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ORIGINAL ARTICLE

Growth, age at sexual maturity, longevity and natural mortality of *Alpheus brasileiro* (Caridea: Alpheidae) from the south–eastern coast of Brazil

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ABSTRACT

We estimated the growth patterns, age at the onset of sexual maturity, longevity, and natural mortality of the snapping shrimp *Alpheus brasileiro* Anker, 2012. The sampling occurred monthly from April 2015 to March 2016 in the estuarine intertidal zone of Cananéia, São Paulo, Brazil. To estimate the growth parameters, all cohorts were adjusted to the Bertalanffy growth model. Longevity was estimated by the inverse growth equation. Natural mortality was calculated following the decrease in abundance over time of each cohort. We obtained the following estimates: $CL_\infty = 9.49$ mm, $k = 0.0077$ day^{-1} (1.64 year^{-1}), $t_0 = -0.7628$ for males, and $CL_\infty = 9.31$ mm, $k = 0.0095$ day^{-1} (1.32 year^{-1}), $t_0 = 0.0374$ for females. The estimated age at the onset of morphological sexual maturity was 94 and 74 days for males and females, respectively. Females take 89 days to reach functional maturity, and have a higher mortality (4.35 year^{-1}) than males (3.67 year^{-1}). We rejected the hypothesis that males and females of *A. brasileiro* have the same growth patterns, longevity, mortality and, reaches sexual maturity at the same age. Our results suggest that physiological aspects and energy allocation strategies modulate the growth, longevity, and mortality of these snapping shrimps.

KEYWORDS

Cananéia, intertidal zone, life history, sex allocation, snapping shrimp

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Introduction

The genus *Alpheus* Fabricius, 1798 is the most speciose of the Family Alpheidae and has more than 300 species described worldwide (De Grave and Fransen, 2011). Alpheid shrimps occur in a wide variety of microhabitats, usually in consolidated and unconsolidated substrates and in tropical and subtropical regions (Bauer, 2004; Anker *et al.*, 2006). The western Atlantic snapping shrimp *Alpheus brasileiro* Anker, 2012, is a common representative of the *Alpheus armillatus* H. Milne Edwards, 1937 species complex, which occurs along the Brazilian coast. It is found in natural pools formed by exposed reef areas and under rocks in estuaries (Anker, 2012; Pescinelli *et al.*, 2017a).

Previous studies investigated the biology of *A. brasileiro* analyzing egg production and social monogamy (Pescinelli *et al.*, 2017a), relative growth (Pescinelli *et al.*, 2018a) and showed that males and females have different relative growth, and that reproduction and recruitment are continuous. The morphology of early larval stages was also analyzed, and led to the conclusion that *A. brasileiro* has an extended larval development in the plankton (Pescinelli *et al.*, 2017b). Although these results combined characterize a great part of the biology of this species, information on population dynamics are still lacking.

Information on the components of population dynamics, such as growth, age at the onset of sexual maturity, longevity, and mortality are essential to understand a species' life history (Stearns, 2000). The energy allocation strategy is also of great interest as it is related to major physiological processes like growth and reproduction (Lika, 2003). In crustaceans, the study of growth is an important tool to estimate growth and mortality rates, as well as the age at the onset of sexual maturity (Sheehy, 1990; Campana, 2001).

In the study of individual growth it is important to consider that the dimensions of a given body part may change at different rates, depending on the species and, within a species, depending on the sex (Hartnoll, 1982). In contrast to fishes or bivalves, for example, crustaceans lack structures with growth rings or layers that can be used to estimate age (Skurdal *et al.*, 1985; King, 1995). The alternative is to use the change in individual body size as a function of time to estimate the age. This can be achieved by monitoring cohorts identified through the size–frequency distribution of a population over a given period (Bertalanffy, 1938; Campos *et al.*, 2011; Fonteles–Filho, 2011). The size–frequency distribution method leads to cohort identification. The mathematical model that has been widely used for this purpose is the one proposed by Bertalanffy (1938) that relates age to size. Through this model it is possible to estimate the maximum size that the individuals can reach, and thus, their longevity. Bertalanffy's model is considered the best one to study age in crustaceans (Davanso *et al.*, 2013; Simões *et al.*, 2013; Santos *et al.*, 2015; Pescinelli *et al.*, 2018b).

Aiming to fill the knowledge gap about the life history of the snapping shrimp *A. brasileiro*, our goal was to analyze the growth patterns and to estimate the longevity, natural mortality rates, and the age at the onset of morphological and functional sexual maturity of the species. This species is socially monogamous (Pescinelli *et al.*, 2017a) which is characterized by the size–assortative pairing, *i.e.*, there is a close association between males and females and a positive correlation between the individual size of a pair. Given that size–assortative pairing results in an absence of sexual dimorphism in body size (Boltaña and Thiel, 2001; Baeza *et al.*, 2016), we hypothesized that males and females have the same growth patterns and reach sexual maturity are the same age, in order to facilitate heterosexual pairing. Due to the formation of heterosexual pairs, males and females share a refuge, divide tasks, live under the same environmental and biotic conditions. Considering that the estimation of longevity and natural mortality takes the growth coefficient into account, we also tested the hypothesis that males and females have equal longevity and natural mortality rates.

Materials and Methods

Study area

The sampling area was an intertidal estuary in the south–eastern Brazilian coast (25°04'11.2"S, 48°03'08.9"W) (Fig. 1). The sediment is composed of a mixture of mud, sand, and small rocks (~ 30 cm) scattered over the area. During low tides the rocks are exposed, but the remaining small puddles of water provide a suitable refuge for *A. brasileiro* (Fig. 2).

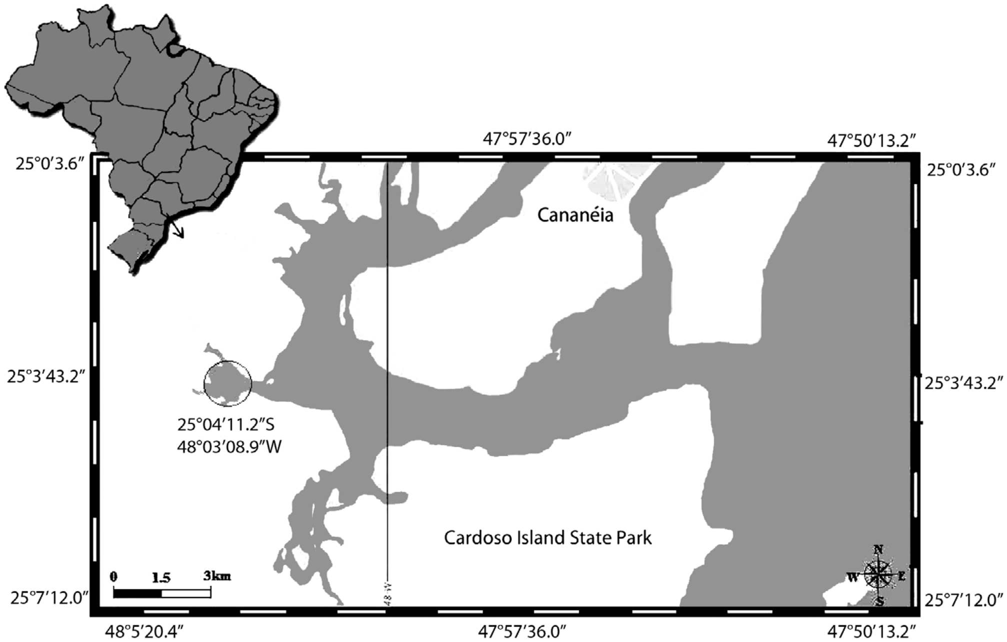

Figure 1. Location of the study area, water represented by dark grey in the map of the intertidal estuarine zone of Cananéia, São Paulo, south–eastern Brazil. Adapted from Pescinelli *et al.* (2017a).

Sampling

The sampling occurred monthly from April 2015 to March 2016. The sampling area was divided in three sub–areas 10 m apart from each other, perpendicular to the water line. Each sub–area was 20 m long and 5 m wide. Inside each sub–area, three 1 m^2 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). Shrimps were collected from under the rocks by two people during the low tide with a total effort of 2 hours per person. Upon sampling, shrimps were kept in coolers with crushed ice. 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 endopod 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), 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.

Growth, longevity, age at sexual maturity, and mortality

The growth analysis was performed separately for males and females, undifferentiated individuals were not used. For each sampling month, the frequency of CL values was distributed in 0.5 mm size classes following Sturges (1926) and modes were calculated using PeakFit software (PeakFit v. 4.06 SPSS Inc. for Windows Copyright 1991–1999, AISN Software Inc., Florence, OR, USA).

To estimate the growth parameters, all cohorts chosen were adjusted to the Bertalanffy growth model (Bertalanffy, 1938), namely $CL_t = CL_\infty\,[1-e^{-k\,(t-t0)}]$, where CL_t is size estimated at age *t*, CL_∞ is asymptotic size, *k* is the growth coefficient, and t_0 is the theoretical age at size zero. The growth parameters CL_∞, *k* and t_0 were estimated using the *Solver* supplement of Microsoft Excel, which minimizes the sum of residues of the comparison between the observed length and the length calculated by the Bertalanffy model. The criteria used to choose the cohorts were based on biological coherence between longevity, growth coefficient and asymptotic size. Growth curves were compared using the *F* test ($P = 0.05$) according to Cerrato (1990). Longevity was estimated by the inverse Bertalanffy

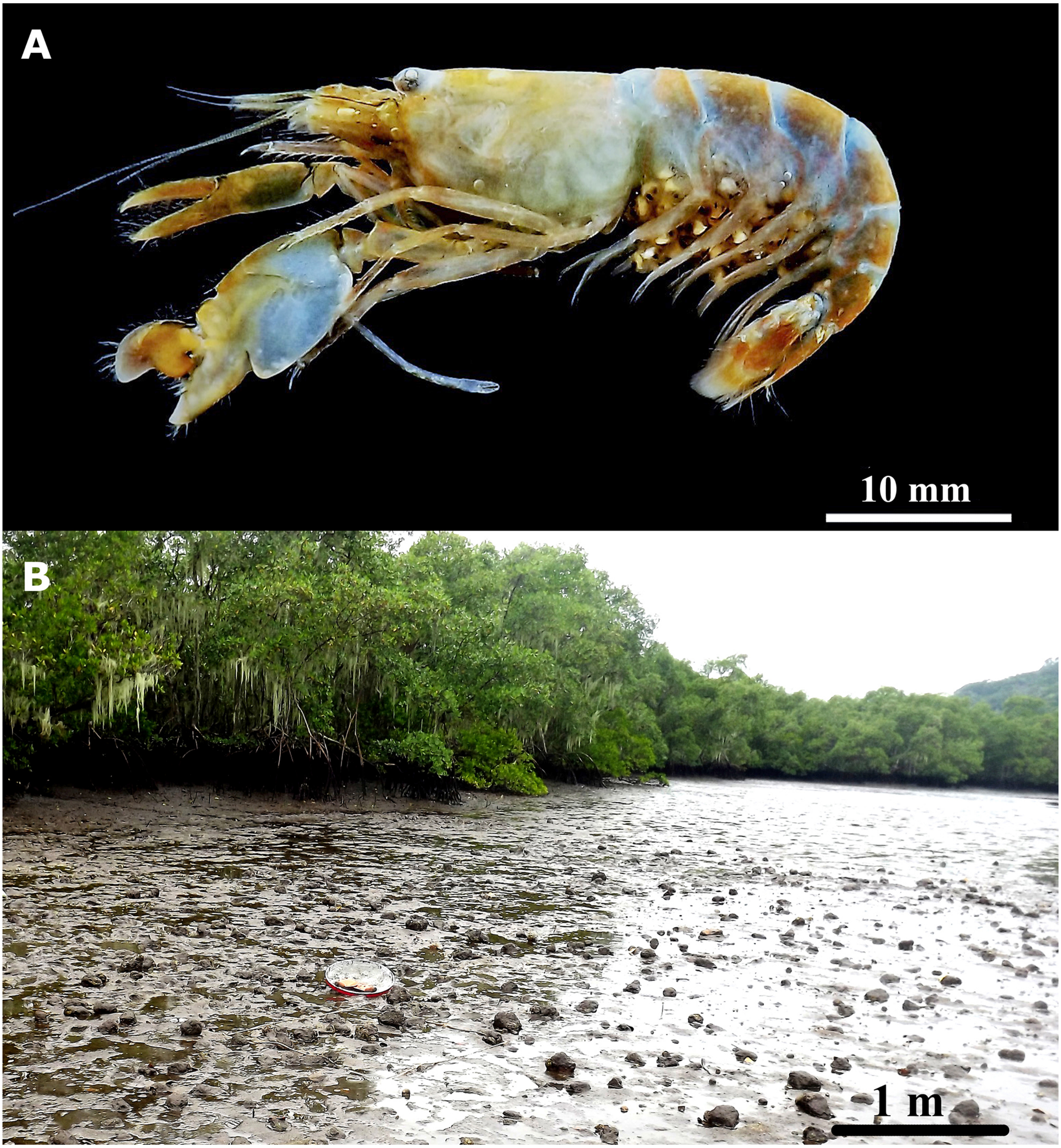

Figure 2. A, Lateral view of an ovigerous female of *Alpheus brasileiro* Anker, 2012; B, sampling area at the intertidal zone of the estuary of Cananéia, São Paulo, south–eastern Brazil.

growth equation, with modifications suggested by D'Incao and Fonseca (1999), $t_0 = 0$ and $CL/CL_\infty = 0.99$, while the longevity equation was $t = (t_0 - (1/k) \ Ln \ (1 - CL_t/CL_\infty))$.

Female functional sexual maturity was estimated using the L_{50} method based on females carrying an egg mass among the pleopods. This method distributes (%) the individuals into size classes using CL as an independent variable and the relative frequencies as a dependent variable. The data were then fitted to a sigmoid curve following the results of the logistic equation ($y = 1/(1 + e^{(-r(CL - CL_{50}))})$), where CL_{50} is the CL at which 50% of females reach functional maturity and r is the slope. The curves were adjusted based on the least squares method (Vazzoler, 1996), estimating the size at maturity (CL_{50}) and using interpolation (50%).

To estimate the age at the onset of the sexual maturity of males and females, the equation suggested by King (1995) was used: Age at maturity = $(t_0 - (1/k)\ \mathrm{Ln}\,(1 - CL_\infty / CL_m))$ where t_0, k, and CL_∞ are the values obtained in the analysis of growth, and CL_m is the size at sexual maturity. The age at maturity was calculated using the information of the size at the onset of functional maturity of females and the morphological maturity of males and females. The size at the onset of morphological maturity used in the calculations (4.9 and 4.7 mm CL for males and females, respectively) was estimated in a previous study that addressed the structure and relative growth of the same population (Pescinelli *et al.*, 2018a).

The empirical natural mortality (M) was estimated based on the growth parameters and by observing the decreasing abundance of a cohort over time, according to methods of Taylor (1959) and Pauly (1980). In order to avoid overestimating or underestimating the natural mortality, we calculated the average of the two methods.

RESULTS

During the study, 313 individuals were collected and measured: 154 males and 147 females and 12 undifferentiated. The size ranges of each demographic class are shown in Table 1. The size–frequency distribution indicated a similar proportion of males and females in the classes of sexually immature and sexually mature individuals (Fig. 3).

Five cohorts of males and females were chosen to compose the growth curves of *A. brasileiro* (Fig. 4). The final curve, obtained by the combination of all curves of each sex, resulted in the following estimates: $CL_\infty = 9.49$ mm, $k = 0.0077$ day^{-1}, $t_0 = -0.7628$ for males; and $CL_\infty = 9.31$ mm, $k = 0.0095$ day^{-1}, $t_0 = 0.0374$ for females (Fig. 4).

The estimated maximum longevity was 598 days (1.64 years) for males and 483 days (1.32 years) for females. The statistical comparison (*F* test) between the estimated curves for both sexes showed significant differences ($F_{calc} = 11.42 > F_{tab} = 2.87$).

Table 1. *Alpheus brasileiro* Anker, 2012. Carapace length of each demographic category of the population of Cananéia, São Paulo state, south–eastern Brazil from April 2015 to March 2016.

Demographic category	N	Min – Max (CL–mm)	Mean ± SD	%
Undifferentiated	12	2.01 – 2.84	2.52 ± 1.58	3.9
Males	154	2.97 – 8.91	5.39 ± 1.60	49.2
Females without eggs	59	2.54 – 8.61	4.42 ± 1.60	18.5
Females with eggs	88	4.83 – 8.91	6.42 ± 1.54	28.4
Total	313	2.01 – 8.91	5.38 ± 1.63	100

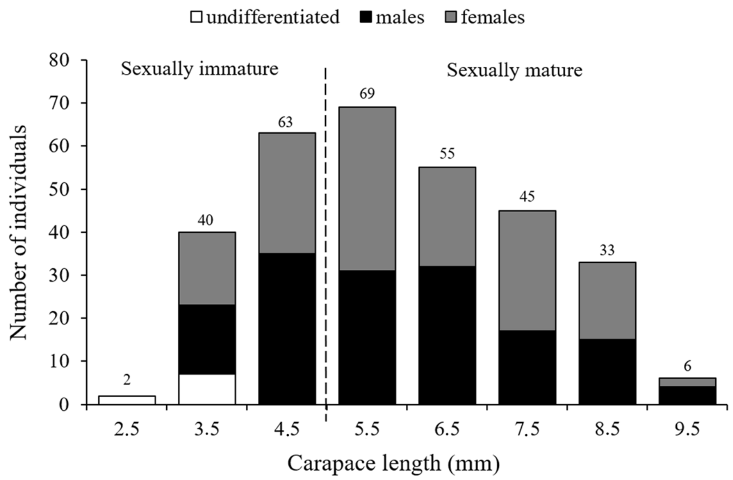

Figure 3. *Alpheus brasileiro* Anker, 2012. Size–frequency distribution of individuals both sexually immature (2.5 to 4.5 mm CL) and sexually mature (5.5 to 9.5 mm CL). Undifferentiated individuals (white bars), males (black bars) and females (dark grey bars). The values of morphological sexual maturity (4.9 and 4.7 mm CL for males and females respectively) are from the study of population structure and relative growth with the same population (Pescinelli *et al.*, 2018a).

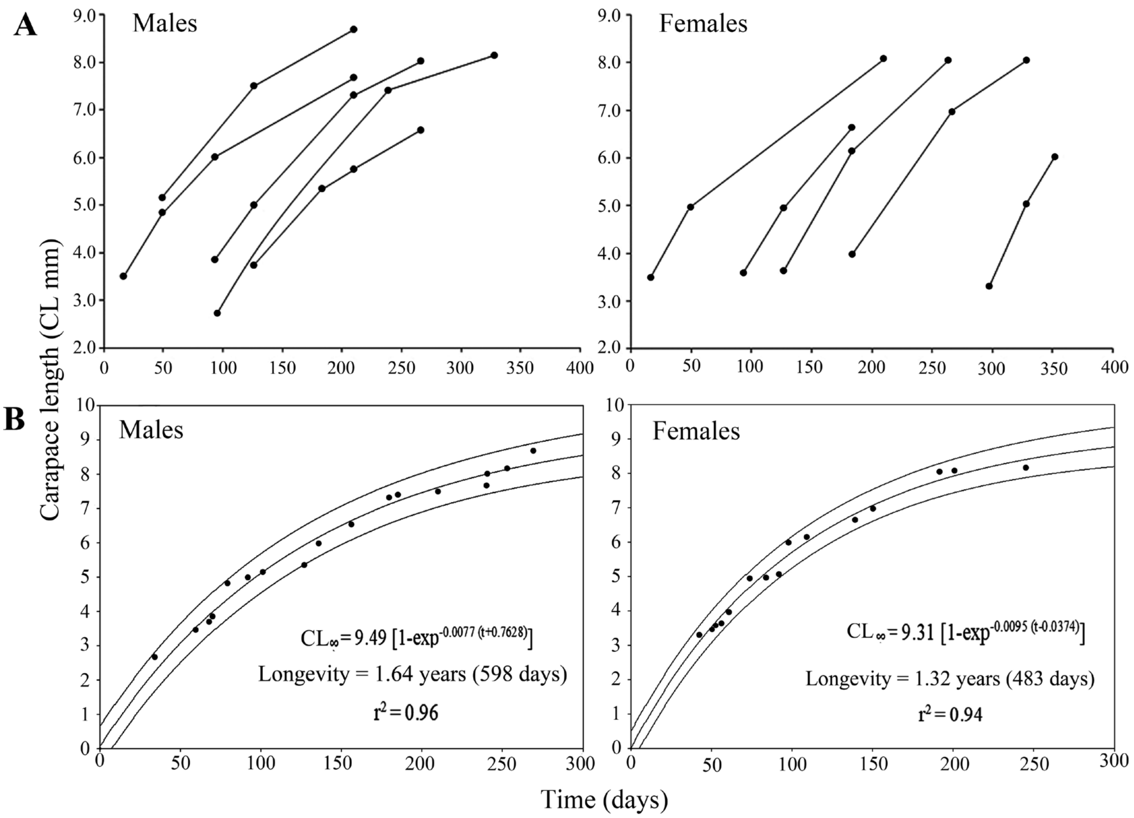

Figure 4. *Alpheus brasileiro* Anker, 2012. A, Cohorts identified during sampling describing the growth of each sex. B, Bertalanffy´s equation parameters estimated for males and females. The central line = mean; external lines = prediction intervals (95%).

The estimated size at onset of the functional sexual maturity, *i.e.*, where 50% of females are sexually mature (CL_{50}), was 5.34 mm CL (Fig. 5). At this size, the estimated age was 89 days. The age at the onset of the morphological sexual maturity of *A. brasileiro* was 94 days, in the case of males, and 74 days, in the case of females.

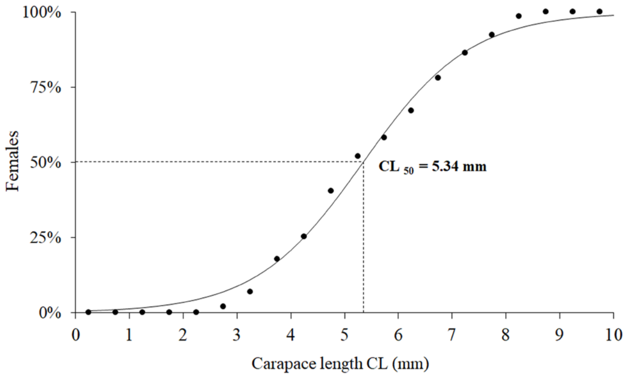

Figure 5. *Alpheus brasileiro* Anker, 2012. Logistic curve interpolation where 50% of females reach functional sexual maturity (CL_{50}).

Natural mortality was estimated at 2.82 $year^{-1}$ (0.23 $month^{-1}$) and 3.48 $year^{-1}$ (0.29 $month^{-1}$) for males and females, respectively (Taylor method) and 4.53 $year^{-1}$ (0.38 $month^{-1}$) and 5.23 $year^{-1}$ (0.43 $month^{-1}$) for males and females, respectively (Pauly method). The mean value of these two methods was therefore 3.67 $year^{-1}$ (0.30 $month^{-1}$) for males, and 4.35 $year^{-1}$ (0.36 $month^{-1}$) for females.

DISCUSSION

Significant differences between the sexes were found in this study, therefore, our initial hypothesis that males and females of *A. brasileiro* had equal growth and longevity was rejected. Males reached larger sizes, grew more slowly, and lived slightly longer than the females. The hypothesis of similar growth was based on the monogamous social system showed by this species, and based on the absence of sexual dimorphism in body size (Pescinelli *et at.*, 2017a). In the monogamous social system, there is a social fidelity between the pair, and cooperation in the defense of territory and maintenance of the refuge (Thiel and Baeza, 2001; Correa and Thiel, 2003). In species with a monogamous social system, body size is an important factor that influences the pair formation. Thus, sexual dimorphism in size is absent or minimal, and there is a positive correlation between the carapace length (CL) of paired males and females, a phenomenon known as a size–assortative pairing (Rodrigues *et al.*, 2009).

The hypothesis that males and females of *A. brasileiro* reached sexual morphology at the same age was also rejected. Males reached morphological sexual maturity later (94 days) than the females (74 days). The differences between the asymptotic size (CL_∞), longevity, and age at sexual maturity of males and females, albeit small, resulted in a different growth coefficient *k*, which was lower in males. Altogether, males grow more slowly and reach larger sizes, live longer, and reach sexual maturity later than the females. This occurs because the parameters CL_∞ and *k* are intrinsically negatively correlated (Pauly, 1980).

The growth coefficient is related to the physiological characteristics of individuals, which in turn are influenced by environmental factors that can trigger or change the reproduction and growth patterns of each sex (Crear *et al.*, 2003; Díaz *et al.*, 2003). Since *A. brasileiro* males and females form pairs that share a specific microhabitat or refuge, it is possible to say that each pair is under the influence of the same environmental factors, like water temperature and salinity, predation, and interspecific competition. Thus, other physiological aspects that were not evaluated in the present study may cause the sex–specific growth coefficients estimated here.

Our results regarding the growth parameters and longevity are consistent with the estimates of the morphological sexual maturity obtained through the use of the relative growth method (Pescinelli *et al.*, 2018a). With this method it was estimated that males reach the sexual maturity at a slightly larger size (4.9 mm CL) than the females (4.7 mm CL). The differential growth between males and females can be explained by different energy allocation strategies. While males invest in growth and, especially, in the development of structures related to agonistic behavior, *i.e.*, territory defense, competition for females, and defense against predators, females invest energy into reproduction, *i.e.*, in the gonadal development and production and maintenance of eggs (Correa and Thiel 2003; Bauer, 2004; Pescinelli *et al.*, 2018a).

Our results showed differences in the growth patterns of males and females and evidence of sex allocation in *A. brasileiro*. Sex allocation is defined as a differential energy allocation to reproductive processes in males and females (Charnov, 1982). Physiological processes, such as growth and reproduction are directly related to the strategy of energy allocation (Lika, 2003). Just as in the relative growth, in which males and females differed in the energy allocation to the growth of body structures, the sex allocation influenced the growth coefficient and longevity of *A. brasileiro.*

We estimated a higher natural mortality for females, also contrary to our hypothesis. In this study, only the natural mortality was analyzed since *A. brasileiro* is not a target of fisheries or another type of catch. It was possible to observe some trends between the natural mortality and growth parameters. We found an inverse relationship between natural mortality and CL, and a direct relationship between natural mortality and the growth coefficient *k*. These relationships could be explained by the link between predation and size, where the natural predation rate is inversely related to the individual size (Fonteles–Filho, 2011). Nonetheless, since males and females of *A. brasilero* live in pairs and share a specific microhabitat or refuge, it is possible to assume that a pair is under the same predation risk. A second factor that can directly influence the natural mortality is the sex–specific differential reproductive effort. Considering that females invest more energy into reproduction, and the fact that the studied population reproduces continuously (Pescinelli *et al.*, 2018a), it may be inferred that the higher mortality and the lower longevity of females is due to the successive reproductive events that take place as soon as they reach sexual maturity. The continuous reproduction demands a high energy investment into ovarian development, and production and maintenance of eggs until the hatching of the larvae (Bauer, 2004). In carideans shrimps with continuous reproduction, the ovarian development usually occurs while the eggs are being incubated (Bauer, 2004). Soon after the larvae hatch, the female can copulate with the paired male and produce a new brood, therefore, they continuously invest in reproduction.

Studies on the individual growth, longevity and mortality of species of *Alpheus* are scarce in the literature, but some comparisons can be made. In a study on the population structure of *A. carlae* on the northern coast of São Paulo, Mossolin *et al.* (2006) estimated the CL_∞ of males and females as 13.90 mm and 14.90 mm, respectively, and longevity as ~1.20 years. A similar result was found for *A. estuariensis* in the northeastern coast of Brazil by Costa–Souza *et al.* (2017) in which there was no difference between the growth parameters of males and females (Tab. 2). Although *A. carlae* and *A. brasileiro* belong to the *A. armillatus* species complex, their growth parameters differed markedly, probably due to the higher values of CL_∞ estimated for *A. carlae*. However, when the study of Mossolin *et al.* (2006) was carried out, it was still unclear which species belonged to this species complex. Since this issue was only elucidated later by Anker (2012), it is possible that other species have been included by Mossolin *et al.* (2006) in the estimation of growth parameters, resulting in an overestimated CL_∞ for *A. carlae*.

In summary, our study showed that males reach larger sizes, grow slower, reach sexual maturity later, and live longer than females. The analyses of individual growth, longevity, and mortality indicate sex–specific energy allocation strategies (sex allocation). Pescinelli *et al.* (2018a) reached the same conclusion by studying the relative growth. Thus, our results suggest that sex–specific physiological aspects are the drivers of the monogamous social system of the studied population. Altogether, our results contribute to a better understanding of the life history of the snapping shrimp *A. brasileiro* and may be used in comparative studies with other species.

Table 2. *Alpheus brasileiro* Anker, 2012. Growth parameters and mortality, CL_∞ is asymptotic size, *k* is the growth coefficient, longevity and M mortality for *Alpheus* species. *Growth parameters with no difference between males and females, and **Growth with the difference between males and females. MF males + females.

Species	Reference	Methods	Parameter	Male	Female
*Alpheus carlae***	Mossolin *et al.* (2006)	Elefan I	CL_∞ (mm)	13.90	15.34
			k (year–1)	2.28	1.89
			Longevity	1.20	1.29
*Alpheus estuariensis**	Costa–Souza *et al.* (2017)	Bhattacharya	CL_∞ (mm)	14.64(MF)	
			k (year–1)	1.21(MF)	
			Longevity	1.07(MF)	
Alpheus brasileiro**	Present study	(PeakFit)	CL_∞ (mm)	9.49	9.31
			k (year–1)	2.92	3.28
			Longevity	1.64	1.32
			M(year–1)	2.82	3.48

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