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Population structure, relative growth and morphological sexual maturity of the snapping shrimp *Alpheus brasileiro* Anker, 2012 (Caridea: Alpheidae) from the south-eastern coast of Brazil

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ABSTRACT

The present study investigated the population structure of the snapping shrimp *Alpheus brasileiro*. We tested the hypotheses that the sex ratio of the population differs from the expected 1:1 and that the growth pattern differs between adults and juveniles and between sexes. Reproductive period, juvenile recruitment and morphological sexual maturity were estimated. Samples were collected in two periods. The first sampling occurred bimonthly from March 2013 to January 2014. The second sampling occurred monthly from April 2015 to March 2016. The population structure was determined based on the size-frequency distribution of different demographic categories. To analyse the relative growth, we measured the second pleuron length, major cheliped propodus length, major cheliped propodus width, major cheliped propodus height, appendix interna length, appendix masculina length. The results showed that the sex ratio did not differ from 1:1 (male:female). Reproduction and juvenile recruitment were continuous throughout the study period. The analysis of relative growth confirmed the hypothesis that males and females, and juveniles and adults, have different growth patterns, indicating distinct strategies of energy allocation. The estimated carapace length at the onset of morphological sexual maturity was 4.9 mm in males and 4.7 mm in females. The results obtained in this study are probably related to the monogamous social behaviour of *A. brasileiro*. Monogamy can influence demographic parameters such as sex ratio and the size at which males and females reach morphological sexual maturity.

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Introduction

The snapping shrimp genus *Alpheus* Fabricius, 1798, is the largest in the family Alpheidae Rafinesque, 1815, with more than 300 species described worldwide (De Grave and Fransen 2011). It is the genus with the second highest number of species in the infraorder Caridea Dana, 1852 (De Grave and Fransen 2011; Almeida et al. 2014). Alpheid shrimps exhibit wide morphological and ecological diversity and exert important ecological functions in the ecosystems they inhabit. Many species live in mutualistic and commensal associations with anemones, corals, sponges, decapods other than shrimps and Gobiidae fishes (Bauer 2004).

Despite the high number of species of *Alpheus*, there are few studies about population biology of the species, especially in comparison with the extensive knowledge about the taxonomy and diversity of the

family Alpheidae. In Brazil, the population biology of a few species has been studied. Mossolin et al. (2006) and Pavanelli et al. (2008) studied the population structure and reproductive strategy of *Alpheus carlae* Anker, 2012 (as *Alpheus armillatus*, H. Milne Edwards, 1837). Pavanelli et al. (2010) studied the effects of environmental conditions on the reproductive performance of different populations of *Alpheus nuttingi* (Schmitt, 1924). Costa-Souza et al. (2014) studied the reproductive biology and heterosexual pairing of *Alpheus estuariensis* Christoffersen, 1984. Pescinelli, Davanso et al. (2017; Pescinelli, Pantaleão et al. 2017), studied fecundity, social monogamy and described the early larval stages of *Alpheus brasileiro* Anker, 2012.

Alpheus brasileiro belongs to the *A. armillatus* species complex and is endemic to the Brazilian coast. Its distribution ranges from the state of Pará to the state of

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Santa Catarina (Anker 2012). Individuals are found in natural pools of exposed reef areas and under rocks in estuarine environments (Anker 2012; Pescinelli, Davanzo et al. 2017). A previous study of the biology of *A. brasileiro* revealed the occurrence of social monogamy (Pescinelli, Davanzo et al. 2017). According to Wickler and Seibt (1981), social monogamy is the closest association between a male and a female (e.g. paired shrimps) that often involves cooperation in breeding activities.

Information on population biology, such as the sex ratio, reproductive period, recruitment and the size at onset of morphological sexual maturity is essential to understand a species' life history (Stearns 2000). The growth pattern of crustaceans is characterized by ontogenetic differences in body structures during development (Hartnoll 1978). Based on that pattern, the study of relative growth is an effective tool to describe the growth type and to estimate the size at onset of morphological sexual maturity (Hartnoll 1978). The strategy of energy allocation is an important factor to be considered because it is directly associated with physiological processes, such as growth and reproduction (Schaffer 1983; Lika 2003). The energy allocation to reproductive processes in males and females is defined as sex allocation (Charnov 1982). Differences

in the growth of body structures of males and females may result from differential energy allocation strategies, i.e. in males the increasing size of the che-liped reflects the importance of this structure in the reproductive processes, whereas in females, the increase in abdomen growth reflects their reproductive potential, since it is a structure that provides protection for eggs (Charnov 1982).

Based on the information of monogamy in the mating system of *A. brasileiro* (Pescinelli, Davanzo et al. 2017), this study aimed to analyse the population structure of this species and to test the hypotheses that population sex ratio differs from the expected 1:1 and growth patterns differ in adults and juveniles and between the sexes. Morphological sexual maturity, reproductive period, juvenile recruitment and a possible relationship between population structure and environmental factors were also investigated to expand the knowledge of the species' life history.

Materials and methods

Study area

The sampling area was set in an intertidal estuary on the south-eastern Brazilian coast (25°04'11.2"S, 48°03'08.9"W;

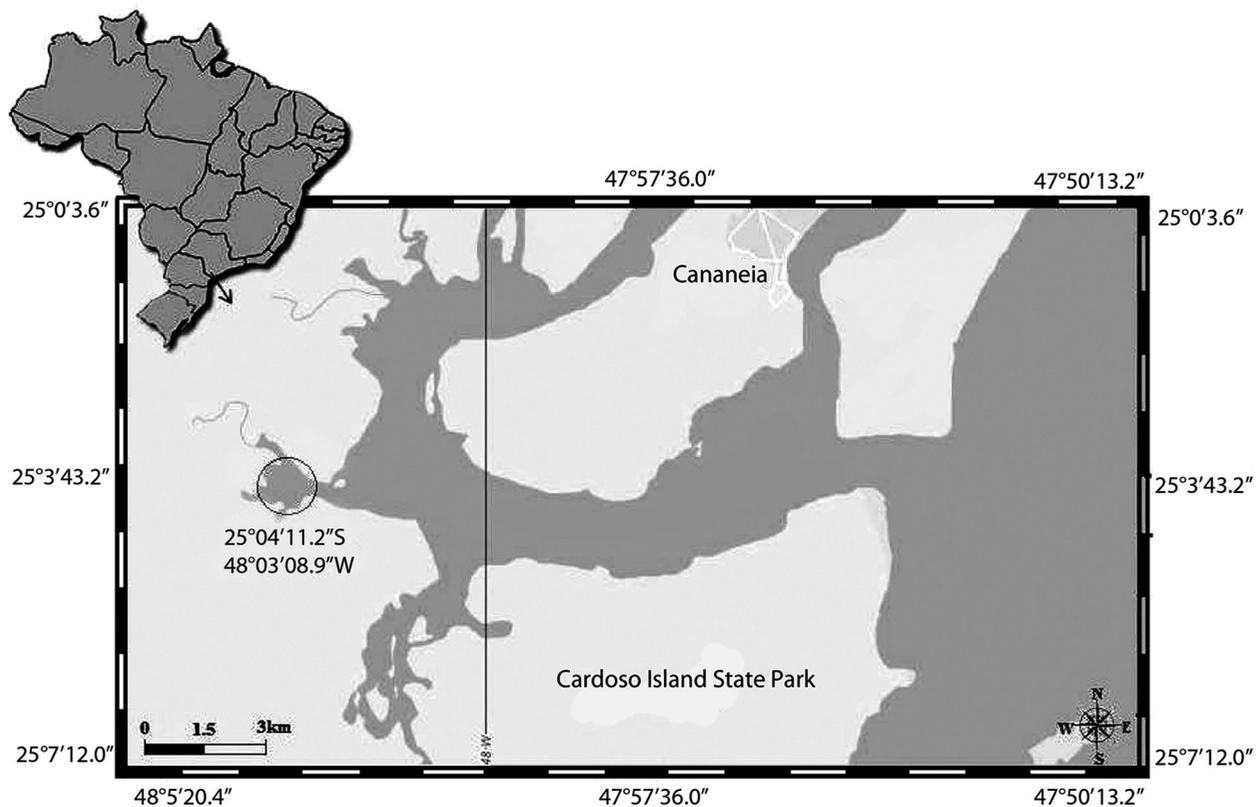


Figure 1. Location of the study area, water represented by dark grey in the map of the intertidal estuarine zone of Cananéia, São Paulo, south-eastern Brazil. Adapted from Pescinelli, Davanzo et al. (2017).

Figure 1). The bottom sediment is composed of a mixture of sand, mud and rocks dispersed throughout the area. Rocks are exposed during low tide, but small puddles of water provide refuge for *A. brasileiro*.

Sampling

Previous samplings showed that the population density of *A. brasileiro* was low at the limited-sized study area (600 m²); therefore, to avoid major disturbances in this population, sampling occurred in two periods. The first sampling occurred bimonthly from March 2013 to January 2014. The second sampling period was delayed more than one year to allow the restructuring of the studied population, thus the samplings occurred monthly from April 2015 to March 2016 and were used in the analyses of the population structure as reproductive period and juvenile recruitment.

The sampling area was divided into three sub-areas perpendicular to the water line. Each sub-area was 20 m long and 5 m wide, and they were sited 10 m apart from each other. Inside each sub-area, three 1-m² units were sampled, yielding nine sampling units per month. These units were equidistant from each other (method adapted from Vergamini and Mantelatto 2008; Costa-Souza et al. 2014). During the low tide, rocks were lifted to collect the shrimps during a sampling effort of 2 h per person. Upon sampling, shrimps were kept in coolers with crushed ice. Paired shrimps were kept together. Next, the shrimp were transported to the laboratory where a number of measurements were recorded.

All specimens captured were classified based on identification keys or information provided by Anker (2012) and Soledade and Almeida (2013). The sex was identified according to the presence (males) and absence (females) of appendices masculinae on the endopods of the second pair of pleopods (Bauer 2004). Individuals smaller than the smallest male found in the study period were considered as undifferentiated. The carapace length (CL) of each individual was measured with a digital calliper of 0.01 mm accuracy. Individuals of small size were measured under a Zeiss Stemi 2000C trinocular stereomicroscope equipped with an ocular micrometer.

Water temperature and salinity were monitored with a mercury thermometer and an optical refractometer, respectively (accuracy = 0.1). Monthly rainfall data were obtained from the Brazilian Integrated Agricultural Weather Data Center (Ciagro).

Population structure

Adult individuals were separated into males, non-ovigerous females and ovigerous females. Juvenile

individuals used in population structure analysis included all the undifferentiated and juvenile males and females. The specimens were analysed in classes of carapace length distributed in intervals of 1 mm in each of the sampled months. Individuals with a CL smaller than 4.9 mm (males) and 4.7 mm (females) were designated as juveniles (estimated through the sexual maturity analysis detailed below). A chi-square test (χ^2) with a significance level of 5% (Sokal and Rohlf 1995) was used to determine whether the sex ratio followed a 1:1 ratio during each month of the first and second sampling period. Undifferentiated individuals were excluded from the analysis of the sex ratio. Months with fewer than 20 individuals were not included in this analysis (Vieira 2011).

Normality was checked using the Shapiro–Wilk test (Zar 1996). The reproductive period was estimated based on the observation of ovigerous females in the population. Juvenile recruitment was estimated based on the occurrence of all juvenile categories (including undifferentiated) in the population. To verify the reproductive period and juvenile recruitment only the data of the second sampling period (April 2015 to March 2016) were used because in this period the collections were monthly.

A cross-correlation (Sokal and Rohlf 1981) was used to evaluate the correlation between environmental factors (water temperature/salinity and rainfall) and the abundance of ovigerous females, undifferentiated juveniles and male and female juveniles. For this analysis, only the data collected from April 2015 to March 2016 were used.

Relative growth and estimation of size at the onset of morphological sexual maturity

For relative growth, a subsample of 166 individuals from the first sampling period (from March 2013 to January 2014) that had intact body structures was used. Measurements included the second pleuron length (SPL), major cheliped propodus length (CPL), major cheliped propodus width (CPW), major cheliped propodus height (CPH), appendix interna length (AIL), appendix masculina length (AML) and CL (Figure 2).

The relative growth analysis detects changes in the growth pattern of particular body structures in relation to a constantly growing body part, e.g. the carapace length (independent variable). The allometric equation $y = ax^b$ was used as a linearized equation ($\log y = \log a + b \log x$) in which y is the dependent variable (body structure), x is the independent variable (CL), b is the allometric coefficient and a is the intercept. The allometric condition b was analysed for each structure

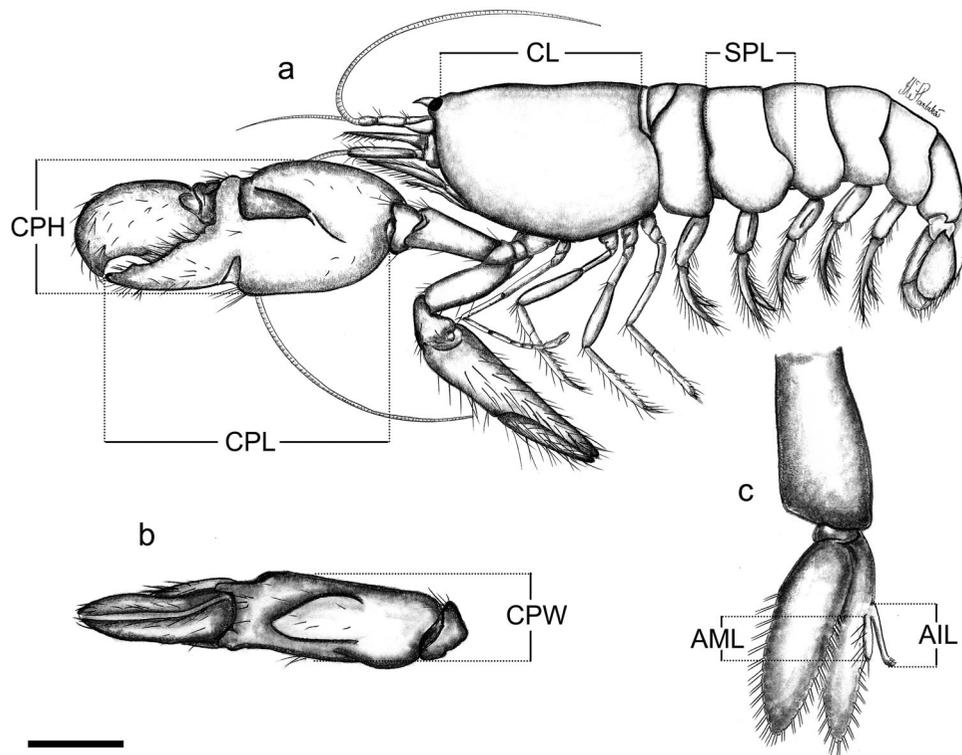


Figure 2. *Alpheus brasileiro* Anker, 2012. Body dimensions used in the morphometric analyses. (a) lateral view, (b) dorsal view of major cheliped propodus and dactylus, (c) second pleopods. SPL, second pleuron length; CPL, major cheliped propodus length; CPW, cheliped propodus width; CPH, major cheliped propodus height; AIL, appendix interna length; AML, appendix masculina length; CL, carapace length. (Scales: a, b = 3 mm, c = 1 mm). Illustrations by João Alberto Farinelli Pantaleão.

($b = 1$: isometry, $b < 1$: negative allometry, $b > 1$: positive allometry) with Student's *t*-test ($H_0: b = 1$; $\alpha = 0.05$; Zar 1996). A non-hierarchical 'K-means clustering' analysis was performed on the log-transformed data. This method distributes the data into a predetermined number of groups. This number is defined by an iterative process that minimizes the variance within groups and maximizes the variance among them. The result of this classification (K-means) was refined by applying a discriminant analysis (DA). To determine the morphological sexual maturity, the relationships where the allometric coefficient changed between the juvenile and adult stage (i.e. different linear equations) were selected. The size of the smallest individual classified as an adult was used as the value at which the species reaches the morphological sexual maturity. This statistical procedure was based on the study of Sampedro et al. (1999).

After the separation of the log-transformed data, an analysis of covariance (ANCOVA) was applied to compare the angular and linear coefficients (slopes and intercepts) for each of six secondary sexual characters by CL and a covariate group (juveniles vs. adults and males vs. females). Juveniles and adults were compared separately for each sex. This analysis determined

whether the data for each relationship were best described by a single straight line or if the demographic groups were best represented by different linear equations (i.e. differential growth between juveniles and adults, and between males and females).

Results

In the first sampling period, water temperature ranged from 20 to 30°C ($24.5 \pm 4.5^\circ\text{C}$), salinity ranged from 4 to 20 ppt (12.4 ± 6.2 ppt) and rainfall ranged from 99 to 418 mm (185 ± 127 mm). In the second sampling period, water temperature ranged from 21 to 28°C ($24.2 \pm 1.93^\circ\text{C}$), salinity ranged from 5 to 29 ppt (15.4 ± 7.7 ppt) and rainfall ranged from 30 to 413 mm (189 ± 108 mm) (Figure 3).

During the study, 498 individuals were collected and measured, 185 in the first sampling period and 313 in the second. The CL ranged from 2.8 to 10.1 mm (5.2 ± 1.5 mm) in the first period, and from 2.5 to 8.9 mm (5.4 ± 1.6 mm) in the second period (Table I). There was no statistically significant difference between the mean sizes of males and females (Mann-Whitney; $P > 0.05$). Oviparous females were more frequent in the size class interval from 4 to 8 mm (Figure 4) and were

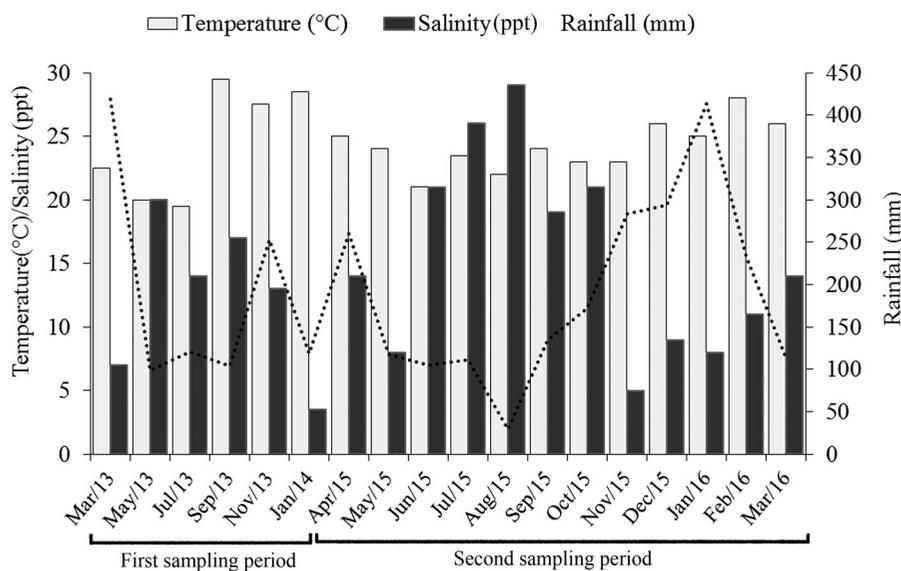


Figure 3. Temporal variation of temperature, salinity and rainfall at Cananéia, São Paulo state, south-eastern Brazil, during the study period.

Note: Rainfall data from Brazilian Integrated Agricultural Weather Data Center (Ciagro).

Table I. *Alpheus brasileiro* Anker, 2012. Carapace length of each demographic category of the population at Cananéia, São Paulo state, south-eastern Brazil, in two periods (March 2013–January 2014 and April 2015–March 2016).

Demographic category (Mar/13–Jan/14)	N	Min – Max (CL-mm)	Mean ± SD	%
Undifferentiated	3	2.8–2.9	2.8 ± 1.5	1.6
Juvenile males	35	2.9–4.9	4.0 ± 1.4	18.9
Adult males	53	4.9–8.5	6.4 ± 1.5	28.6
Juvenile females	32	2.9–4.6	3.7 ± 1.4	17.3
Females without eggs	27	4.8–10.0	5.9 ± 1.4	14.6
Females with eggs	35	4.8–10.0	5.9 ± 1.5	18.9
Total	185	2.8–10.0	5.2 ± 1.5	100
(Apr/15–Mar/16)	N	Min-Max (CL-mm)	Mean ± SD	%
Undifferentiated	12	2.5–2.8	2.6 ± 1.7	3.8
Juvenile males	64	2.9–4.9	3.9 ± 1.6	20.5
Adult males	90	4.9–8.9	6.5 ± 1.6	28.8
Juvenile females	46	2.9–4.7	3.9 ± 1.5	14.7
Females without eggs	13	4.8–8.6	6.3 ± 1.8	3.8
Females with eggs	88	4.8–8.9	6.4 ± 1.7	28.2
Total	313	2.5–8.9	5.4 ± 1.6	100

observed in all months in the second period (April 2015 to March 2016) (Figure 5). There was no statistically significant correlation between the abundance of ovigerous females and water temperature, salinity or rainfall (cross-correlation, $P > 0.05$). Juveniles were collected every month in the second period of sampling except August 2015 (Figure 5). As with the ovigerous females, there was no statistically significant correlation between the abundance of juveniles and water temperature, salinity or rainfall (cross-correlation, $P > 0.05$). The overall sex ratio was 1:0.99 and did not differ statistically from the expected 1:1 ($P = 0.891$), and also did not differ when analysed in each of the months ($P > 0.05$) (Table II).

All growth equations for different morphological structures differed significantly in either slopes or

intercepts between juveniles and adults (ANCOVA, $P < 0.05$), except AML vs. CL ($P > 0.05$) (Table III). Similarly, the allometric growth of males and females differed significantly, indicating a sex-specific growth rate of all studied body structures (ANCOVA, $P < 0.05$) (Table IV).

The relationship that best represented the changes in the growth of secondary characters between juveniles and adults was CPL vs. CL in males and SPL vs. CL in females. The estimated CL of males and females at morphological sexual maturity were 4.9 and 4.7 mm, respectively (size estimated based on the relative growth analyses) (Figure 6). The allometric relationships are in Table V. The main changes in allometry were found in the relationships SPL vs. CL in females with negative allometry in juveniles and positive

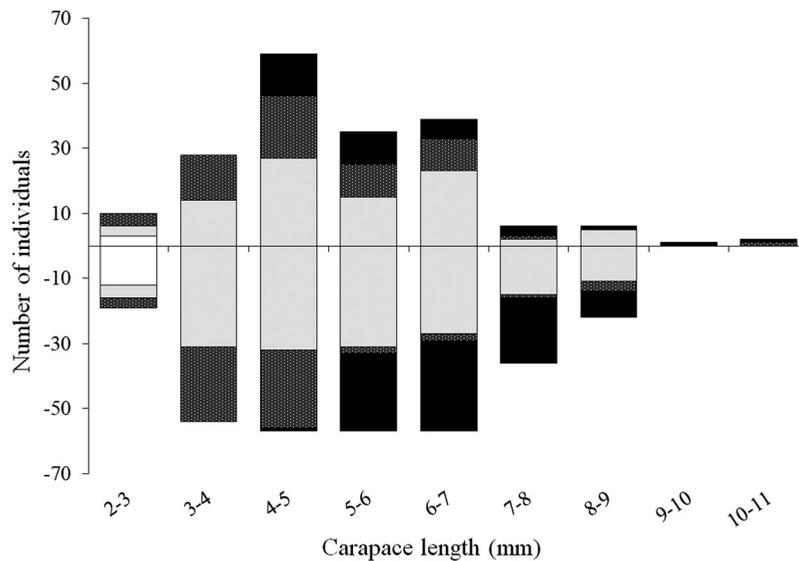


Figure 4. *Alpheus brasileiro* Anker, 2012. Size-frequency distribution of undifferentiated juveniles (white bars), juvenile + adult males (light grey bars), juvenile + adult females without eggs (dotted dark grey bars) and females with eggs (black bars) (all individuals sampled, $n = 497$) at Cananéia, São Paulo state, south-eastern Brazil. Values above the x-axis refer to March 2013–January 2014 and the values below the x-axis refer to April 2015–March 2016. Class interval of 1 mm (CL).

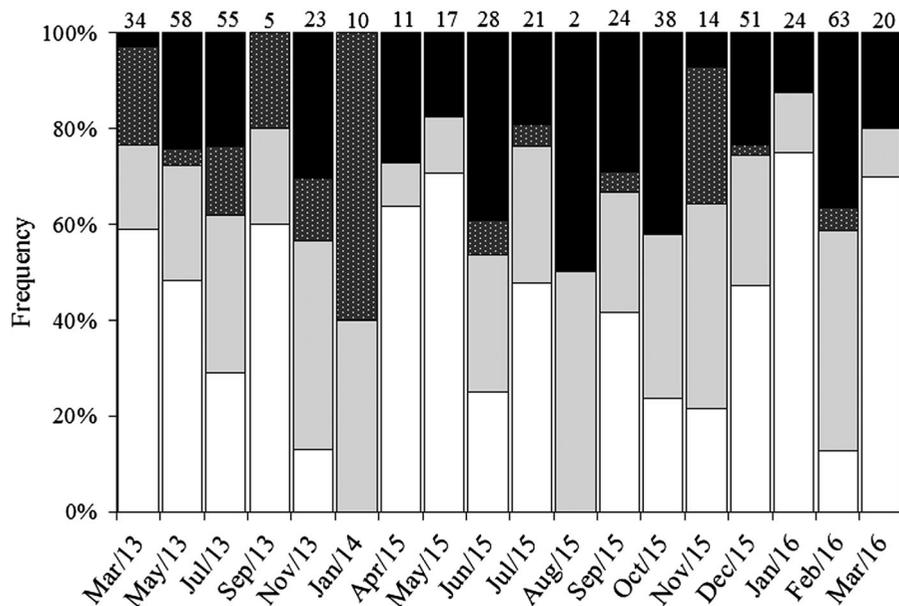


Figure 5. *Alpheus brasileiro* Anker, 2012. Monthly per cent frequency of the juveniles (white bars), adult males (light grey bars), adult females (dotted dark grey bars) and females with eggs (black bars), at Cananéia, São Paulo state, south-eastern Brazil. The numbers on the top of the bars correspond to the number of individuals sampled in every month.

allometry in adult females, CPL vs. CL and CPW vs. CL in males with positive allometry in juveniles and isometric in adult males (Table V).

Discussion

The snapping shrimp *A. brasileiro* did not show sexual dimorphism in body size, which can be explained by

its social and reproductive behaviour that may include social monogamy (Pescinelli, Davanzo et al. 2017). A monogamous sexual system is a strategy of fidelity between sexes that defend and share a specific microhabitat or refuge (Thiel and Baeza 2001; Correa and Thiel 2003). In monogamic species, the size difference between sexes is minimal and often absent (Correa and Thiel 2003) because body size is a crucial

Table II. *Alpheus brasiliro* Anker, 2012. Proportion of males and females at Cananéia, São Paulo state, south-eastern Brazil (undifferentiated individuals were excluded). The deviation from an equal sex ratio was tested for each month. The test was applied only for monthly samples >20 individuals.

Month	Males	Females	<i>P</i>	χ^2	Male/Female
Mar/13	14	20	0.300	1.050	1:1.42
May/13	31	28	0.690	0.151	1:0.90
Jul/13	28	27	0.890	0.010	1:0.96
Sep/13	3	2	–	–	–
Nov/13	12	11	0.830	0.041	1:0.92
Jan/14	4	6	–	–	–
Apr/15	5	5	–	–	–
May/15	6	8	–	–	–
Jun/15	12	16	0.449	0.571	1:1.33
Jul/15	12	9	0.512	0.428	1:0.75
Aug/15	1	1	–	–	–
Sep/15	9	12	0.512	0.428	1:1.33
Oct/15	17	18	0.865	0.028	1:1.06
Nov/15	7	6	–	–	–
Dec/15	25	21	0.563	0.333	1:0.85
Jan/16	12	12	1	0	1:1
Feb/16	35	29	0.385	0.753	1:0.80
Mar/16	9	9	–	–	–
Total	242	240	0.891	0.018	1:0.99

Table III. *Alpheus brasiliro* Anker, 2012. Results of analysis of covariance (ANCOVA) between juveniles and adults of males and females for each relationship at at Cananéia, São Paulo state, south-eastern Brazil. SPL, second pleuron length; CPL, cheliped propodus length; CPW, cheliped propodus width; CPH, cheliped propodus height; AIL, appendix interna length; AML, appendix masculina length; CL, carapace length; J, juvenile; A, adult. Par = parameter, F = statistic values; *P* = significance *Significant difference *P* < 0.05 (different growth between juveniles and adults of males and females).

Relationship	Factor (group)	Par. (Log)	<i>F</i>	<i>P</i>
SPL vs. CL	Male (J vs. A)	intercept	7.228	0.008*
		slope	0.025	0.874
	Female (J vs. A)	–	–	–
CPL vs. CL	Male (J vs. A)	slope	49.025	0.000*
		slope	13.112	0.000*
	Female (J vs. A)	intercept	4.050	0.047*
CPW vs. CL	Male (J vs. A)	slope	0.058	0.808
		intercept	29.389	0.000*
	Female (J vs. A)	slope	1.785	0.185
CPH vs. CL	Male (J vs. A)	intercept	33.249	0.000*
		slope	1.096	0.298
	Female (J vs. A)	intercept	33.862	0.000*
AIL vs. CL	Male (J vs. A)	slope	0.058	0.810
		slope	11.988	0.000*
	Female (J vs. A)	–	–	–
AML vs. CL	Male (J vs. A)	slope	8.612	0.004*
		slope	6.718	0.011*
	Female (J vs. A)	intercept	0.043	0.834
CPL vs. CL	Male (J vs. A)	intercept	0.240	0.625
		slope	3.159	0.079
	Female (J vs. A)	–	–	–

factor in pair formation, and individuals with a large size difference do not pair (Rodrigues et al. 2009). A positive correlation between the carapace length of

Table IV. *Alpheus brasiliro* Anker, 2012. Results of analysis of covariance (ANCOVA) between males and females for each relationship at Cananéia, São Paulo state, south-eastern Brazil. SPL, second pleuron length; CPL, cheliped propodus length; CPW, cheliped propodus width; CPH, cheliped propodus height; AIL, appendix interna length; CL, carapace length. Par = parameter, *F* = statistic values; *P* = significance *Significant difference *P* < 0.05 (different growth).

Relationship	Factor (group)	Par. (Log)	<i>F</i>	<i>P</i>
SPL vs. CL	Males vs. Females	slope	68.777	0.000*
CPL vs. CL	Males vs. Females	slope	69.154	0.000*
CPW vs. CL	Males vs. Females	slope	6.071	0.014*
CPH vs. CL	Males vs. Females	slope	7.022	0.008*
AIL vs. CL	Males vs. Females	slope	8.612	0.004*

paired males and females (size-assortative pairing) was also observed in *A. brasiliro* (Pescinelli, Davanso, et al. 2017).

The sex ratio in the studied population did not differ from the expected 1:1. This is probably related to the monogamous social behaviour in which the pair formation results in an equal distribution of the sexes in the population, thus producing a sex ratio close to or equal to 1:1 (Correa and Thiel 2003). Similar results were found in populations of *A. carlae* (as *A. armillatus*) (Mossolin et al. 2006), *Alpheus dentipes* Guérin, 1832 (Fernández-Muñoz and Garcia-Raso 1987) and *Alpheus angulosus* McClure, 1995 (Mathews 2002). These results corroborate the idea that the 1:1 sex ratio may be related to the pairing behaviour of these species.

The reproductive activity of *A. brasiliro* in the second sampling period was continuous, with the presence of ovigerous females from April 2015 to March 2016. A continuous reproductive period was reported in a population of *A. carlae* (as *A. armillatus*) in the south-eastern coast of Brazil (Mossolin et al. 2006) and of *A. estuariensis*, from the north-eastern coast of Brazil (Costa-Souza et al. 2014). *Synalpheus longicarpus* Herrick, 1891 and *A. dentipes* also exhibited continuous reproduction in the eastern Gulf of Mexico and in southern Spain, respectively (Erdman and Blake 1987; Fernández-Muñoz and Garcia-Raso 1987).

In tropical and subtropical regions, environmental factors, such as temperature and photoperiod, usually show little variation (Sastry 1983). Furthermore, the availability of food tends to be consistent over the year (Sastry 1983), which may favour continuous reproduction. In caridean shrimps with continuous reproduction, the ovarian development commonly occurs during the embryo incubation (Bauer 2004). Thus, shortly after larvae hatch, females can copulate and produce new embryos (Bauer 2004). The lack of correlation between the abundance of ovigerous females and temperature, salinity or rainfall indicates that

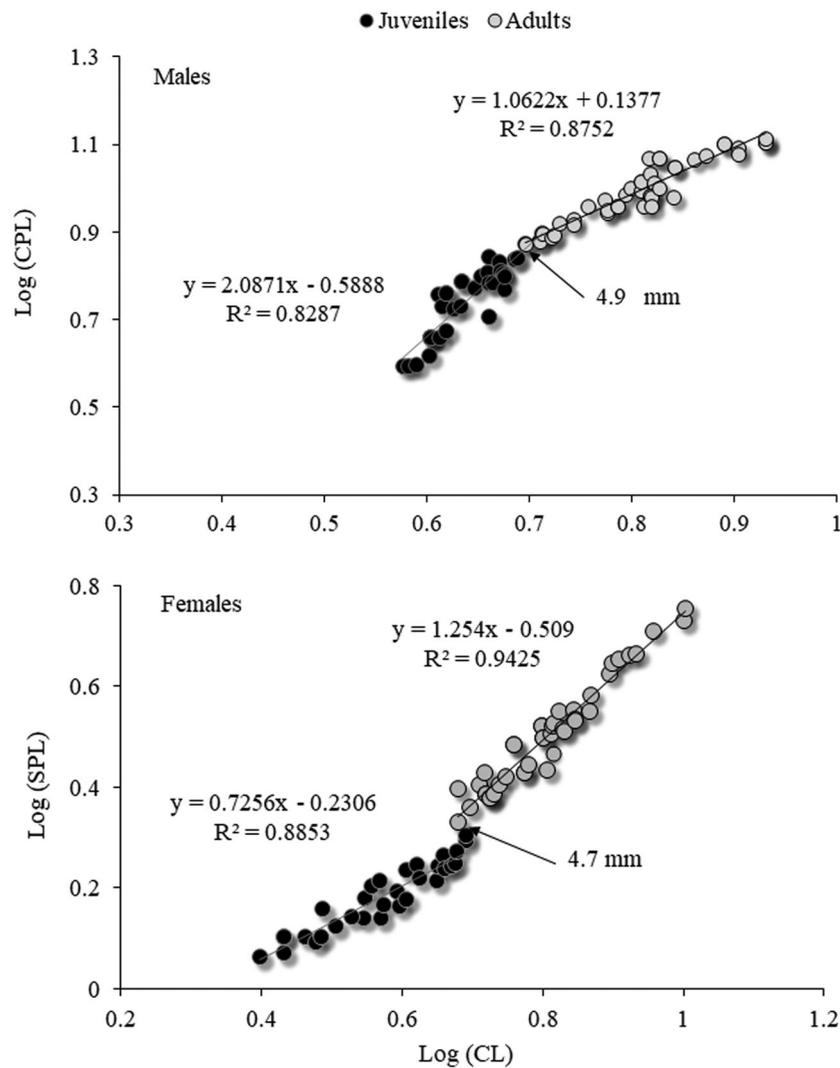


Figure 6. *Alpheus brasileiro* Anker, 2012. Estimated size of morphological sexual maturity for males and females at Cananéia, São Paulo state, south-eastern Brazil. The estimated size refers to the smallest individual after the inflection point of the equations for juveniles and adults. CPL, cheliped propodus length; SPL, second pleuron length; CL, carapace length.

these factors are not modulating reproduction in this population.

The availability of food resources is an important factor in the development of embryos and the subsequent release of the planktonic larvae into the environment (Sastry 1983). Thus, species living in estuarine environments benefit because they have a high level of nutrients available throughout the year (Levinton 1995). These conditions are found in the region where the study was conducted (Schaeffer-Novelli et al. 1990).

The period and intensity of recruitment can vary substantially among alpheid populations. Some alpheids exhibit continuous recruitment, as in *S. longicarpus* (Erdman & Blake 1987) and *A. dentipes* (Fernández-Muñoz & García-Raso 1987); or seasonal recruitment, as observed in *Synalpheus fritzmuelleri*

Coutière, 1909 (Felder 1982). As in the reproductive period *A. brasileiro* exhibited continuous recruitment in the second sampling period (April 2015 to March 2016). Juveniles were collected in all months except August 2015, however this may have been related to a sampling-related bias caused by the incomplete exposure of the sampled area during the low tide resulting in only two individuals being collected in this month. The intensity of recruitment is associated with several factors, including the constancy of embryo production and the temporal variation in the mortality of planktonic larvae and/or juveniles (Bauer 1989). The juvenile recruitment of *A. brasileiro* remained within the expected range for populations from tropical and subtropical regions in which reproduction and recruitment are continuous (Bauer 1989; Vergamini and Mantelatto 2008).

Table V. *Alpheus brasileiro* Anker, 2012. Allometric analyses of transformed morphometric data (log) using carapace length as independent variable at Cananéia, São Paulo state, south-eastern Brazil. SPL, second pleuron length; CPL, cheliped propodus length; CPW, cheliped propodus width; CPH, cheliped propodus height; AIL, appendix interna length; AML, appendix masculina length; CL, carapace length; JM = juvenile males, AM = adult males, JF = juvenile females, AF = adult females; b = allometric coefficient; a = where the line intersects the y-axis; r^2 = determination coefficient; T = statistic values; P = significance; + = positive allometry, 0 = isometry, - = negative allometry.

Relationship	Sex phase	N	a	b	r^2	$T (b = 1)$	P	Allometry
SPL vs. CL	JM	34	-0.353	0.897	0.721	1.122	<0.001	-
	AM	46	-0.299	0.878	0.770	1.706	<0.001	-
	JF	35	0.230	0.725	0.885	5.124	<0.001	-
	AF	51	-0.509	1.254	0.942	5.110	<0.001	+
CPL vs. CL	JM	33	-0.509	2.087	0.828	3.531	<0.001	+
	AM	47	0.138	1.062	0.875	1.245	>0.001	0
	JF	44	0.312	0.711	0.671	4.289	<0.001	-
CPW vs. CL	AF	42	0.321	0.738	0.665	3.168	<0.001	-
	JM	31	-0.565	1.071	0.754	0.627	<0.001	+
	AM	49	-0.367	0.902	0.776	1.374	>0.001	0
CPH vs. CL	JF	29	-0.439	0.821	0.619	1.446	<0.001	-
	AF	57	-0.273	0.680	0.693	5.047	<0.001	-
	JM	33	-0.255	0.995	0.791	0.109	>0.001	0
AIL vs. CL	AM	47	-0.154	0.968	0.815	0.463	>0.001	0
	JF	33	-0.348	1.105	0.846	1.103	<0.001	+
	AF	53	0.035	0.618	0.640	5.902	<0.001	-
AML vs. CL	JM	39	-1.065	0.972	0.750	1.017	>0.001	0
	AM	41	-1.394	1.350	0.772	2.870	<0.001	+
	JF	41	-1.325	1.460	0.824	4.263	<0.001	+
AML vs. CL	AF	45	-1.354	1.423	0.751	3.156	<0.001	+
	JM	34	-1.432	1.284	0.832	2.871	<0.001	+
	AM	46	-1.641	1.553	0.812	4.867	<0.001	+

The relative growth showed different allometric coefficients, confirming the hypothesis that males and females and adults and juveniles have different growth patterns. The varied growth pattern of body structures of males and females may reflect distinct strategies of energy allocation. Thus, the body structures that best indicated the size at which individuals reach morphological sexual maturity were different for males than for females. The major cheliped propodus in males and the second abdominal pleuron in females showed changes in the growth pattern between the different demographic categories (juveniles and adults).

The major cheliped propodus size in males is important in the agonistic behaviour (disputes over females and territory), defence against predators and construction of burrows. It is essential for the cheliped to reach a functional size during the process that culminates in maturity, influencing the reproductive success of males (Nolan and Salmon 1970; Versluis et al. 2000). Therefore, differences of the growth of cheliped propodus between juvenile and adult stages can be used to estimate morphological sexual maturity in *A. brasileiro*.

The increased growth of the second pleuron in females occurred after morphological sexual maturity was reached, with the increased size providing a larger space for carrying the eggs. In caridean females, the size of the second pleuron is an important adaptation for egg incubation and is one of the factors influencing reproductive success (Bauer 2004).

The slight difference between the estimated values of sexual maturity of males and females indicated that both sexes reach maturity at similar sizes. The socially monogamous behaviour and the size-assortative pairing in *A. brasileiro* (Pescinelli, Davanzo et al. 2017) probably influence the similar values of sexual maturity of males and females.

The negative allometric growth of the major cheliped propodus in females and of the second abdominal pleuron in males reflects the different energy allocation strategy of each sex. In crabs, this situation is very common. Males are likely to invest more energy in the major cheliped propodus growth because of its use in territorial disputes and intra- and interspecific interactions.

The allometric growth of the appendix masculina was positive in *A. brasileiro* juveniles and adults. Studies on caridean shrimps indicated that this appendix is important during the spermatophore transfer from the male to the female (Bauer 1976; Berg and Sandifer 1984). The allometric growth of the appendices internae of the second pleopod in males varied from isometric in juveniles to positive in adults. Alternatively, in females, the growth was positive in juvenile and adults. This small structure has a hook-like shape known as *cincinnuli* (Bauer 1976), that helps in the synchronized movement of the pleopods during swimming. Therefore, the growth of this structure is important for locomotion and in the construction and maintenance of shrimp burrows.

The current study has brought forward new information on the population biology of *A. brasileiro*, and the results reinforce the influence of the monogamous social behaviour on the species' population biology. This information may improve the understanding of the species' life history and may be used in other comparative ecological or behavioural studies.

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