

# Life History Traits of the Snapping Shrimp *Alpheus carlae* (Decapoda: Alpheidae) from the South-eastern Coast of Brazil

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The life history traits of the snapping shrimp *Alpheus carlae* were investigated. We evaluated the relative growth, morphological sexual maturity, sexual dimorphism, handedness, fecundity, and egg volume. Sampling was performed monthly in an estuarine region of Cananéia, in the south-eastern coast of Brazil. The following structures were measured to perform the relative growth analysis: length of carapace and second pleonal pleuron, length, width and height of major cheliped propodus, and length of appendix interna and appendix masculina. Juveniles and adults males and females have different growth patterns, indicating distinct strategies of energy allocation. The estimated carapace length at the onset of morphological sexual maturity of females and males was 5.6 mm and 6.2 mm, respectively. The sexual dimorphism of specific body structures was evident, mainly in the appendix interna of females and major cheliped of males. There was no evidence of handedness in females or males. The mean fecundity of females was  $364 \pm 204$  eggs (mean  $\pm$  SD) eggs and was positively correlated with the carapace length. The egg volume differed between developmental stages I and II, and I and III, with an overall volume increase of 73.23% and 95.45%, respectively. The results contribute to the knowledge about *A. carlae* and its life history in natural environment.

**Key words:** Caridea, Relative growth, Sexual dimorphism, Egg production.

## BACKGROUND

The life history theory is based on optimization models that assume extrinsic and intrinsic factors (Stearns 2000) such as environmental conditions and tradeoffs among life history traits, respectively. These factors can change the patterns of resource allocation of species in order to maintain reproductive success (Schaffer 1974; Stearns 2000). The key factor of this theory is understanding what influences the survival and reproduction of individuals of different ages or stages of development, how traits are interconnected and their constraints. Age, size at sexual maturity, and reproductive investment are the main life history

traits and they have a significant impact on mortality rates, fecundity, and tradeoffs (Stearns 2000; Lika and Kooijman 2003).

Tradeoffs between age and size at sexual maturity and between reproductive investment and lifespan are common throughout an individual life history (Stearns 2000; Lika and Kooijman 2003). Growth and reproduction are antagonist processes and represent a typical tradeoff during development (Koene and Ter Maat 2004), therefore an increase in the allocation of resources devoted to reproduction results in decreased growth. The allocation of resources for reproductive processes may be different in males and females of the same species as a result of their different roles in the

population; this is defined as sex allocation (Charnov 1982).

In crustaceans, the allocation of energy toward reproduction occurs at the expense of somatic growth and results in the development of secondary sexual characters and is an example of this type of tradeoff (Lika and Kooijman 2003; Marochi et al. 2019). Crustaceans are characterized by having ontogenetic differences in the growth pattern of certain body structures during development (Hartnoll 1978). Therefore, the study of relative growth is an effective tool to analyze the type of growth among stages of development and sexes and to estimate the size at morphological sexual maturity (Hartnoll 1978). Furthermore, it can reveal different energy allocation strategies between males and females of different species to improve their reproductive potential (Charnov 1982). The energy allocated to reproduction can also be evaluated by estimating the fecundity and volume of eggs in females (Corey and Reid 1991).

Snapping shrimps of the genus *Alpheus* Fabricius, 1798 are the most representative genus of the family Alpheidae Rafinesque, 1815, with more than 300 species described worldwide (De Grave and Fransen 2011). *Alpheus* species commonly have a monogamic mating system characterized by the close association between one male and one female (Boltaña and Thiel 2001; Mathews 2002). Our target species, *Alpheus carlae* Anker, 2012, is a common representative of the *A. armillatus* H. Milne Edwards, 1837 [in H. Milne Edwards 1834–1840] species complex. This snapping shrimp has a wide distribution in the Brazilian coast, from the state of Ceará to the state of São Paulo (Anker 2012). Individuals are found in a wide variety of ecological microhabitats such as coral fragments, under rocks, in tidal pools of estuarine areas, and in mangrove root holes (Baeza and Thiel 2007; Anker 2012; Pescinelli et al. 2018). Some biological aspects of *A. carlae* have already been studied (Mossolin et al. 2006; Pavanelli et al. 2008, as *A. armillatus*), but the correct status of the species in the *A. armillatus* complex was not clear when these studies were conducted. The fecundity (Soledade et al. 2017), growth, and sexual maturity (Costa-Souza et al. 2019) were estimated for populations of *A. carlae* from northeastern Brazil. Although *A. carlae* has been increasingly studied in recent years, there is a lack of information about the life history traits of populations from the south-eastern Brazilian coast. There are only records of the species in the São Paulo state (Almeida et al. 2018) and a description of the first larval stages (Pantaleão et al. 2020).

Considering the tradeoff between energy allocation to reproduction or somatic growth in crustaceans

(Hartnoll 1985; Lika and Kooijman 2003), knowledge on sex allocation are fundamental to understanding the life history traits of a species. Besides the close association between males and females, *Alpheus* species are characterized by a heterosexual size-assortative pairing when individuals are under the same environmental and biotic conditions. Our goal is to analyze the following life history traits of the snapping shrimp *A. carlae*: relative growth, morphological sexual maturity, sexual dimorphism, handedness, fecundity, and egg volume.

## MATERIALS AND METHODS

### Study area, sampling and data analysis

Sampling was conducted monthly from April 2015 to March 2016 in an intertidal estuary in Cananéia, São Paulo, in the south-eastern Brazilian coast (25°04'11.2"S 48°03'08.9"W) (Fig. 1). The sediment is composed of mud with rocks dispersed throughout the area (Fig. 2A). The rocks are exposed during low tides, forming small puddles of water that provide refuge to shrimps. The sampling area was divided into three sub-areas (20 m long × 5 m wide) perpendicular to the water line and 10 m apart from each other. Samples were taken from three 1 m<sup>2</sup> units equidistant from each other, a total of nine sampling units per month (method adapted from Pescinelli et al. 2017). *Alpheus carlae* (Fig. 2B) individuals were manually taken from under rocks during daylight and low tide and were individualized for transportation. All the ovigerous females were individualized separately to avoid loss and damage to eggs. In laboratory, males and females were identified according to the presence or absence of the appendix masculina in the endopod of the second pair of pleopods, respectively (Bauer 2004).

Morphological analyses were conducted based on the following measurements taken under a stereomicroscope (0.01 mm): Carapace length (CL), second pleonal pleuron (SPP), major cheliped propodus length (CPL), major cheliped propodus width (CPW), major cheliped propodus height (CPH), appendix interna length (AIL), and appendix masculina length (AML) (Fig. 3).

The normality of data was tested using the Shapiro-Wilk test (Zar 1996). Differences in the relative growth of body structures indicated the pattern of energy allocation used by individuals for somatic growth or reproduction in the different stages of development. These differences were analyzed using the allometric equation ( $y = a \cdot x^b$ ) used in the linearized version ( $\log y = \log a + b \log x$ ), where  $y$  is the dependent variable

or the dimension studied (SPL, CPL, CPW, CPH, AIL and AML),  $x$  is the independent variable (CL),  $b$  is the allometric coefficient, and  $a$  is the point at which the straight line intersects the ordinate axis (Hartnoll 1978). The allometric condition  $b$  of each body structure was analyzed ( $b = 1$ : isometry;  $b < 1$ : negative allometry;  $b > 1$ : positive allometry) using the Student's t-test (Ho:  $b = 1, \alpha = 0.05$ ) (Zar 1996).

A non-hierarchical  $K$ -means clustering analysis was performed with the log-transformed data. This method distributes the data into a predetermined number of groups (two groups: juvenile and adults) (Sampedro et al. 1999). The result of this classification ( $K$ -means) was refined by a discriminant analysis (DA). Angular and linear coefficients (slopes and intercepts) were compared for each relationship using an analysis of covariance (ANCOVA). The ANCOVA determines if the data from 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) (Sampedro et al. 1999).

The morphological sexual maturity was estimated

based on the relationships in which the allometric coefficient changed between the juvenile and adult stage (*i.e.*, different linear equations). The size of the smallest adult was used as the value at which the species reaches the morphological sexual maturity (Sampedro et al. 1999).

The sexual dimorphism was analyzed by comparing the allometric coefficient resulting from the growth of body structures. The Mann-Whitney test ( $\alpha = 0.05$ ) was used to verify the differences between the size of each body structure of males and females. Handedness was verified according to the proportion of right and left chelipeds with a Chi-square test ( $\chi^2$ ) ( $\alpha = 0.05$ ).

The eggs were carefully removed from the pleopods of ovigerous females using a brush; they were placed in a Petri dish, counted, and classified visually into one of the following stages of embryonic development: Early stage (I), with no eyes and yolk occupying 75 L 100% of egg volume; intermediate stage (II), with vestigial eyes and yolk occupying about 50 L 75% of egg volume; and final stage (III), with developed eyes and yolk occupying 25 L 50%

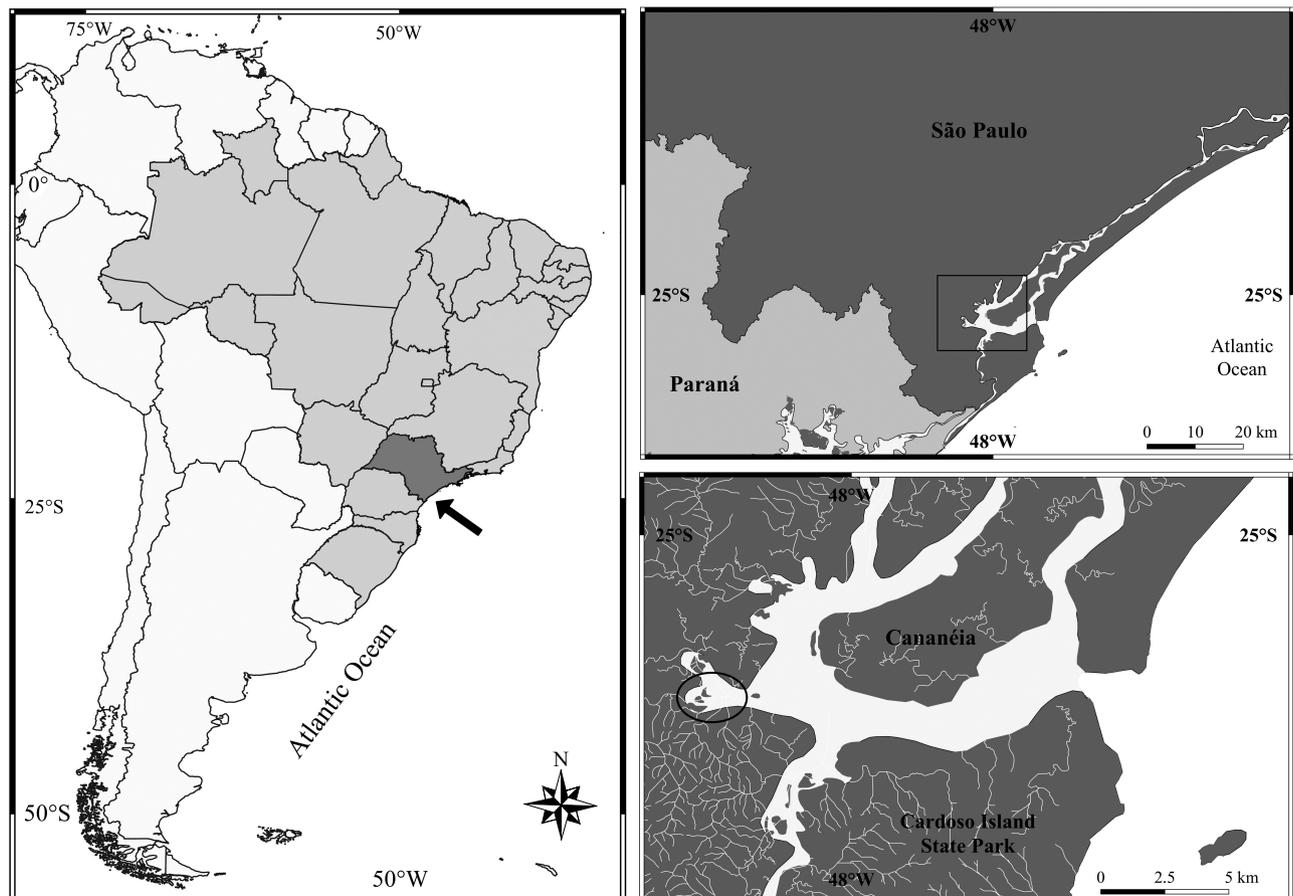


Fig. 1. Location of the study area in the intertidal estuarine complex of Cananéia, São Paulo, south-eastern Brazil.

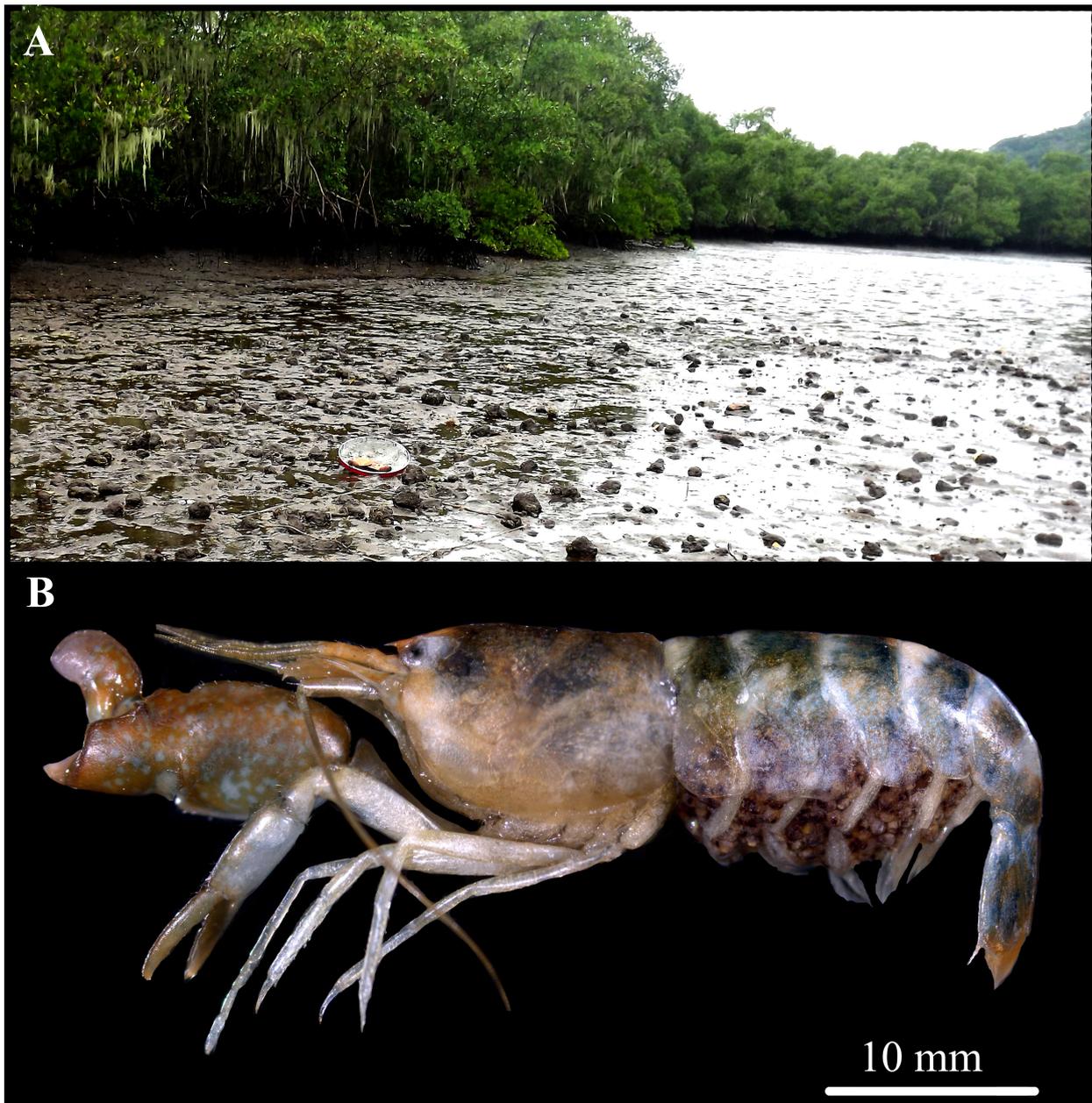
of egg volume (Wehrtmann 1990). Ten eggs were randomly selected from each female and the longest and shortest diameters of each egg were measured under a stereomicroscope equipped with an ocular micrometer to estimate the volume using the formula:  $[v = 1/6 * \pi * (d1)^2 * d2]$ , where d1 and d2 correspond to the longest and shortest diameters, respectively (Bauer 1991).

To avoid egg losses and changes in volume during embryonic development, only females with recently produced eggs (Stage I) were included in the fecundity. The Pearson correlation ( $\alpha = 0.05$ ) was used to analyze

the relationship between female size and fecundity and the relationship between female size and egg volume. The Kruskal-Wallis test ( $\alpha = 0.05$ ) was used to determine differences in the number and volume of eggs between stages of development.

## RESULTS

A total of 188 individuals were sampled, 96 females and 92 males. The minimum and maximum CL



**Fig. 2.** (A) Sampling area at the intertidal zone of the estuary of Cananéia, São Paulo, south-eastern Brazil. (B) Lateral view of an ovigerous female of *Alpheus carlae* Anker, 2012.

of females and males was 3.14–10.16 mm (mean  $\pm$  SD,  $6.11 \pm 1.55$  mm) and 3.18–9.48 mm (mean  $\pm$  SD,  $6.40 \pm 1.36$  mm), respectively. Data had a normal distribution (Shapiro-Wilk,  $P > 0.05$ ). All growth equations calculated for the morphological structures significantly differed between juveniles and adults in either slopes or intercepts (ANCOVA,  $P < 0.05$ ), with the exception of the relationships CPL vs. CL and CPH vs. CL in males (Table 1). The allometric growth was also different between males and females, showing a sex-specific growth rate in the analyzed body structures (ANCOVA,  $P < 0.05$ ) (Table 2).

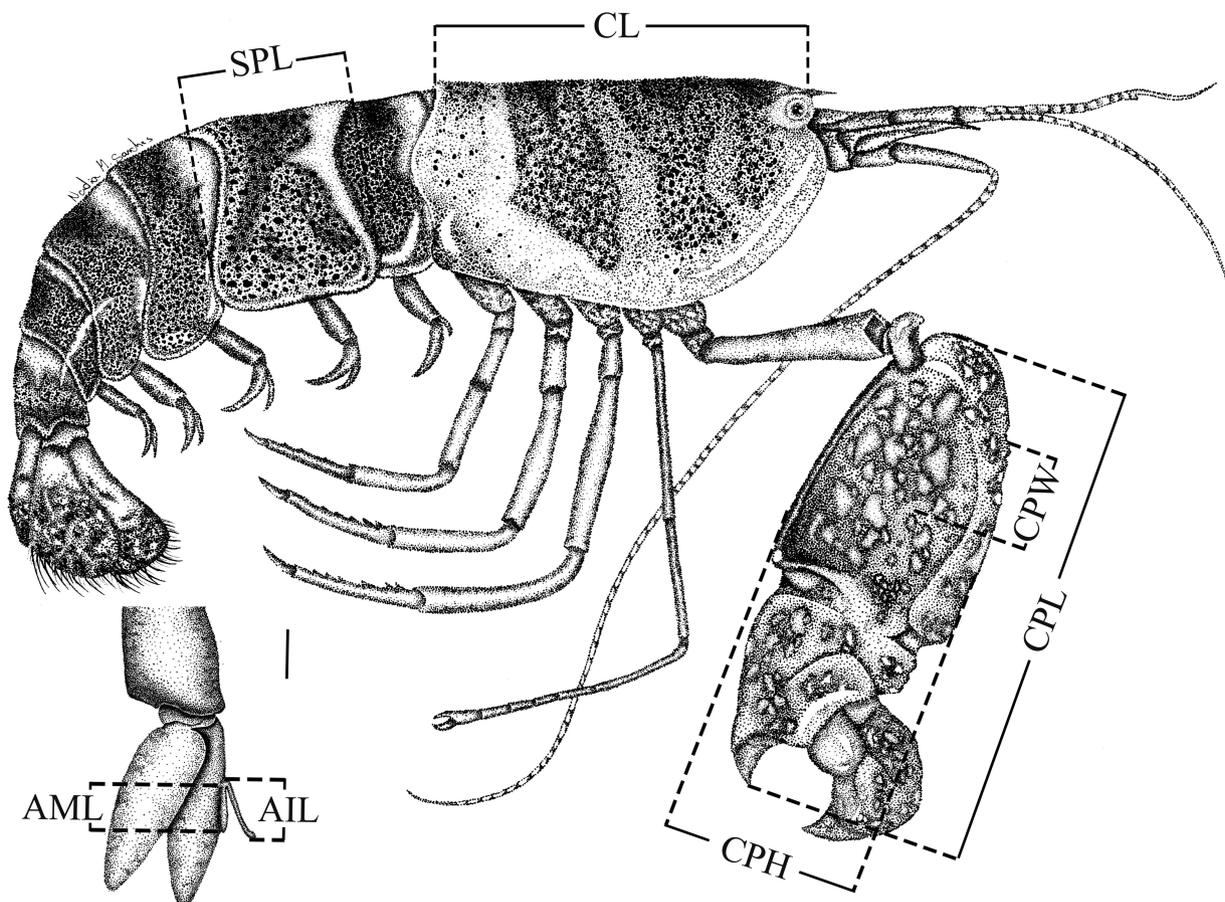
All allometric relationships are detailed in Table 3. The relationships that best demonstrated changes in the growth pattern between juveniles and adults were AIL vs. CL for females and CPW vs. CL for males, with CL at morphological sexual maturity of 5.6 and 6.2 mm, respectively (Fig. 4).

All allometric relationships tested for females showed changes across the growth of juveniles and adults. A positive allometric growth was observed in

juveniles followed by an isometric growth in adults for the relationships SPL vs. CL and AIL vs. CL. The relationships CPL vs. CL and CPH vs. CL had isometric growth in juveniles followed by a negative allometry in adults. CPW vs. CL had a positive allometry in juveniles followed by a negative allometry in adults (Table 3).

All allometric relationships tested for males had changes during the growth pattern of juveniles and adults, except for AIL vs. CL that had negative allometry in both juveniles and adults. The relationships between CPL vs. CL, CPH vs. CL, and CPW vs. CL had a positive allometry in juveniles followed by an isometry in adults. The relationship AML vs. CL had a negative allometry in juveniles followed by an isometry in adults (Table 3).

There were no statistical differences between the size (CL) of males and females (Mann-Whitney test,  $P > 0.05$ ). However, the size of body structures was different between sexes; the length, width, and height of major cheliped were larger in males (Mann-Whitney test,  $P < 0.05$ ). Females had larger second pleonal



**Fig. 3.** *Alpheus carlae* Anker, 2012. Body dimensions used in the morphometric analyses. Carapace length (CL), second pleonal pleuron (SPP), major cheliped propodus length (CPL), major cheliped propodus width (CPW), major cheliped propodus height (CPH), appendix interna length (AIL), and appendix masculina length (AML). Illustrations by Nádia de Moraes Sanches.

pleuron and appendix interna (Fig. 5). The sexual dimorphism of *A. carlae* was also evident considering the growth of body structures; all growth equations differed significantly between the slopes of males and females (ANCOVA,  $P < 0.05$ ) (Table 2). There was no evidence of laterality in the chelipeds of *A. carlae*, one cheliped was larger than the other without a constancy regarding the side.

A total of 34 females with eggs at different stages of development were analyzed: stage I (N = 19), stage

II (N = 10) and stage III (N = 5). There was a positive correlation between CL and number of eggs (Pearson's correlation,  $P < 0.05$ ), with a proportional increase in egg number according to female size (Fig. 6A). The mean fecundity was  $364 \pm 204$  eggs (mean  $\pm$  SD) per individual (min-max, 66–735).

The egg volume increased throughout the development:  $0.074\text{--}0.144 \text{ mm}^3$  (mean  $\pm$  SD,  $0.099 \pm 0.021$ ) in stage I,  $0.115\text{--}0.0181 \text{ mm}^3$  (mean  $\pm$  SD,  $0.145 \pm 0.024$ ) in stage II, and  $0.166\text{--}0.220 \text{ mm}^3$  (mean  $\pm$  SD,

**Table 1.** *Alpheus carlae* Anker, 2012. Results of analysis of covariance (ANCOVA) between juveniles and adults of males and females for each relationship. SPL = second pleuron length; CPL = cheliped propodus length; CPH = cheliped propodus height; CPW = cheliped propodus width; AIL = appendix interna length; AML = appendix masculina length; CL = carapace length; Par = parameter;  $F$  = statistic values;  $P$  = significance \*Significant difference  $P < 0.05$ )

Relationship	Factor (group)	Par. (Log)	$F$	$P$
SPL vs. CL	Females (J vs. A)	A	55.51	0.00*
		B	3.62	0.06
	Males (J vs. A)	A	5.48	0.02*
		B	0.42	0.52
CPL vs. CL	Females (J vs. A)	A	-	-
		B	5.93	0.02*
	Males (J vs. A)	A	0.56	0.45
		B	1.36	0.25
CPH vs. CL	Females (J vs. A)	A	-	-
		B	7.28	0.01*
	Males (J vs. A)	A	0.51	0.47
		B	0.33	0.56
CPW vs. CL	Females (J vs. A)	A	-	-
		B	28.79	0.00*
	Males (J vs. A)	A	-	-
		B	5.36	0.02*
AML vs. CL	Males (J vs. A)	A	-	-
		B	3.98	0.05*
AIL vs CL	Females (J vs. A)	A	16.81	0.00*
		B	1.65	0.20
	Males (J vs. A)	A	33.28	0.00*
		B	0.03	0.86

**Table 2.** *Alpheus carlae* Anker, 2012. Results of analysis of covariance (ANCOVA) between males and females for each relationship. Par = parameter;  $F$  = statistic values;  $P$  = significance; \* significant difference ( $P < 0.05$ )

Relationship	Factor (group)	Par. (Log)	$F$	$P$
SPL vs. CL	Females vs. Males	Slope	74.531	0.000*
CPL vs. CL	Females vs. Males	Slope	21.551	0.000*
CPH vs. CL	Females vs. Males	Slope	19.132	0.000*
CPW vs. CL	Females vs. Males	Slope	19.909	0.000*
AIL vs. CL	Females vs. Males	Slope	73.574	0.000*

0.189 ± 0.019) in stage III. The egg volume differed significantly between developmental stages I and II and I and III (Kruskal-Wallis/Dunn,  $P < 0.05$ ), with an overall volume increased of 73.23% and 95.45%, respectively (Fig. 6B).

### DISCUSSION

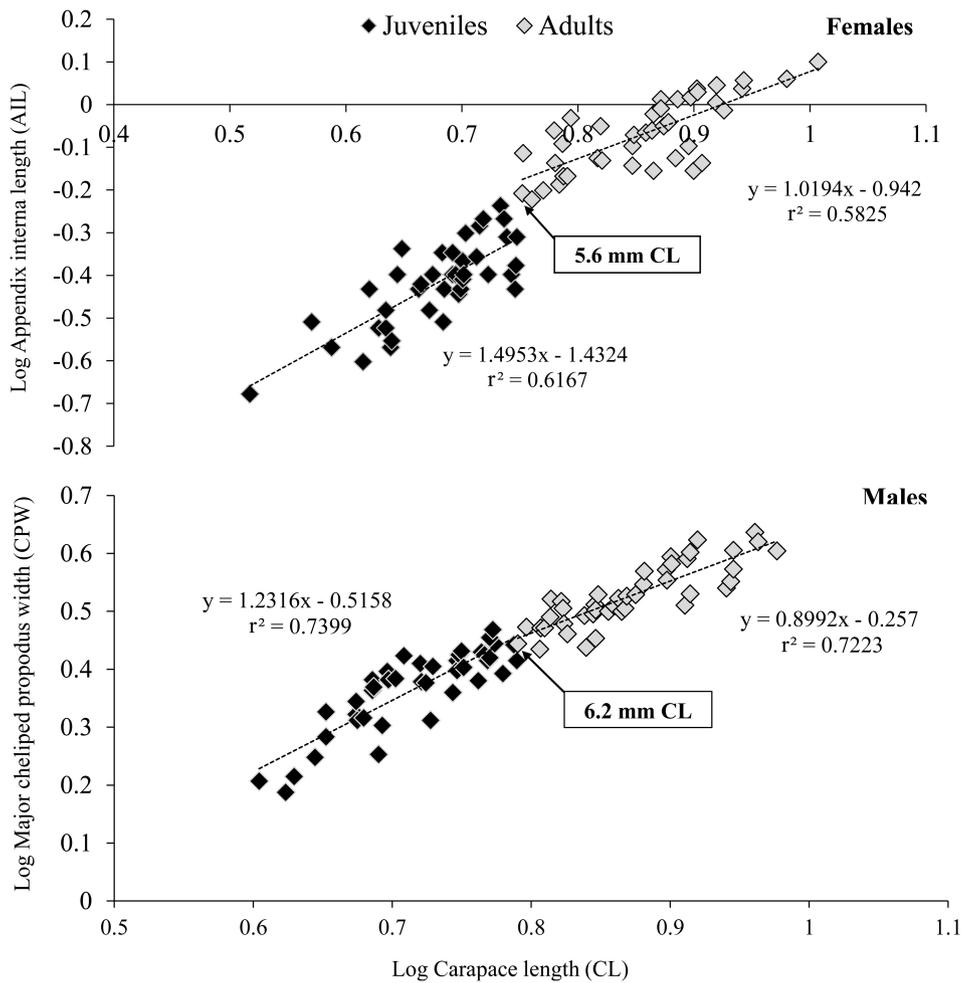
This study provided detailed insights into the life-history traits of the snapping shrimp *A. carlae* from an estuarine complex in south-eastern Brazil. Our study demonstrated a differential growth pattern between juveniles and adults and between males and females. The body structures that best indicated the size at morphological sexual maturity of males and females were also distinct and there was a sexual dimorphism in the mean size of body structures. This finding suggests a tradeoff between the energy allocation for reproduction and somatic growth before and after reaching

morphological sexual maturity, demonstrating that there is a sex allocation to the growth of body structures linked to agonistic behavior and reproduction. All these results revealed distinct strategies of energy allocation in *A. carlae*.

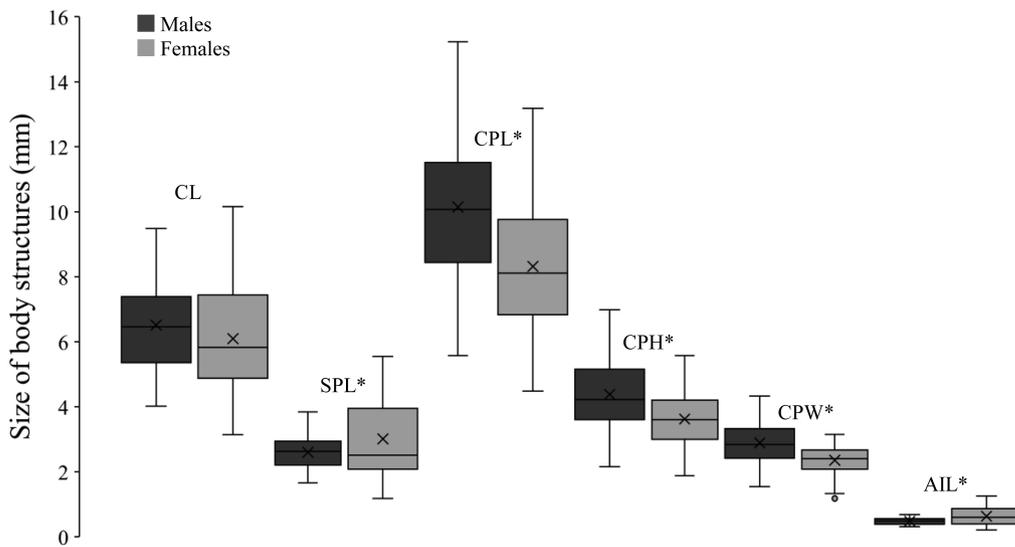
Comparisons between the relative growth of males and females revealed different strategies of energy allocation and a sexual dimorphism in body structures. This dimorphism is associated with the monogamous sexual behavior of *Alpheus* species that consists of an association between one male and one female, usually of similar sizes, cooperating in breeding activities (Wickler and Seibt 1981; Heuring and Hughes 2020). Males invest more energy in weapon structures, such as larger chelipeds, and females in structures directly associated with reproduction such as abdomen and second pleonal pleuron, providing a large area to carry the eggs (Bauer 2004). Both chelipeds and abdomen are related to the reproductive process that requires a large amount of energy, culminating in the reduction of energy allocated

**Table 3.** *Alpheus carlae* Anker, 2012. Analysis of morphometric data using the carapace length (CL) as an independent variable. SPL = second pleuron length; CPL = cheliped propodus length; CPH = cheliped propodus height; CPW = cheliped propodus width; AIL = appendix interna length; AML = appendix masculina length; JM = juvenile males; AM = adult males; JF = juvenile female; AF = adult female;  $b$  = allometric coefficient;  $a$  = intercept;  $r^2$  = determination coefficient;  $T$  = statistic values;  $P$  = significance; + = positive allometry; = isometry; - = negative allometry

Relationship	Sex	N	$a$	$b$	$r^2$	$T(b = 1)$	$P$	Allometry
SPL vs. CL	JF	47	-0.4629	1.1303	0.8388	1.78	< 0.001	+
	AF	38	-0.1659	0.8914	0.6693	1.00	< 0.001	0
	JM	35	-0.3024	0.8706	0.7424	1.44	< 0.001	0
	AM	48	-0.2002	0.7691	0.6063	2.55	< 0.001	-
CPL vs. CL	JF	40	0.1403	1.001	0.7347	0.01	< 0.001	0
	AF	52	0.3544	0.7316	0.6408	3.41	< 0.001	-
	JM	44	0.0208	1.2303	0.8045	2.47	< 0.001	+
	AM	45	0.1313	1.0819	0.7879	0.95	< 0.001	0
CPH vs. CL	JF	31	-0.2937	1.1095	0.7094	0.85	< 0.001	0
	AF	53	0.0098	0.7126	0.6507	8.35	< 0.001	-
	JM	39	-0.3632	1.2543	0.7344	2.05	< 0.001	+
	AM	50	-0.3017	1.1616	0.7314	1.60	< 0.001	0
CPW vs. CL	JF	27	-0.5875	1.2963	0.735	2.07	< 0.001	+
	AF	56	0.0817	0.3982	0.354	8.35	< 0.001	-
	JM	41	-0.5158	1.2316	0.7399	1.92	< 0.001	+
	AM	44	-0.257	0.8992	0.7223	1.11	< 0.001	0
AML vs. CL	JM	29	-0.9318	0.4786	0.1864	2.74	> 0.001	-
	AM	52	-1.1894	0.9202	0.5528	0.67	< 0.001	0
AIL vs. CL	JF	37	-1.4324	1.4953	0.6167	2.45	< 0.001	+
	AF	42	-0.942	1.0194	0.5825	0.06	< 0.001	0
	JM	37	-0.8974	0.666	0.5587	3.40	< 0.001	-
	AM	48	-0.8494	0.6879	0.6041	3.87	< 0.001	-



**Fig. 4.** *Alpheus carlae* Anker, 2012. Minimum estimated size of morphological sexual maturity for females and males. The estimated size refers to the smallest individual after the inflection point of the equations for juveniles and adults.



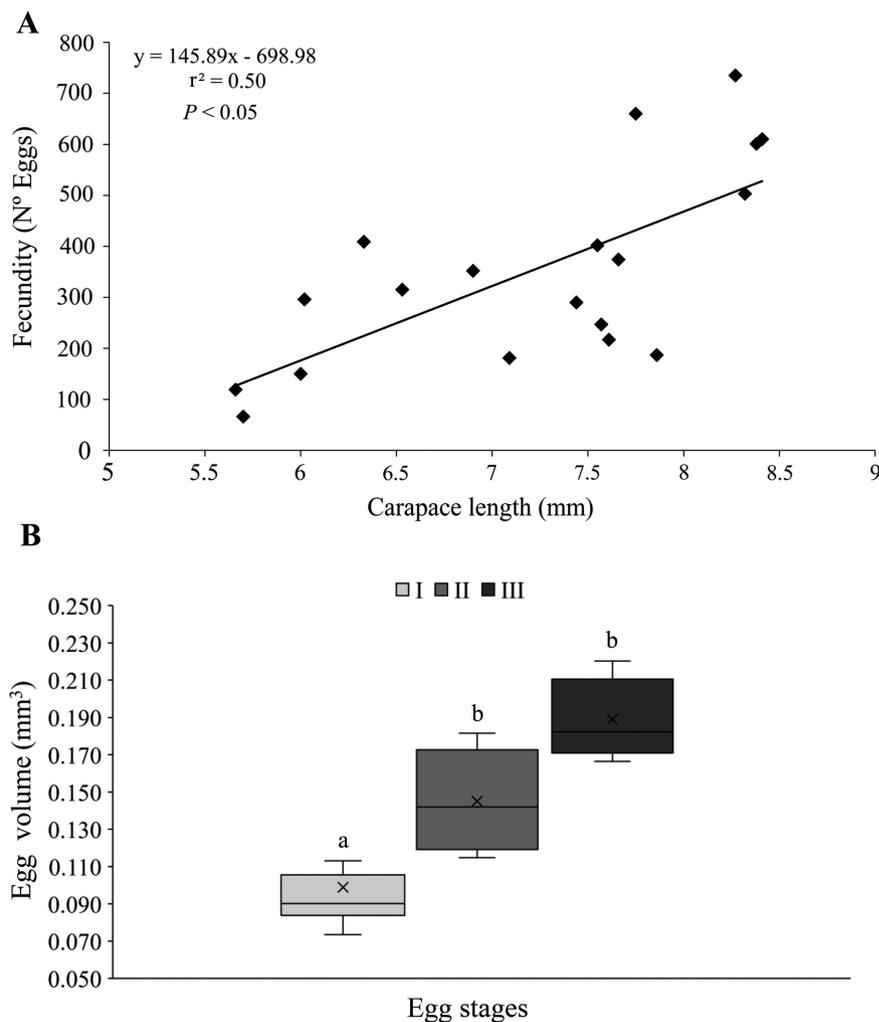
**Fig. 5.** Sexual dimorphism in *Alpheus carlae* Anker, 2012. Minimum, maximum, median (horizontal line) e average (X). \*Significant difference (Mann-whitney,  $P < 0.05$ ). Carapace length (CL), second pleuron length (SPL), major cheliped propodus length (CPL), major cheliped propodus width (CPW), major cheliped propodus height (CPH), appendix interna length (AIL).

to somatic growth and in the development of secondary sexual characters (Marochi et al. 2019).

Males of *Alpheus carlae* exhibited an allometric growth pattern of chelipeds. In all relationships, there was a positive allometry in juveniles followed by an isometry in adults, results similar to those found by Pescinelli et al. (2018) in *Alpheus brasileiro* Anker, 2012. The development of chelipeds in males is related to intra and interspecific factors and to sexual selection (Marochi et al. 2019). Males have a characteristic agonistic behavior in which they use the major cheliped to defend against predators in disputes over territory and females, partner guarding, to the construction of burrows, among other inter and intra-specific activities (e.g., Correa and Thiel 2003; Hughes et al. 2014; Pescinelli et al. 2018; Costa-Souza et al. 2019). Thus, the differential growth of the major cheliped of juveniles and adults is an important parameter for estimating the

morphological sexual maturity.

Females undergo isometric growth of the second pleonal pleuron and appendix interna during the juvenile stage, followed by a positive allometric growth in adults. The growth of the appendix interna had the highest change in the allometric coefficient, representing the best relationship for estimating the size at which females reach sexual morphological maturity. The development of this structure in females is related to a possible increase in the area of the incubator chamber, facilitated by a small hook-shaped structure known as *cincinulli* that connects pleopods together (Bauer 2004). This condition of connected pleopods increases the reproductive potential since the connection of the pleopods to each other provides a greater protection to the egg mass (Pescinelli et al. 2018). In addition, the characteristic development of the pleonal pleuron in caridean females is an important adaptation for egg



**Fig. 6.** *Alpheus carlae* Anker, 2012. (A) Correlation between carapace length and the fecundity of females with eggs in development stage I. (B) Comparison of egg volume at the early (I), intermediate (II), and final stage of development (III). Minimum, maximum (whiskers), median (horizontal lines) and mean (x). Different letters indicate significant differences among egg stages.

incubation, influencing the reproductive success (Bauer 2004).

Males reached sexual morphological maturity at larger sizes than females, similar to what was found for *A. brasiliense* (Pescinelli et al. 2018) and *Alpheus estuariensis* Christoffersen, 1984 (Costa-Souza et al. 2019). This may be related to the males' agonistic behavior. If males delay their sexual maturity, they can direct more energy into the somatic growth and structures related to agonistic behavior, such as chelipeds (Marochi et al. 2019). As a result, males can increase their reproductive and survival success. Larger males may have higher efficiency in obtaining resources, higher sperm production, higher aggressiveness during territorial defense, and higher chances of survival in disputes with other males (Heuring and Hughes 2020). On the other hand, females invest more energy into reproduction, *i.e.*, gonadal development and production and maintenance of eggs (Correa and Thiel 2003; Bauer 2004). Thus, our analyses of the growth of *A. carlae* made it evident that the species has a sex allocation strategy. However, there does not seem to be a pattern in relation to the size in which males and females reach sexual maturity considering the results found by Costa-Souza et al. (2019) for *Alpheus* species including *A. carlae* in which females have reached sexual maturity in larger sizes than males. As in the present study, the sex allocation strategy was observed by Hamasaki et al. (2020) for crayfish *Procambarus clarkii* (Girard 1852), in which reproductive males were found to have wider and longer chelipeds than reproductive females and non-reproductive males and females. The growth pattern of each sex is directly related to the strategy of energy allocation and the influence of physiological processes such as growth and reproduction in the species life history (Lika and Kooijman 2003).

In some species of the genus *Alpheus*, mainly those living at low latitudes, females have continuous reproduction throughout the year (Soledade et al. 2017). Therefore, by the time the females hatch their eggs, they have already restarted the gonadal development process (Bauer 2004) and are able to mate again as soon as spawning is finished. The reproductive effort of females during reproductive events is higher than males since they invest a lot of energy in the development of the ovary, and production and maintenance of eggs. This excessive effort is reflected in a low longevity of females in comparison with males (*e.g.*, Pescinelli et al. 2020).

The positive correlation between the females size and egg production reinforces the high energy investment allocated to reproductive processes in *A. carlae*. The more the female grows, the larger the area available for incubation and accommodation of eggs in the abdomen and the higher the egg production, which

is decisive to reproductive success (Bauer 1991). The fecundity in the studied population of *A. carlae* (mean size 6.4 mm CL) was higher than in other species of the genus, such as *A. brasiliense* (mean size 5.8 mm CL) (Pescinelli et al. 2017), *A. estuariensis* (mean size 9.0 mm CL) (Costa-Souza et al. 2014), or even when compared to another population of *A. carlae* (mean size 8.6 mm CL) from northeast Brazil (Soledade et al. 2017). The variation in egg production can be influenced by environmental factors, such as temperature, salinity, and photoperiod, by genetic factors, and by the availability and quality of food available in the area where these individuals live (Bertini and Baeza 2014). However, the possibility that the analyzed populations adopt the reproductive strategy of multiple spawning throughout the year remains unclear.

Although the number of females analyzed is low, meaning that caution is needed when analyzing the results and conclusions, the increase in egg volume was constant and was evident by the increased rate between stages I and II, and stages I and III. The increase in the egg volume is a result of embryonic growth and the increased membrane permeability close to the moment of larval hatching (Pavanelli et al. 2008). This happens in response to the osmotic regulation process, which allows higher water absorption during this egg development stage, facilitating the rupturing of the membrane (*e.g.*, Pavanelli et al. 2008; Mossolin et al. 2010; Oliveira et al. 2018).

## CONCLUSIONS

In summary, our study contributed to the knowledge about *A. carlae* and its life history in the natural environment. Throughout life, males and females direct their energy toward the growth of different body structures, reflecting the different strategies of energy and behavioral allocation. Males invest more in somatic growth and weaponry structures, crucial during female searching, burrows protection and maintenance, and female guarding. Females invest more energy in the growth of structures directly related to reproductive processes and gonadal development, egg production and maintenance. These differences between the energy allocation of males and females are fundamental to the reproductive success of the species.

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