Thalassas (2018) 34:1–11
DOI 10.1007/s41208-017-0036-z

Population Structure of the Shrimp *Alpheus estuariensis* (Caridea: Alpheidae) in a Tropical Estuarine Tidal Mudflat

Ana Carla Costa-Souza[1] · **José Roberto Botelho de Souza**[1] ·
Marina de Sá Leitão Câmara de Araújo[2] · **Alexandre Oliveira Almeida**[1]

Received: 28 April 2017 / Accepted: 18 July 2017 / Published online: 7 August 2017

Abstract This study investigated recruitment, sex ratio, growth, longevity, density, and distribution pattern of a population of the snapping shrimp *Alpheus estuariensis* in a tropical estuarine tidal mudflat in northeastern Brazil. Individuals were captured monthly from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil. In total, 863 shrimps were collected: 311 males, 305 females (134 breeding and 171 non-breeding), and 247 juveniles. Individuals smaller than 5.9 mm (carapace length of the smallest breeding female) were considered juveniles. Both adults and juveniles occurred throughout the sampling period. Although there was no relationship between abundance and environmental factors (temperature, rainfall, and salinity), some months had more individuals than others. Recruitment was continuous. Total and monthly sex ratio did not differ from 1:1 (M:F). The sex ratio by size-frequency class (carapace length) was similar to Wenner's "Standard Pattern"; however, no deviation in favor of males was observed in the largest size classes. Compared with Gompertz and logistic functions, the von Bertalanffy Growth model gave the best fit to the data, describing growth with the equation: Length = $14.64*(1\text{-}e^{(-1.21*(\text{age-}0.03))})$. The estimated life span of *A. estuariensis* was 1.07 years. Juveniles and adults were more abundant in small grain size sediments, which might facilitate excavation during shelter construction.

Keywords Crustacea · Snapping shrimp · Recruitment · Sex ratio · Longevity · Distribution

Introduction

Many aspects of organismal ecology may be explained by population processes and structure such as size-frequency distribution, sexual maturity, reproductive period, recruitment, longevity, mortality, and sex ratio. This knowledge is crucial in the study of local and global ecological processes, to propose trends on population features, and to support studies on species conservation (Bauer 1992; Almeida et al. 2012a; Ardovine 2014). Understanding the population structure of decapod crustaceans of economic interest is necessary for the development of conservation strategies, guidelines, and regulations to control their consumption (Almeida et al. 2012a; Hirose et al. 2015; Pinheiro and Almeida 2015; Santos et al. 2016).

Despite the vast diversity and wide geographical distribution of decapod crustaceans (Martin and Davis 2001), common trends in the population structure can be clearly observed in several species. Populations are shaped and/or affected by abiotic factors that change with latitude, and after considering these factors, generalizations can be proposed (Bauer 1989, 1992; Cobo and Fransozo 2003; Castilho et al. 2007; Lardies et al. 2008). Populations from temperate regions tend to have larger individuals with late sexual maturity and short and seasonal reproductive period and recruitment (Bauer 1992; Litulo 2005). On the contrary, subtropical and tropical populations have smaller individuals with early sexual maturity and

---

✉ Ana Carla Costa-Souza
accostabio@yahoo.com.br

[1] Universidade Federal de Pernambuco (UFPE), Centro de Biociências, Departamento de Zoologia, Avenida Professor Moraes Rêgo, 1235, Cidade Universitária, Recife, Pernambuco 50670-901, Brazil

[2] Universidade de Pernambuco, Faculdade de Ciências, Educação e Tecnologia de Garanhuns (FACETEG), Magano, Garanhuns, Pernambuco 55294-902, Brazil

continuous reproductive period and recruitment (Bauer 1992; Litulo 2005; Almeida et al. 2012a; Hirose et al. 2012).

Sex ratio is another important aspect that might portray the behavior of species (e.g., sexual behavior or mating system), as well as the sexual system (gonochorism and hermaphroditism). The composition and population dynamics of a species might vary over time along the life cycle (Wenner 1972; Correa and Thiel 2003; Terossi and Mantelatto 2010). Wenner (1972) analyzed the sex ratio of some marine crustaceans according to size and proposed four patterns: (1) Standard: the sex ratio is proportional in most size classes, but it is male-biased in the largest size classes; (2) Reversal: represented by a sigmoid curve, the proportion of the sexes varies sharply as individuals grow; it is mostly observed in populations with sexual reversion; (3) Intermediate: juveniles are incorporated into the population in different proportions, resulting in a sex ratio different from 1:1; and (4) Anomalous: the 1:1 ratio is maintained in smaller size classes; there is a deviation towards females in the intermediate classes, and towards males in the larger classes. Terossi and Mantelatto (2010) proposed the “Predominance” pattern, when studying *Hippolyte obliquimanus* from São Paulo (Brazil), in which females are predominant in almost all size classes (female-biased).

The genus *Alpheus* comprises a rich and diverse group known as snapping shrimps, with more than 300 species described (De Grave and Fransen 2011; Almeida et al. 2014). The genus is widely distributed in tropical and subtropical marine and estuarine habitats, occurring from the intertidal to the deep sea (Chace 1988; Anker et al. 2006). Basic studies on population biology of *Alpheus* are still scarce maybe due to its complicated taxonomy, which includes the presence of species complexes (Mathews and Anker 2009). These shrimps are ecologically cryptic (see Felder 1982), which makes monthly samplings difficult and contributes to the lack of information about the life-history of most species.

Alpheus estuariensis is a burrowing shrimp from the Western Atlantic, found from the eastern coast of Florida (USA) down to Santa Catarina, southern Brazil (Christoffersen 1984; Almeida and Mantelatto 2013). They are commonly found in burrows excavated in muddy sediments of estuaries, under rocks and debris, as well as in rotting wood, from the intertidal to 22 m deep (Christoffersen 1984; Almeida et al. 2012b). In these environments, *A. estuariensis* build deep and complex burrows which are also used as shelter by other crustaceans with which they are associated (Costa-Souza et al. 2014; Oliveira et al. 2015). They are functionally bioturbators, according to Berke’s classification (Berke 2010).

The breeding biology and heterosexual pairing of *A. estuariensis* in an intertidal mudflat in northeastern Brazil was studied by Costa-Souza et al. (2014). Similar to other tropical species, the population showed continuous breeding, and the proportion of ovigerous females varied along the year. However, the fecundity was lower than in other species of the genus. Approximately 20% of the sampled animals were found in heterosexual pairs of similar-sized individuals, suggesting the occurrence of monogamy. However, despite the wide latitudinal distribution of *A. estuariensis*, studies on its population structure have not been published until the present moment.

In this study the population structure of *A. estuariensis* was analyzed and compared with other tropical caridean shrimp populations. We analyzed the size frequency distribution, recruitment, sex ratio, growth, longevity, distribution, and density of shrimps according to sediment type (granulometry). To conclude, we evaluated whether *A. estuariensis* is well established in the study area, a mangrove remnant situated in an urbanized area.

Materials and Methods

Study Area and Sampling Protocol

The Pontal Bay (14°48′31.1″ S 39°02′08.3″ W), located in Ilhéus, Bahia state, northeastern Brazil, is an estuary formed by the rivers Cachoeira, Fundão, and Santana (Fig. 1). The estuary is formed by muddy areas with mangroves and sandbanks in the lower part of the alluvial plain (Nacif et al. 2003). The bay is surrounded by the city and it is affected by domestic sewage discharge (see Almeida et al. 2006; Souza et al. 2009). The study area comprised an intertidal plain of muddy sediments and sparse rocks that are exposed during the spring tide. Samplings were taken monthly from September 2011 to October 2012 during spring low tide. No samplings occured in October 2012 due to heavy rainfall.

At the sampling site, three 30 m long transects (T1, T2, and T3) were arranged parallel to the shoreline. The distance between transects was 24 m between T1 and T2 and 12 m between T2 and T3. Between T2 and T3 there was a concave area that was always flooded, even at low tide. In order to avoid placing the transect in such conditions, T3 had to be placed 24 m away from T2. Ten sampling units of 1 m^2 were randomly selected from each transect every month, totaling 30 sampling units per month.

Individuals of *A. estuariensis* were captured from the sampling units using a 50 mm diameter pump made of a PVC pipe. This pump was used as a corer. All burrow openings within the units were pumped. The number of times that the pump was used in each opening was not standardized. The sediment taken with the pump was sieved using a 1.8 mm fine mesh. Individuals were sorted and placed into plastic bottles filled with water from the sampling site and transported to the laboratory for further analyses. Sediment samples were also taken from each transect.

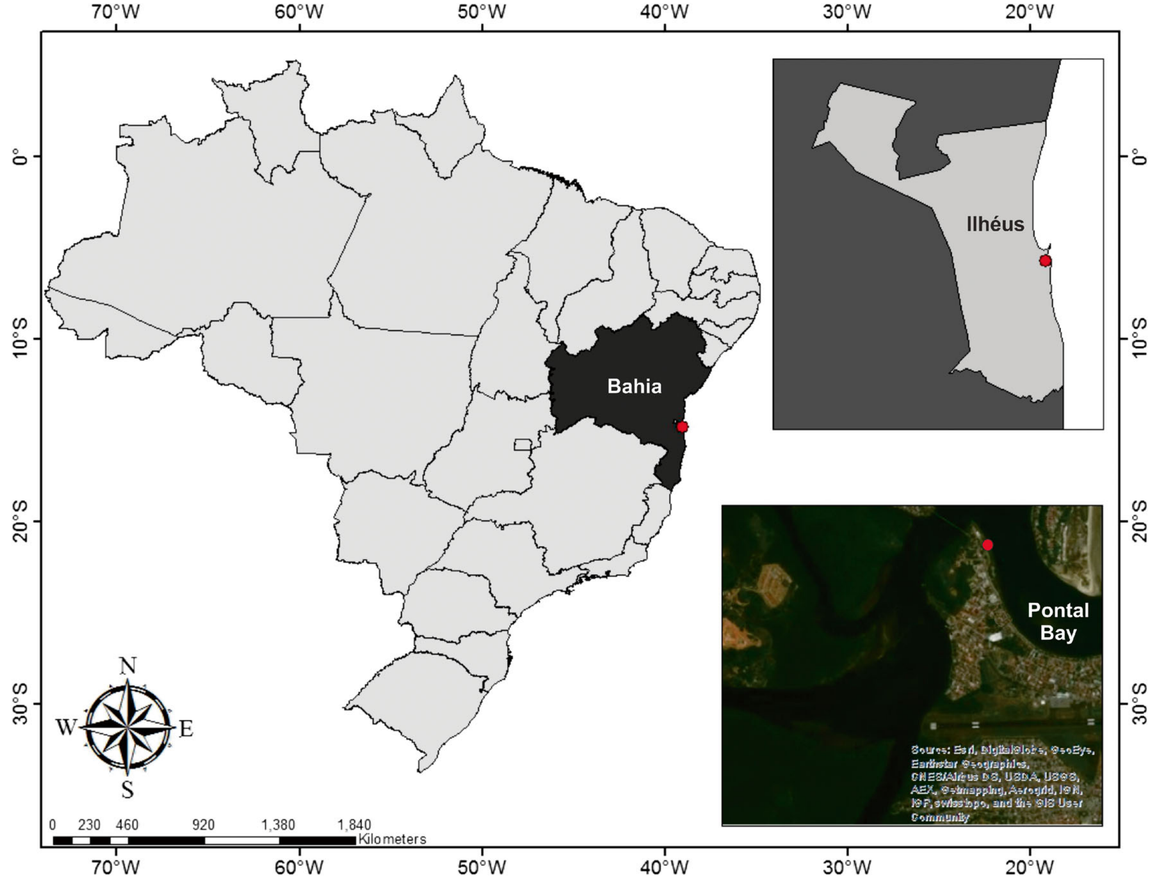

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Fig. 1 Location of the study area in Pontal Bay, Ilhéus, Bahia, Brazil

Laboratory Measurements

In the laboratory, each individual was anesthetized on ice and preserved in 70% ethanol. Males were identified based on the presence of the *appendix masculina* on the endopod of the second pair of pleopods (Bauer 2004). Females were identified based on the absence of the *appendix masculina* and/or presence of embryos underneath the abdomen (Bauer 2004). Individuals smaller than 5.9 mm of carapace length (smallest breeding female) were considered juveniles (see Costa-Souza et al. 2014); at this stage, the *appendix masculina* is undeveloped, preventing sex recognition.

The carapace length (CL) of each shrimp (the distance from the tip of the rostrum to the posterior margin of the carapace) was measured with a digital caliper to the nearest 0.01 mm. Small individuals were measured with a stereomicroscope equipped with a *camera lucida* and ocular micrometer.

Air temperature, rainfall (precipitation), and salinity data were recorded monthly. Air temperature data were obtained from the "Centro de Previsão de Tempo e Estudos Climáticos — CPTEC/INPE" website (http://bancodedados.cptec.inpe.br/estatisticas/). Rainfall data were obtained from the "Instituto do Meio Ambiente e Recursos Hídricos do Estado da Bahia — INEMA-BA" website (http://www.inema.ba.gov.br/monitoramento/indice-precipitacao/). Salinity was recorded with a portable refractometer (Instrutherm). Methods used for the granulometric analysis of T1, T2, and T3 were described by Oliveira et al. (2015) in a natural history study of the alpheid shrimp *Salmoneus carvachoi* in the same area.

Statistical Analyses

The data samples were grouped in CL classes of 0.5 mm and histograms of size-frequency distribution were used to analyze the population structure (juveniles, males, and females). Recruitment was assessed based on the abundance of individuals smaller than 5.9 mm throughout the year. The sex ratio was defined as the total number of males/total number of females; the chi-squared test with Yates correction was used to compare the total and monthly percentages of males and females. Wenner's curve was plotted with male data using the percentage of individuals by size class (see Wenner 1972). A significance level of 5% was adopted for all statistical analyses.

To estimate growth parameters males and females were grouped, as the length structure was similar in both sexes, and the sex ratio was ≈1. The CL frequency distribution was used to estimate the growth parameters of the model. Modes were identified by the Bhattacharya method (Bhattacharya 1967), with size-class intervals of 0.5 mm, using FISAT II v. 1.2.2 (Gayanilo et al. 2005). The routine 'linking of means' was used to obtain the growth increments. The growth parameters were estimated based on three different mathematical functions: Von Bertalanffy Growth Function (VBGF), Gompertz Growth Function (GGF), and Logistic Growth Function (LGF). The growth curve that best represented the data was chosen based on the Akaike Information Criteria (AIC) (Akaike 1974), using the following equation:$AIC = 2\log\varphi + 2K$, where Φ = a minimum likelihood and K = number of model parameters. Afterwards, the variation of the smallest value of AIC (Δi) and the importance of each model (W_i), defined as $w_i = e^{(-0.5\Delta_i)100/\sum\Delta_i}$, was calculated. The upper and lower limits (95%) for the confidence intervals of each estimated growth parameter were established using likelihood and bootstrap analyses, both with 1000 interactions (Hood 2006). Longevity was estimated by the growth parameters of the best model, based on the length that represented the 99th percentile of the population (L99%) (Sparre and Venema 1998).

The mean total density and the density of each group (juveniles, females, and males) was calculated for each transect. To calculate density, the total number of individuals per sampling unit (1 m^2) in each transect was considered. Differences between densities were analyzed using the Kruskal-Wallis test and Mann-Whitney test *a posteriori*. Total abundance and per group (total, juveniles, females, and males) were related to the grain size distribution obtained for each transect.

Statistical analyses were performed with PAST - Paleontological Statistics version 2.16 (Hammer et al. 2001). The map was built using the program ArcMap version 10 (ArcGis). All the figures were modified using CorelDRAW Graphics Suite X7.

Results

Environmental Data

The mean air temperature in the study area varied from 22 °C (September 2011) to 27 °C (January and February 2012) (25 ± 2.8 °C; mean ± standard deviation). Rainfall was well distributed throughout the study period, with monthly means varying from 0.1 ± 0.2 cm (September 2012) to 13.9 ± 22.9 cm (August 2012). Drought periods were not observed. The mean salinity varied from 24.5 (December 2011) to 34.3 (May 2012) (30.6 ± 2.3) (Fig. 2). The grain size analysis evidenced small differences in grain size composition between transects, with predominance of coarse silt in T1, fine sand in T2, and very fine sand in T3.

Population Structure

A total of 863 individuals were collected, of which 311 (36.0%) were males, 305 (35.4%) females — 134 (43.9%) breeding and 171 (56.1%) non-breeding — and 247 (28.6%) juveniles (Fig. 3). The CL ranged from 5.9 to 14.0 mm (8.2 ± 1.4) in males, from 5.9 to 13.0 mm (7.5 ± 1.6) in females; and from 1.9 to 5.8 mm (4.6 ± 0.8) in juveniles. Males and females did not differ significantly in size ($P = 0.660$; Mann-Whitney rank sum test). Adults represented more than 50% of the population in most months, except in January 2012 (Fig. 4). Small individuals (< 5.9 mm) occurred in all months, with peaks in December 2011, January 2012, May 2012, and July 2012, indicating a continuous recruitment. The frequency of adult and juvenile shrimps throughout the year was not related to rainfall and temperature distribution (Multiple R: 0.669; $P > 0.05$).

Sex Ratio

The total male/female sex ratio (M:F) was 1:1.02 along the year (Table 1). In the sex ratio by size class, the frequency of males and females was proportional in most classes, except in the 5.5–6.0 mm class. In that size class, females were more frequent, while males were dominant in the 11.5–12.0 mm class (Fig. 5).

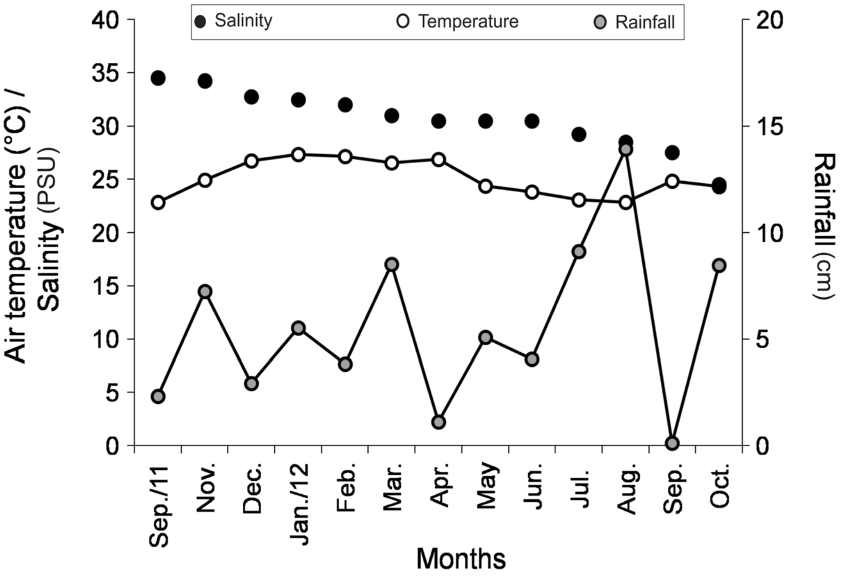
Growth

The three growth models were fitted to the data, and two of them achieved a very similar value of AIC (Table 2). Among them, the VBGF was the growth model with the best fit [$\text{Length} = 14.64*(1-e^{(-1.21*(\text{age}-0.03))})$] and lowest AIC value (Fig. 6). Age explained 99% of length variation. The estimated longevity of *A. estuariensis* was 1.07 years.

Population Distribution

Of the total number of individuals, 596 (69%) were captured in T1, 81 (9%) in T2, and 186 (22%) in T3. The total mean density was 2.2 ± 2.1 ind. m^{-2}. Considering the mean density per transect, the highest value was observed in T1 (4.8 ± 1.9 ind. m^{-2}), followed by T3 (1.6 ± 1.3 ind. m^{-2}), and T2 (0.4 ± 0.7 ind. m^{-2}) (Fig. 7). Density was significantly different between transects (Kruskal-Wallis test and Mann-Whitney *posteriori*: $P < 0.005$). The mean density of juveniles, females, and males was also higher in T1, followed by T3 and T2 (Fig. 8). The density of males and females in T1 did not differ significantly (Kruskal-Wallis test and Mann-Whitney *a posteriori*: $P = 0.979$) and was higher than that of juveniles (Kruskal-Wallis test and Mann-Whitney *a posteriori*: $P = 0.016$). In the other transects, the densities of the three groups did not differ significantly (T2: Kruskal-Wallis test and

Fig. 2 Monthly variation of abiotic factors (temperature, rainfall, and salinity) from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil



Mann-Whitney *a posteriori*: *P* = 0.550; T3: Kruskal-Wallis test and Mann-Whitney *a posteriori*: *P* = 0.560).

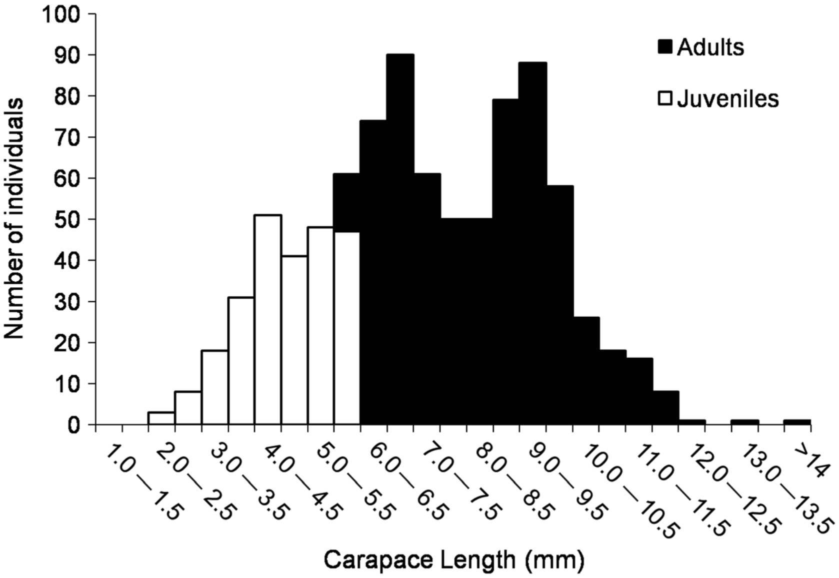
Discussion

Population Structure

Adults and juveniles were observed throughout the studied period, with dominance of adults in most months. However, the abundance in each size class was variable. In general, this structure resembles that of many tropical (and few subtropical) marine crustaceans. In these regions, individuals of almost all size classes are often found during all year (Bauer 1989, 1992; Bezerra and Mathews-Cascon 2006, 2007; Vergamini and Mantelatto 2008; Terossi and Mantelatto 2010; Silva et al. 2016). This tendency is directly related to high temperatures with small variation throughout the year seen in tropical regions. High temperatures allow a rapid gonadal development and continuous reproduction, providing a constant input (renewal) of individuals to the population (Sastry 1983; Bauer 1992; Cobo and Fransozo 2003; Litulo 2005). Costa-Souza et al. (2014) recorded a continuous reproductive period for the same population of *A. estuariensis*, which maintains this population size throughout the years.

Nutrient availability is another determinant factor in the population structure and survival of individuals (Bauer 1992; Bauer and Lin 1994; Litulo 2005). Tropical estuarine

Fig. 3 Frequency distribution by size-class (CL) of the total number of individuals (males, females, and juveniles) of the shrimp *Alpheus estuariensis* sampled in Pontal Bay, Ilhéus, Bahia, Brazil



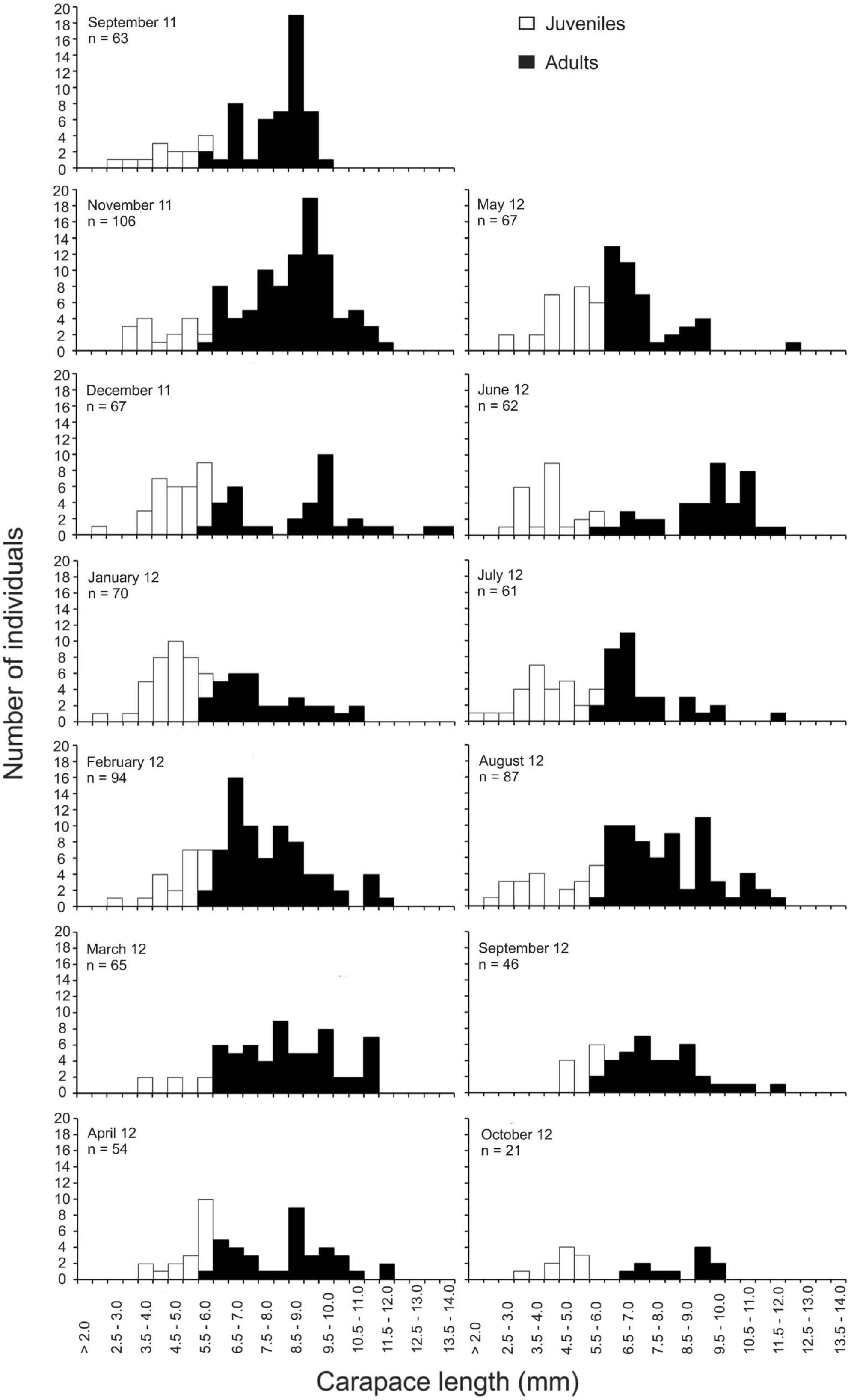


Fig. 4 Monthly abundance by size-class (CL) of the shrimp *Alpheus estuariensis* sampled from September 2011 to October 2012 in Pontal Bay, Ilhéus, Bahia, Brazil

Table 1 Sex ratio (males:females) of the shrimp *Alpheus estuariensis* sampled in Pontal Bay, Ilhéus, Bahia, Brazil, from September 2011 to October 2012

Month	Sex-ratio (M:F)	χ^2
September 2011	29:26	0.132
November 2011	45:47	0.100
December 2011	15:21	1.54
January 2012	17:16	0.011
February 2012	39:32	0.540
March 2012	28:32	0.365
April 2012	17:18	0.055
May 2012	23:18	0.501
June 2012	22:18	0.314
July 2012	17:18	0.304
August 2012	33:35	0.615
September 2012	21:19	0.059
October 2012	06:05	0.069

Table 2 Growth parameters of the shrimp *Alpheus estuariensis* sampled in Pontal Bay, Ilhéus, Bahia, Brazil, from September 2011 to October 2012, for the three tested growth models: von Bertalanffy Growth function (VBGF), Gompertz (GGF), and Logistic (LGF); and analysis of the Akaike information criterion curves. L∝ = asymptotic length; K = growth constant; to = age in the length; ΔI = variation from the smallest value of AIC; wi = importance of each model

	VBGF	Upper limits	Lower limits	GGF	LGF
$L_{\propto}$	14.64	17.19	13.17	12.33	11.5
K=	1.21	1.51	0.89	2.48	3.75
t_0=	0.03	0.07	−0.005	0.39	0.46
AIC	8.64			9.54	9
Δi	0			0.95	0.36
wi	0.52			0.25	0.44

environments have a constant supply of resources, due to a high organic matter input(Little 2000; Silva et al. 2016). Although the abundance of *A. estuariensis* was not related to abiotic factors, the small temperature variation and constant food availability (characteristic of an estuarine environment) probably are the main factors favoring the persistency of the species and modulating its population.

Despite the scarce information on alpheid shrimp populations, the tropical and subtropical marine populations previously studied showed a similar composition to that of *A. estuariensis*. Populations of *Alpheus dentipes* (south of Spain), *A. carlae* (as *A. armillatus*) (São Paulo, Brazil), and *Synalpheus fritzmuelleri* (Texas, USA) (Felder 1982; Fernández-Muñoz and García-Raso 1987; Mossolin et al. 2006) also had adults and juveniles in most months. The exception was the alpheid *Salmoeus carvachoi*, studied at the same time and site as *A. estuariensis*, which had a lower abundance and was even absent in some months (Oliveira et al. 2015).

The presence of juveniles along the entire year indicates a continuous recruitment in the study area. Many subtropical and tropical crustacean species, including typical mudflat species, exhibit continuous recruitment (Bauer 1992; Litulo 2005; Bezerra and Mathews-Cascon 2006, 2007). However, in *A. estuariensis*, the abundance in the first two size classes (i.e., supposedly the youngest) was extremely low and was only observed in 4 months. This might indicate a higher mortality of juveniles in the first life stages. In caridean shrimps,

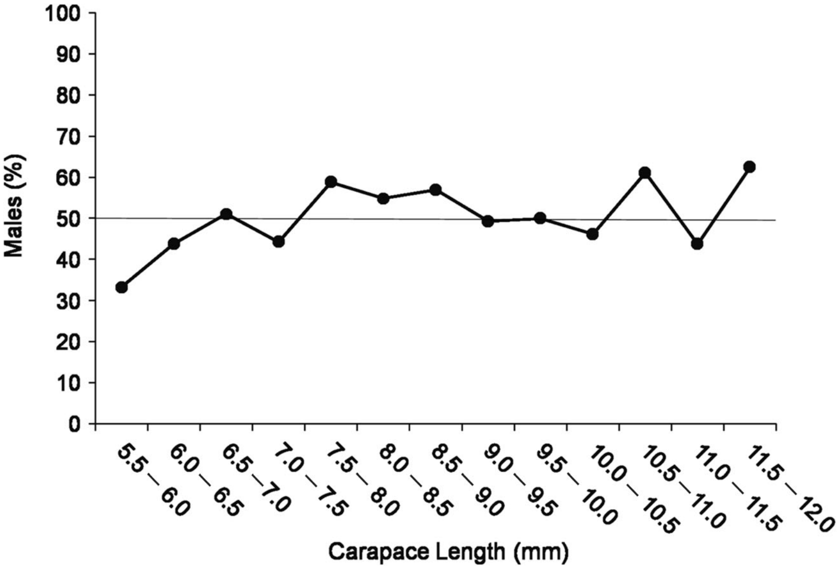


Fig. 5 Percentage of males by size-class (CL) of the shrimp *Alpheus estuariensis* sampled in Pontal Bay, Ilhéus, Bahia, Brazil

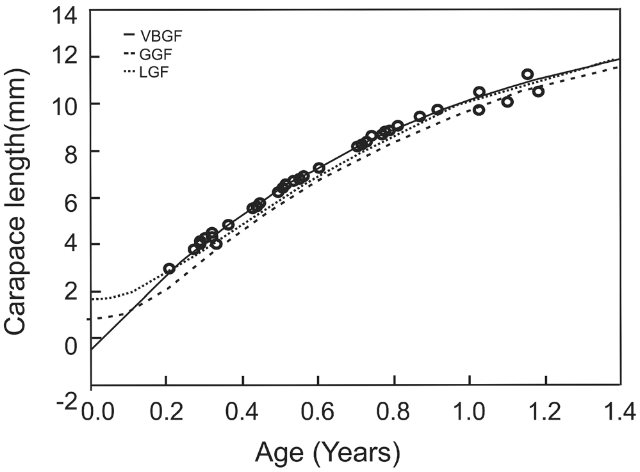


Fig. 6 Age, growth curves, and fitted in von Bertalanffy Growth function (VBGF), Gompertz (GGF) and Logistic (LGF) of the shrimp *Alpheus estuariensis* sampled in Pontal Bay, Ilhéus, Bahia, Brazil

the decapodid (megalopa) larva settles on the substrate just before the molt into juvenile (Anger 2006; Chak et al. 2015). Like other burrowing species (e.g., Strasser and Felder 1998), decapodids of *A. estuariensis* might excavate the sediment where it will shelter, becoming more exposed and vulnerable to predation, increasing the likelihood of early mortality. Juveniles of *A. estuariensis* probably share the same habitat of the adults, despite the low number of individuals found in the first size classes. On the contrary, Fernández-Muñoz and García-Raso (1987) suggested that small juveniles of *A. dentipes* (south of Spain) possibly do not live in the same habitat as larger juveniles and adults.

Males and females of *A. estuariensis* were very similar in size. In some species of *Alpheus*, such as *A. inca*, *A. carlae*, *A. normanni*, and *A. heterochaelis* (Nolan and Salmon 1970; Boltaña and Thiel 2001; Mossolin et al. 2006) males are slightly smaller than females. In other species, e.g., *A. heterochaelis*, females are slightly smaller than males (Rahman et al. 2003). However, despite these small variations among species, the genus *Alpheus* lacks size dimorphism.

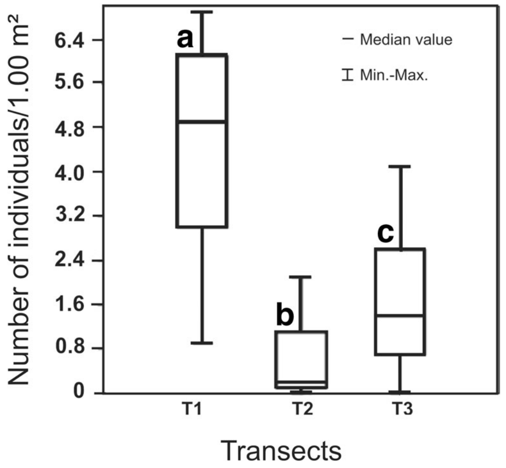


Fig. 7 Total densities, per sampling unit (1 m^2) and transect, of the shrimp *Alpheus estuariensis* sampled in Pontal Bay, Ilhéus, Bahia, Brazil. Boxplots with equal letters did not differ significantly

Sex Ratio

The total and monthly sex ratio observed did not differ from the expected 1:1. The sex ratio of a population of *A. carlae* also did not differ from the expected 1:1 (Mossolin et al. 2006). In *A. dentipes*, both the total and monthly sex ratio were also similar to the ratio obtained for *A. estuariensis* (Fernandez-Muñoz and García-Raso 1987).

In many species of *Alpheus*, including the studied population, individuals are found in heterosexual pairs in the field (Knowlton 1980; Mathews 2002; Correa and Thiel 2003; Bauer 2004; Costa-Souza et al. 2014; Pescinelli et al. 2016). Some of these populations are considered monogamous (Knowlton 1980; Mathews 2002; Pescinelli et al. 2016). Some ecological characteristics of the genus *Alpheus* may be considered, such as low population density, the high inter and intraspecific competition for refuges, and the cryptic habit. Those features, along with the pairing behavior, are probably the main adaptive factors that contribute to the equal abundance of males and females in the populations (Knowlton 1980; Mathews 2002; Correa and Thiel 2003). Although monogamy has not been confirmed in this population of *A. estuariensis* (see Costa-Souza et al. 2014), the presence of males paired with ovigerous and non-ovigerous females, the occurrence of size-assortative pairing, and the cryptic habit of those animals may have contributed to the 1:1 sex ratio.

The frequency of males and females was very similar in all size classes. Considering the five sex ratio patterns by size class that have been proposed (see Wenner 1972; Terossi and Mantelatto 2010), the sex ratio observed in *A. estuariensis* resemble the "Standard Pattern". According to Wenner (1972), this pattern indicates that the frequencies of males and females are the same in most size classes. However, in the largest classes ahigher prevalence of males might reflect a larger growth of these individuals or the existence of a differential behavior between sexes when they reach certain sizes. Differently, in *A. estuariensis* the frequency of both sexes in the largest size classes was similar.

Growth

The presence of size-assortative pairing, similar size structure in both sexes, and a 1:1 sex ratio in all size classes indicate that males and females of *A. estuariensis* have similar growth and mortality rates. In other crustaceans, differences in growth

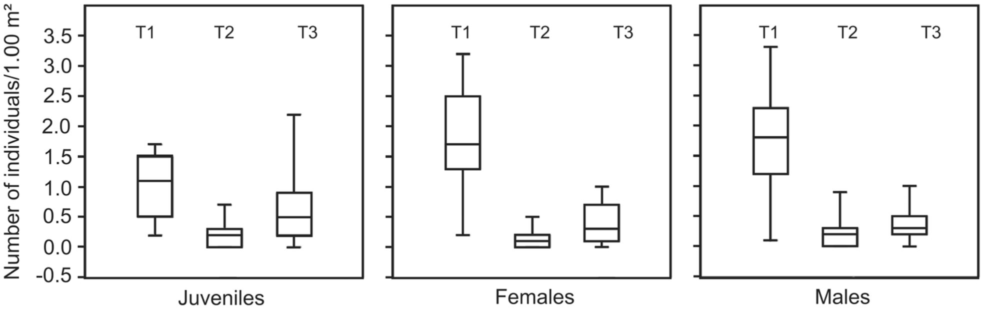


Fig. 8 Densities per sampling unit (1 m^2) of juveniles, females, and males per transect of the shrimp *Alpheus estuariensis* sampled in Pontal Bay, Ilhéus, Bahia, Brazil

between males and females are common. In *Callinectes danae*, females have slower growth because they direct energy towards reproduction and spawning migration (Shinozaki-Mendes et al. 2012). In penaeoid shrimps, females are often larger, have lower growth rates and live longer, which is probably an adaptation to increase egg production (Castilho et al. 2012). Different mortality rates between sexes may result in different size structure and sex ratio: in *Callichirus major* the sex ratio is 1:1 in young adults but the proportion of females increases with size due the higher mortality of males as a result of their agonistic behavior (Souza et al. 1998).

The estimated longevity for *A. estuariensis* (1.07 years, ~13 months) can be considered intermediate when compared to other caridean shrimps with short life cycles such as *Thor manningi* (males with 3.5 months~; females with 5 months) (Bauer 1986), and to carideans with long life cycles, such as *Palaemon adspersus* (males: 3.07 years; females: 2.83 years) (Glamuzina et al. 2014). The longevity of *A. estuariensis* was very similar to *A. carlae* and *A. dentipes* from populations from the subtropical region (Fenandez-Muñoz and Garcia-Raso 1987; Mossolin et al. 2006).

Population Distribution

The highest abundance and density of adults and juveniles was observed in T1, located in the lower intertidal zone. The grain size of T1 (coarse silt) was smaller than that of T2 and T3 (Oliveira et al. 2015). Individuals of *S. carvachoi*, one of the shrimps associated with *A. estuariensis* in the study area, were also more abundant in the same transect (Oliveira et al. 2015). The choice of substrate to settle may be influenced by factors such as surface texture (including type of sediment), adult-related cues, salinity, estuarine water, vegetation, and presence of shells (in hermit crabs) [see Strasser and Felder (1998, 1999) and references therein; Anger (2006) and references therein]. The type of sediment might affect burrow structure, density, and distribution of burrowing crustaceans, which also might influence the distribution of burrow-associated fauna (Dworschak 1983; Yanagisawa 1984; Hall-Spencer and Atkinson 1999; Palomar et al. 2005). The higher number of individuals found in T1 indicates that late larval stages might "select" sediments of small grain sizes for settlement. Fine sediments are characterized by the reduced space between particles, poor drainage, lower oxygen concentration, higher organic matter concentration, and "cohesive" properties. Such cohesiveness is extremely important for burrowing organisms and allows the construction and maintenance of their refuges in the sediments, which would be more difficult in the sand (Little 2000). Probably, *A. estuariensis* selects substrates with fine sediments due to their particular properties. Higher cohesive properties might facilitate burrowing due to the sediment's poor drainage capacity, which prevents drought during the low tide. Also, the high concentration of organic matter of fine sediments decreases the shrimps' exposure time during foraging.

According to the results obtained in this study, we conclude that the population structure of *A. estuariensis* resembles several other tropical crustacean populations. The abundance of individuals is constant throughout the year, as well as recruitment, which is probably related to low variation in temperature and the constant food availability in the studied region. Additionally, although the study site is situated in a mangrove remnant near an urban area, the population seems to be well established. As in other species of *Alpheus*, males and females of *A. estuariensis* show similar size and the sex ratio is 1:1. These shrimps do not have long lifespans as other co-generic populations. Finally, we conclude that *A. estuariensis* prefers to build shelters in fine-grained sediments.

Acknowledgements The authors are thankful to the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) (APP 0035/2011) and to the Universidade Estadual de Santa Cruz (UESC) (00220.1100.1065) for financing the Project "Biologia e Ecologia de Camarões da Família Alpheidae (Crustacea: Decapoda: Caridea)". To the Programa de Pós-Graduação em Zoologia of UESC for the support. A.C. Costa-Souza thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the master's scholarship grant. AOA thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the research scholarship support (PQ 305939/2015-7). To Patricia Santos, Guidomar Soledade, Andressa Cunha, Mário Vitor Oliveira, David Weber, João Mário Macêdo, Aline Reis, Midian

Salgado, Karen Martins, Yamid Mera, Milane Correa, Luciano Oliveira, Paulo Ribeiro, and Ivanise Hora for their support in the field samplings and to Dr. Erminda Couto and Dr. Fernanda Jordão for their support with sediment analysis.

References

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Autom Control 19:716–725

Almeida AO, Coelho PA, Santos JTA, Ferraz NR (2006) Crustáceos decápodos estuarinos de Ilhéus. Bahia, Brasil. Biota Neotrop 6(2): doi:10.1590/S1676-06032006000200024

Almeida AO, Mantelatto FLM (2013) Extension of the southern distributions of three estuarine snapping shrimps of the genus *Alpheus* Fabricius, 1798 (Caridea: Alpheidae) in South America. Crustaceana 86:1715–1722

Almeida AC, Baeza JA, Fransozo V, Castilho AL, Fransozo A (2012a) Reproductive biology and recruitment of *Xiphopenaeus kroyeri* in a marine protected área in the Western Atlantic: implications for resource management. Aquat Biol 17:57–69

Almeida AO, Boehs G, Araújo-Silva CL, Bezerra LEA (2012b) Shallow water caridean shrimps from southern Bahia, Brazil, including the first record of *Synalpheus ul* (Ríos & Duffy, 2007) (Alpheidae) in the southwestern Atlantic Ocean. Zootaxa 3347:1–35

Almeida AO, Terossi M, Mantelatto FL (2014) Morphology and DNA analyses reveal a new cryptic snapping shrimp of the *Alpheus heterochaelis* Say 1818 (Decapoda: Alpheidae) species complex from the western Atlantic. Zoosystema 36:53–71

Anger K (2006) Contributions of larval biology to crustacean research: a review. Invertebr Reprod Dev 49:175–205

Anker A, Ahyong ST, Noel PY, Palmer AR (2006) Morphological phylogeny of alpheid shrimps: parallel preadaptation and the origin of a key morphological innovation, the snapping claw. Evolution 60: 2507–2528

Ardovine C (2014) Crabs global diversity, behavior and environmental threats. Nova publishers, New York

Bauer RT (1986) Sex change and life history pattern in the shrimp *Thor manningi* (Decopoda: Caridea): a novel case of partial protandric hermaphroditism. Biol Bull 170:11–31

Bauer RT (1989) Continuous reproduction and episodic recruitment in nine caridean shrimp species inhabiting a tropical seagrass meadow. J Exp Mar Biol Ecol 127:175–187

Bauer RT (1992) Testing generalizations about latitudinal variation in reproductive and recruitment patterns with caridean and sicyoniid shrimps. J Invertebr Reprod Dev 22:193–202

Bauer RT (2004) Remarkable shrimps: adaptations and natural history of the carideans. University of Oklahoma Press, Norman

Bauer RT, Lin J (1994) Temporal patterns of reproduction and recruitment in populations of the penaeid shrimps *Trachypenaeus similis* (Smith) and *T. constrictus* (Stimpson) (Crustacea: Decapoda) from the Northcentral Gulf of Mexico. J Exp Mar Biol Ecol 182:205–222

Berke SK (2010) Functional groups of ecosystem engineers: a proposed classification with comments on current issues. Integr Comp Biol 50:147–157

Bezerra LEA, Matthews-Cascon H (2006) Population structure of the fiddler crab *Uca leptodactyla* Rathbun, 1898 (Brachyura: Ocypodidae) in a tropical mangrove of northeast Brazil. Thalassas 22:65–75

Bezerra LEA, Matthews-Cascon H (2007) Population and reproductive biology of the fiddler crab *Uca thayeri* Rathbun, 1900 (Crustacea: Ocypodidae) in a tropical mangrove from Northeast Brazil. Acta Oecol 31:251–258

Bhattacharya CG (1967) A simple method of resolution of a distribution into Gaussian components. Biometrics 23:115–135

Boltaña S, Thiel M (2001) Associations between two species of snapping shrimp *Alpheus inca* and *Alpheopsis chilensis* (Decapoda: Caridea: Alpheidae). J Mar Biol Assoc U K 81:633–638

Castilho AL, Gavio MA, Costa RC, Boschi EE, Bauer RT, Fransozo A (2007) Latitudinal variation in population structure and reproductive pattern of the endemic south American shrimp *Artemesia longinaris* (Decapoda: Penaeoidea). J Crustac Biol 27:548–552

Castilho AL, Wolf MR, Simões SM, Bochini GL, Fransozo V, Costa RC (2012) Growth and reproductive dynamics of the South American red shrimp, *Pleoticus muelleri* (Crustacea: Solenoceridae), from the southeastern coast of Brazil. J Marine Syst 105–108: 135–144

Chace FA Jr (1988) The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907-1910, Part 5: Family Alpheidae. Smithsonian Contributions to Zoology 466:1–99

Chak STC, Bauer R, Thiel M (2015) Social Behaviour and Recognition in Decapod Shrimps, with Emphasis on the Caridea. In: Aquiloni L, Tricarico E (eds) Social Recognition in Invertebrates. Springer International Publishing, Cham, pp 57–84

Christoffersen ML (1984) The western Atlantic snapping shrimps related to *Alpheus heterochaelis* Say (Crustacea. Caridea), with the description of a new species. Papéis Avulsos de Zoologia 35(19):189–208

Cobo VJ, Fransozo A (2003) External factors determining breeding season in the red mangrove crab *Goniopsis cruentata* (Latreille) (Crustacea, Brachyura, Grapsidae) on the São Paulo State northern coast, Brazil. Revista Brasileira de Zoologia 20:213–217

Correa C, Thiel M (2003) Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. Rev Chil Hist Nat 76:187–203

Costa-Souza AC, Rocha SS, Bezerra LEA, Almeida AO (2014) Breeding and heterosexual pairing in the snapping shrimp *Alpheus estuariensis* (Caridea: Alpheidae) in a tropical bay in northeastern Brazil. J Crustac Biol 34:593–603

De Grave S, Fransen CHJM (2011) Carideorum Catalogus: The Recent Species of the Dendrobranchiate, Stenopodidean, Procarididean and Caridean Shrimps (Crustacea: Decapoda). Zoologische Mededelingen 85:195–589

Dworschak PC (1983) The biology of *Upogebia pusilla* (Petagna) (Decapoda, Thalassinidea). I. The burrows, Publicazzioni della Stazione Zoologica di Napoli I. Mar Ecol 4:19–43

Felder D (1982) Reproduction of the snapping shrimps *Synalpheus fritzmuelleri* and *S. apioceros* (Crustacea: Decapoda: Alpheidae) on a sublittoral reef off Texas. J Crustac Biol 2:535–543

Fernández-Muñoz R, Garcia-Raso JE (1987) Study of a population of *Alpheus dentipes* Guerin, 1832 from calcareous bottoms in the southern Spain. Investigaciones Pesqueras 51:343–359

Gayanilo FC Jr, Sparre P, Pauly D (2005) FAO-ICLARM stock assessment tools II (FISAT II)—User's guide. FAO Computerized Information Series (Fisheries). No. 8, Revised version. Rome: FAO

Glamuzina L, Conides A, Prusina I, Cukteras M, Klaoudatos D, Zacharaki P, Glamuzina B (2014) Population structure, Growth, Mortality and Fecundity of *Palaemon aspersus* (Rathke 1837; Decapoda: Palaemonidae) in the Parila Lagoon (Croatia, SE Adriatic Sea) with notes on the population management. Turk J Fish Aquat Sci 14:677–687

Hall-Spencer JM, Atkinson RJA (1999) *Upogebia deltaura* (Crustacea: Thalassinidea) in Clyde Sea maerl beds. J Mar Biol Assoc U K 79: 871–880

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4:1-9

Hirose GL, Fransozo V, Tropea C, Lopez-Greco LS, Negreiros-Fransozo ML (2012) Comparison of body size, relative growth and size at onset sexual maturity of *Uca uruguayensis* (Crustacea: Decapoda:

Ocypodidae) from different latitudes in the southwestern Atlantic. J Mar Biol Assoc U K 93:781–788

Hirose GL, Souza LS, Silva SLR, Alves DFR, Negreiros-Fransozo ML (2015) Population structure of the red mangrove crab, *Goniopsis cruentata* (Decapoda: Grapsidae) under different fishery impacts: Implications for resource management. Rev Biol Trop 63:443–457

Hood GM (2006) Pop Tools version 2.7. Software. Available at: http://www.cse.csiro.au/poptools

Knowlton N (1980) Sexual selection and dimorphism in two demes of a symbiotic, pair bonding snapping shrimp. Evolution 34:161–173

Lardies M, Medina MH, Correa JA (2008) Intraspecific biogeographic pattern breakage in the snapping shrimp *Betaeus emarginatus* caused by coastal copper mine tailings. Mar Ecol Prog Ser 358:203–210

Little C (2000) The biology of soft shores and estuaries. Oxford University Press, New York

Litulo C (2005) Population biology of the fiddler crab *Uca annulipes* (Brachyura: Ocypodidae) in a tropical East African mangrove (Mozambique). Estuar Coast Shelf Sci 62:283–290

Martin JW, Davis GE (2001) An updated classification of the recent Crustacea, Science Series 39. Los Angeles, CA: Natural History Museum of Los Angeles County 39:1–124

Mathews LM (2002) Tests of the mate-guarding hypothesis for social monogamy: does population density, sex ratio, or female synchrony affect behavior of male snapping shrimp (*Alpheus angulatus*)? Behav Ecol Sociobiol 51:426–432

Mathews LM, Anker A (2009) Molecular phylogeny reveals extensive and ongoing radiations in a snapping shrimp species complex (Crustacea, Alpheidae, *Alpheus armillatus*). Mol Phylogenet Evol 50:268–281

Mossolin EC, Shimizu RM, Bueno SLS (2006) Population structure of *Alpheus armillatus* (Decapoda, Alpheidae) in São Sebastião and Ilhabela, southeastern Brazil. J Crustac Biol 26:48–54

Nacif P, Costa L, Soadi A, Fernandes-Filho E, Ker J, Costa O, Moreau M (2003) Ambientes naturais da bacia hidrográfica do rio Cachoeira. Available at: http://www.corredores.org. br/?pageId = adminOpenDoc&docId = 1664. Accessed in 24 abril 2011

Nolan BA, Salmon M (1970) The Behavior and Ecology of Snapping Shrimp (Crustacea: *Alpheus heterochaelis* and *Alpheus normanni*). Forma et functio 2:289–335

Oliveira MV, Costa-Souza AC, Guimarães FJ, Almeida AO, Baeza JA (2015) Observations on the life history of a rare shrimp, *Salmoneus carvachoi* (Crustacea: Caridea: Alpheidae), a possible simultaneous hermaphrodite. Mar Biodiversity Rec 8:e141

Palomar N, Juinio-Meñez MA, Karplus I (2005) Behavior of the burrowing shrimp *Alpheus macellarius* in varying gravel substrate conditions. J Ethol 23:173–180

Pescinelli RA, Davanso TM, Costa RC (2016) Social monogamy and egg production in the snapping shrimp *Alpheus brasileiro* (Caridea: Alpheidae) from the south eastern coast of Brazil. J Mar Biol Assoc UK. doi:10.1017/S0025315416000904

Pinheiro MAA, Almeida R (2015) Monitoramento de populações do caranguejo-uçá, *Ucides cordatus* (Brachyura, Ucididae). In: Turra A, Denadai MR, Protocolos para o Monitoramento de Habitats Bentônicos Costeiros Rede de Monitoramento de Habitats Bentônicos Costeiros. Instituto Oceanográfico da Universidade de São Paulo, São Paulo, pp 122–133

Rahman N, Dunham DW, Govind C (2003) Social monogamy in the big clawed snapping shrimp *Alpheus heterochaelis*. Ethology 109:457–473

Santos LCM, Pinheiro MAA, Dahdouh-Guebas F, Bitencourt MD (2016) Population status and fishery potential of the mangrove crab, *Ucides cordatus* (Linnaeus, 1763) in North-eastern Brazil. J Mar Biol Assoc UK. doi:10.1017/S0025315416001259

Sastry AN (1983) Ecological aspects of reproduction. In: Vernberg FJ, Vernberg WB, eds, The Biology of Crustacea – Behavior and Ecology, New York, pp 179–270

Shinozaki-Mendes RA, Silva AAG, Mendes PP, Lessa R (2012) Age and growth of *Callinectes danae* (Brachyura: Portunidae) in a tropical region. J Crustac Biol 32:906–915

Silva FMRO, Ribeiro FB, Bezerra LE (2016) Population biology and morphometric sexual maturity of the fiddler crab *Uca* (*Uca*) *maracoani* (Latreille, 1802) (Crustacea: Decapoda: Ocypodidae) in a semi-arid tropical estuary of northeastern Brazil. Lat Am J Aquat Res 44:671–682

Souza JRB, Borzone CA, Brey T (1998) Population dynamics and secondary production of *Callichirus major* (Crustacea: Thalassinidea) on a southern brazilian sandy beach. Arch Fish Mar Res 46:151–164

Souza MFL, Eça GF, Silva MAM, Amorim FAC, Lôbo IP (2009) DistribuiÃ§Ã£o de nutrientes dissolvidos e clorofila-a no estuÃ¡rio dorio Chachoeira, nordeste do Brasil. AtlÃ¢ntica 31(1):107-121

Sparre P, Venema SC (1998) Introduction to tropical fish stock assessment. FAO Fisheries Technical Papers I 306:1–276

Strasser KM, Felder DL (1998) Settlement cues in successive developmental stages of the ghost shrimps *Callichirus major* and *C. islagrande* (Crustacea: Decapoda: Thalassinidea). Mar Biol 132:599–610

Strasser KM, Felder DL (1999) Settlement cues in an Atlantic coastal population of the ghost shrimp *Callichirus major* (Crustacea: Decapoda: Thalassinidea). Mar Ecol Prog Ser 183:217–225

Terossi M, Mantelatto FL (2010) Sexual ratio, reproductive period and seasonal variation of the gonochoric shrimp *Hippolyte obliquimanus* (Caridea: Hippolytidae). Mar Biol Res 6:213–219

Vergamini FG, Mantelatto FL (2008) Microdistribution of juveniles and adults of the mud crab *Panopeus americanus* (Brachyura, Panopeidae) in a remnant mangrove area in the southwest Atlantic. J Nat Hist 23:581–1589

Wenner AM (1972) Sex-ratio as a function of size in marine Crustacea. Am Nat 106:321–350

Yanagisawa Y (1984) Studies on the interspecific relationship between gobiid fish and snapping shrimp. 2. Life history and pair formation of snapping shrimp *Alpheus bellulus*. Publ Seto Mar Biol Lab 29:93–116