced fewer and larger embryos. Thus, as the population of *A. buckupi* was distinct from the population of *A. carlae* regarding embryo size and number, it may suggest different reproductive strategies.

The mode of larval development may influence the reproductive strategies followed by a species (see Bauer 1989). Wehrtmann and Albornoz (2002) observed differences between the reproductive strategies of the sibling species *A. saxidomus* Holthuis 1980 from Eastern Pacific, and *A. simus* Guérin-Méneville, 1855 from western Atlantic. These shrimps have different larval development patterns: The development of *A. simus* is abbreviated and the larvae hatch in a more advanced stage, the decapodid, whereas the development of *A. saxidomus* follows a more typical pattern for alpheids with several zoeal stages. The duration of

embryonic development in crustaceans is directly related to embryo size due to the amount of yolk required to sustain the larval development until the first feeding stage, although this pattern is not seen in some species (see Bauer 1991). Larger and fewer embryos were observed in *A. simus* and attributed to the abbreviated development (Wehrtmann and Albornoz 2002). Such developmental features of *A. simus* are possibly an adaptation to the lower primary productivity of Caribbean waters that result in lower food availability during the larval development, as compared to eastern Pacific waters where *A. saxidomus* occurs (Wehrtmann and Albornoz 2002). However, differently from *A. saxidomus*–*A. simus*, differences in fecundity and embryo size between *A. buckupi* and *A. carlae* might not be directly related to different developmental strategies (see Strathmann 1977; Rabalais and Gore 1985). The larval development of both snapping shrimps remain to be investigated which prevents more precise explanations at this moment.

The influence of environmental factors on the reproductive strategy of different populations of the same species, or of allopatric species (as shown in the sibling species pair *A. saxidomus*–*A. simus*; Wehrtmann and Albornoz 2002) is well documented. Here we found differences between species coexisting in the intertidal zone. Different adaptive strategies

Fig. 2 Correlation between carapace length and fecundity (number of embryos) of two species of *Alpheus* Fabricius 1798, from the coast of Bahia, northeastern Brazil, July 2012–May 2013



apparently have been adopted by these shrimps, possibly to increase the allocation of resources for reproduction, or to reduce the impacts of predation on adults (in the intertidal zone) and to reduce larvae mortality (in the plankton). Furthermore, behavioral differences might also influence the reproduction of these sympatric species, such as advantages in the obtaining of energy resources for reproduction.

This adaptive advantage in obtaining resources can often be related to the size of individuals. The larger size of *A. buckupi* females can make them better competitors in relation to *A. carlae* females, which might result in a higher reproductive potential. Territoriality and agonistic behavior are recognized traits in some species of *Alpheus* (e. g., Nolan and Salmon 1970; Mathews 2002), and larger size might represent a competitive advantage over sympatric species regarding resource allocation for reproduction. Moreover, Bauer (1991) observed a positive allometric correlation between CL and embryo production in *A. normanni* Kingsley 1878, which suggests morphological or physiological adaptations that allow a higher reproductive output with the increase in female size. Indeed, differences in fecundity have been previously associated with the mean size of females. Pavanelli et al. (2010) observed higher embryo production in *A. nuttingi* in relation to one sympatric population of *A. carlae* from São Sebastião, São Paulo, and attributed this difference to the larger size of *A. nuttingi*. Therefore, the larger size of *A. buckupi* females would explain the higher embryo production, as compared to *A. carlae*.

The populations studied here had low fecundity in relation to other species of the genus. Even the mean fecundity found in *A. buckupi* (117 ± 80 embryos) is below the values of other congeners (Table 2). Again, the female size might be the main factor involved here. In caridean shrimps, which incubate embryos under the abdomen, the larger the body size, the greater the capacity for carrying embryos (Bauer 1991). The brooding females analyzed in this study have the smallest mean size among all females of species of *Alpheus* studied so far (Table 2). Their fecundity is only higher when compared to the fecundity of small species of alpheid shrimps (Table 2). Species of *Synalpheus*, for example, produce fewer embryos in comparison to genera that include larger species, such as *Alpheus* and *Betaeus* (see Table 2). These differences might initially be related to size of the species within each genus. Furthermore, species with direct or abbreviated development tend to produce larger and fewer embryos (Wehrtmann and Albornoz 2002). This is the pattern observed in *Synalpheus*, especially in eusocial species (Corey and Reid 1991; Duffy 1996).

The fecundity and reproductive output of the *A. carlae* population from Bahia are lower than those found for a population from southeastern Brazil (Pavanelli et al. 2008). Variation between populations of species with wide distribution has been attributed to latitudinal factors and food

availability (e. g., Lardies and Wehrtmann 2001; Lardies et al. 2008; Mantelatto et al. 2010; Wehrtmann et al. 2011). The increase in embryo volume in populations from higher latitudes of the alpheid *Betaeus truncatus* Dana 1852 from the Chilean coast was related to higher protection (i. e., thermal isolation) against lower water temperatures (Lardies and Wehrtmann 2001).

Populations of alpheid shrimps in lower latitudes reproduce continuously throughout the year (e. g., *A. normanni*; see Bauer 1989) whereas populations in higher latitudes tend to reproduce seasonally (e. g., *S. fritzmulleri* Coutière 1909 and *S. apioceros* Coutière 1909; see Felder 1982). Other alpheids such as *A. carlae* (Mossolin et al. 2006), *S. longicarpus* (Herrick 1891), *S. brooksi* Coutière 1909 and *S. pectiniger* Coutière 1907 (Erdman and Blake 1987) have continuous reproduction with peaks at certain times. Due to energy costs, species that reproduce continuously tend to allocate less energy to each reproductive event. This would be a further explanation for the lower fecundity and RO observed here in comparison with the studies performed on the southeastern coast of Brazil. However, the possibility that the populations analyzed adopt the strategy of multiple spawning throughout the year remains to be tested.

Our data indicate a low embryo loss during incubation in *A. buckupi*. In caridean shrimps, the percentage of embryo loss from the first to the final stage of embryo development might exceed 30% (Corey and Reid 1991; Lardies and Wehrtmann 1997). This might be due to the increase in embryo volume during development, which leads to losses, especially of embryos placed on the outer side of brood masses (Corey and Reid 1991). Behavioral factors, such as intraspecific agonistic interactions or escape from predators might also contribute to embryo loss (see Pavanelli et al. 2010). However, the cryptic habits of alpheid shrimps and their heterosexual pairing behavior might reduce the intensity of these factors (Pavanelli et al. 2010).

The embryos differ substantially in volume and shape throughout development in *A. buckupi* (33% of total increase). This increase is similar to that found for a population of *A. brasileiro* Anker 2012 from Cananéia, southeastern Brazil (35.4%, Pescinelli et al. 2017). Although, this percentage is smaller than that observed in *A. carlae* (64.3%) and *A. nuttingi* (87.4%) populations of southeastern Brazil (Pavanelli et al. 2008, 2010). In other alpheids, the final increment might be even higher (up to 200%; Lardies and Wehrtmann 1997, 2001). The main reason for this increase is the absorption of water by the embryos during incubation (Lardies and Wehrtmann 1997). In addition, the embryos acquire a more oval shape, especially in stage III, in contrast to the more rounded shape of stage I. These changes in embryo shape have been previously reported for the group and are common in decapods (Pavanelli et al. 2008, 2010).

Table 2 Female size (CL), fecundity, embryo volume (EV), and reproductive output (RO) of alpheid shrimps

	N	CL		Fecundity		EV	RO	Locality	Reference
		Min.	Max.	Min.	Max.				
McClure 2002	11	4.78	7.02	9	48	0.13	-	Bahia, Brazil	Present study
<i>Alpheus armillatus</i>	4	7.4	8.8	145	504	0.18	-	Florida, USA	Corey and Reid (1991)
	6	6.29	9.34	27	43	0.13	-	Bahia, Brazil	Present study
<i>Alpheus brasileiro</i>	28	5.30	8.37	149 ± 93	0.12	-		São Paulo, Brazil	Pescinelli et al. 2017
<i>Alpheus buckupi</i>	47	6.79	12.04	32	322	0.10	0.06	Bahia, Brazil	Present study
<i>Alpheus carlae</i>	36	6.69	12.1	12	83	0.13	0.04	Bahia, Brazil	Present study
<i>Alpheus carlae</i> (as <i>A. armillatus</i>)	31	7.7	14.1	42	1979	0.10	0.12	São Paulo, Brazil	Pavanelli et al. (2008)
<i>Alpheus dentipes</i> Guérin 1832	-			-	836	-	-	Málaga, Spain	Fernández-Muñoz and Garcia-Raso (1987)
<i>Alpheus estuariensis</i>	46	7.5	12.2	33	443	0.11	-	Bahia, Brazil	Costa-Souza et al. (2014)
<i>Alpheus euphrosyne euphrosyne</i> de Man 1897	41	11.0	19.2	141	1553	0.004	0.18	Cochin, India	Harikrishnan et al. (2010)
<i>Alpheus glaber</i> (Olivi 1792)	15	8.5	10	180	330	-	-	Off Ancona, Central Adriatic	Atkinson et al. (2003)
<i>Alpheus heterochaelis</i> Say 1818	5	10.0	13.4	133	336	0.91	-	Florida, USA	Corey and Reid (1991)
<i>Alpheus normanni</i>	7	10.0	17.4	68	584	0.09	-	Florida, USA	Corey and Reid (1991)
<i>Alpheus normanni</i>	35	4.1	7.4	-	-	0.03	-	Puerto Rico	Bauer (1991)
<i>Alpheus nuttingi</i>	27	11.0	18.6	949	4222	0.09	0.07	São Paulo, Brazil	Pavanelli et al. (2010)
<i>Alpheus saxidomus</i>	5	10.1	17.4	-	-	0.25	0.44	Costa Rica	Wehrtmann and Graeve (1998)
<i>Betaeus emarginatus</i> (H. Milne Edwards, 1837)	38	9.0	16.3	94	615	0.21	0.09	Valdivia, Chile	Lardies and Wehrtmann (1997)
<i>Betaeus truncatus</i>	25	5.3	11.7	-	1067	0.06	0.07	Guanaquero, Chile	Lardies and Wehrtmann (2001)
<i>Betaeus truncatus</i>	19	-	8.9	-	498	0.09	0.13	Metri, Chile	Lardies and Wehrtmann (2001)
<i>Betaeus truncatus</i>	57	6.54	-	-	731	0.10	0.18	Putemún, Chile	Lardies and Wehrtmann (2001)
<i>Synalpheus agelas</i> Pequegnat and Heard 1979	5	4.2	5.6	16	65	0.27	-	Gulf of Mexico	Corey and Reid (1991)
<i>Synalpheus apioceros</i>	46	3.8	7.4	8	310	-	0.18	Bocas del Toro, Panama	Rebolledo et al. (2014)
<i>Synalpheus brooksi</i>	10	3.4	4.5	3	11	0.50	-	Florida, USA	Corey and Reid (1991)
<i>Synalpheus herricki</i> Coutière 1909	4	3.5	5.1	11	81	0.22	-	Florida, USA	Corey and Reid (1991)
<i>Synalpheus fritzmulleri</i>	13	3.8	6.5	39	484	0.09	-	Florida, USA	Corey and Reid (1991)
<i>Synalpheus longicarpus</i>	21	5.5	8.0	27	349	0.17	-	Florida, USA	Corey and Reid (1991)
<i>Synalpheus pectiniger</i>	31	3.5	4.6	4	17	0.75	-	Florida, USA	Corey and Reid (1991)
<i>Synalpheus yano</i> (Ríos and Duffy 2007)	84	3.7	9.6	6	246	0.06	0.51		Hernaiz et al. (2010)

The RO of *A. buckupi* and *A. carlae*, both around 5% of female body mass, are low compared with other alpheids (Table 2). Previously studied alpheids showed values around 10% (Table 2). Reproductive investment seems to follow an increasing gradient towards high latitudes (e. g., Lardies and Wehrtmann 2001; Lardies et al. 2008). Alpheid shrimps also seem to follow this pattern (Table 2). The low RO value observed in this study for *A. carlae* compared to the population studied in southeastern Brazil (Pavanelli et al. 2008) might also be related to latitudinal factors. *Alpheus buckupi* has not been previously studied, therefore, other populations along the latitudinal gradient need to be analyzed in future studies to verify the relationship between RO and latitude.

Our results indicate that reproductive features differ between sympatric lineages. *Alpheus buckupi* invests more in the number of embryos, whereas *A. carlae* has lower fecundity and higher embryonic volume. These differences suggest that the reproductive strategies of these shrimps are under the influence of different selective forces even though, as sympatric species, they are exposed to similar environmental pressures. This seems to be related to female size differences among species in which the larger size of *A. buckupi* might grant it a competitive advantage, influencing fecundity. The present study provides the first insights on the embryo production of *A. buckupi* in the Western Atlantic and of *A. carlae* in northeastern Brazil.

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Compliance with Ethical Standards

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