

## Population and reproductive biology of two caprellid species (Crustacea: Amphipoda) associated to *Sargassum cymosum* (Phaeophyta: Fucales) on the southeast coast of Brazil

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### ABSTRACT

Caprellid amphipods are common crustaceans at *Sargassum* beds of southeastern Brazil and constitute an important link between primary producers and marine consumers. The goal of this study is to evaluate population and reproductive biology of two caprellid species: *Paracaprella tenuis* Mayer, 1903 and *Pseudaeginella montoucheti* Quitete, 1971. *Sargassum cymosum* Agardh, 1820 samples were collected monthly between October 2010 and September 2011 in a rock shore in southeastern Brazil. The caprellids were identified, counted, measured and classified as males, immature females, sexually mature females, ovigerous females and juveniles. Eggs were counted and measured. Higher densities of *P. tenuis* and *P. montoucheti* were found mainly in winter and lower densities in fall and summer. Density variation is probably related to organic matter supply and substrate availability. Both species showed continuous reproduction with reproductive peaks. *Pseudaeginella montoucheti* larger egg volume indicates a longer incubation period. The egg volume was directly related to female size. The number of eggs was weakly related to female size, indicating that fecundity may be driven by other factors, such as the physiological conditions. Sex ratio deviated for males suggests a higher longevity of males. The present study highlighted important data of two caprellids species that occur in algal beds of different regions.

### KEYWORDS

Brown algae, *Pseudaeginella montoucheti*, *Paracaprella tenuis*, density, fecundity.

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## INTRODUCTION

Studies with phytal communities associated to rock shore macrophytes show that peracarid crustaceans, including amphipods, normally occur in high species abundance and richness, especially in coastal environments dominated by brown seaweeds (Edgar, 1983; Jacobucci *et al.*, 2002; Leite *et al.*, 2007; Jacobucci *et al.*, 2009a). The caprellid amphipods are represented by more than 360 described species (De Broyer, 2014; Mauro and Serejo, 2015) in eight families, widely distributed in marine environments and often represent dominant members in epibenthic communities (Lowry and Myers, 2013). They typically inhabit macroalgae, hydroids, sponges, ascidians, anthozoans, bryozoans, sponges, seagrasses and sediment (McCain, 1968; Takeuchi and Hirano, 1992; Guerra-García, 2001; González *et al.*, 2008; Jacobucci *et al.*, 2009a). The size and biomass of algae (Takeuchi *et al.*, 1987), and also biomass of epiphytes (Edgar, 1983) and hydrozoan cover (Cunha *et al.*, 2018) are important in their substrate selection.

Caprellid life cycle usually lasts on average 40 days (Takeuchi *et al.*, 2001). They are dioic with external fertilization and females present brood pouch, a unique attribute of Peracarida (Borowsky, 1991), to carry eggs and incubate their embryos (Schram, 1986). After releasing the juveniles, some females show parental care, assuring feeding, protection against predators (Clutton-Brock, 1991) and guaranteeing their growth (Aoki, 1997). Many species present continuous reproduction (Bynum, 1978; Imada and Kikuchi, 1984) with peaks of recruitment (Masunari, 1982; Edgar, 1983).

Most information published on caprellids is related to taxonomical papers, including descriptions of new taxa (*e.g.*, Guerra-García, 2003) and inventory of species (*e.g.*, De-La-Ossa-Carretero *et al.*, 2010). Studies involving population and reproductive biology are still particularly scarce (Prato *et al.*, 2013; De Paula *et al.*, 2016; Nuñez-Velazquez *et al.*, 2017). Population structure data are particularly important providing basic information about ecological stability of populations, including seasonal abundance, population size structure, birth rates and mortality (Hutchinson, 1981; Santos *et al.*, 1995). Fecundity analyzes have been considered an important tool to evaluate the reproductive potential of crustacean species, as well as

their population size, allowing inferences about their reproductive adaptations to environmental conditions (Mantelatto and Fransozo, 1997).

Caprellid amphipods, among other crustaceans, are quite frequent inhabitants of brown algae of the genus *Sargassum* in temperate and tropical areas (Imada and Kikuchi, 1984; Martin-Smith, 1993; Jacobucci *et al.*, 2002), and play an important trophic link between primary producers and higher trophic levels (Woods, 2009). In southeastern Brazil, in shallow coastal areas, these algal beds are very common, representing over 80% of the biomass in some areas in the states of São Paulo and Rio de Janeiro (Paula and Oliveira-Filho, 1980). Most caprellids in *Sargassum* beds belong to the genus *Caprella* but other species also occur in variable densities (Jacobucci and Leite, 2002; Jacobucci *et al.*, 2009a). This is the case of *Paracaprella tenuis* Mayer, 1903 and *Pseudaeginella montoucheti* Quitete, 1971 (Lacerda and Masunari, 2011). Both species are smaller than *Caprella* species and were recorded in sympatry in *Sargassum* beds of the northern coast of São Paulo State (Jacobucci *et al.*, 2002; Jacobucci *et al.*, 2009a).

Temporal variation was already recorded for both species with higher densities in summer (Jacobucci *et al.*, 2009a). Although belonging to the same subfamily and having a dominant detritivore feeding habit (Guerra-García and Figueroa, 2009), *P. tenuis* were recorded in much higher densities than *P. montoucheti* (Jacobucci *et al.*, 2009a). This situation suggests these species could present different reproductive strategies, which could result in particular patterns of population fluctuation. Thus the aim of this study was to investigate population structure and reproductive patterns of these two caprellid species throughout the year.

## MATERIAL AND METHODS

### Study area

The present study was carried out at Lázaro beach, located at Fortaleza inlet (23°30'S 45°08'W), Ubatuba municipality, north coast of São Paulo state (Fig. 1). This region presents large beds of the brown seaweed *Sargassum cymosum*. Lázaro beach is moderately protected, but it can be exposed to strong wave action, depending on the wind intensity and direction (Széchy and Paula, 2000).

### Sampling and processing

*Sargassum cymosum* samples were collected monthly between October 2010 and September 2011. At each month twenty-five seaweed fronds were sampled at the sublittoral region, at 2–2.5 m depth, using snorkeling. The fronds were enclosed individually in 0.2 mm mesh bags and removed from the rock shore using a spatula.

At the laboratory, each frond was washed separately in freshwater to detach the animals from the algae. The water left from the washing process was filtered in a 0.2 mm mesh to retain the remaining epifauna. According to Taylor and Cole (1994), this procedure is efficient and removes around 99% of the amphipods present in the algae. The epifauna removed was preserved in 70% ethanol.

The caprellids were separated and identified at species level with the help of a stereomicroscope, using specific keys (Lacerda and Masunari, 2011; Paz-Ríos et al., 2014).

All specimens of *P. tenuis* and *P. montoucheti* were counted and measured using a stereomicroscope with a graduated eyepiece. The body segments of each caprellid were measured separately (Fig. 2). Next they were classified as males (M), immature females (F), sexually mature females (MF), ovigerous females (OF) and juveniles (J), according to Bynum (1978) criteria and counted. The immature females could be distinguished from males by the presence of oostegites in pereonites 3 and 4, which appeared as small buds between gills at the beginning of sexual maturity. The smallest individual found among all the

sampled individuals that presented these small buds was used as sexual reference. All specimens smaller than the standard individuals were classified as juveniles with unknown gender. Individuals larger than the standard without oostegites were characterized as males. Females were characterized as sexually mature when the oostegites were fully developed, forming the brood pouch. Females carrying eggs or juveniles in their brood pouch were characterized as ovigerous.

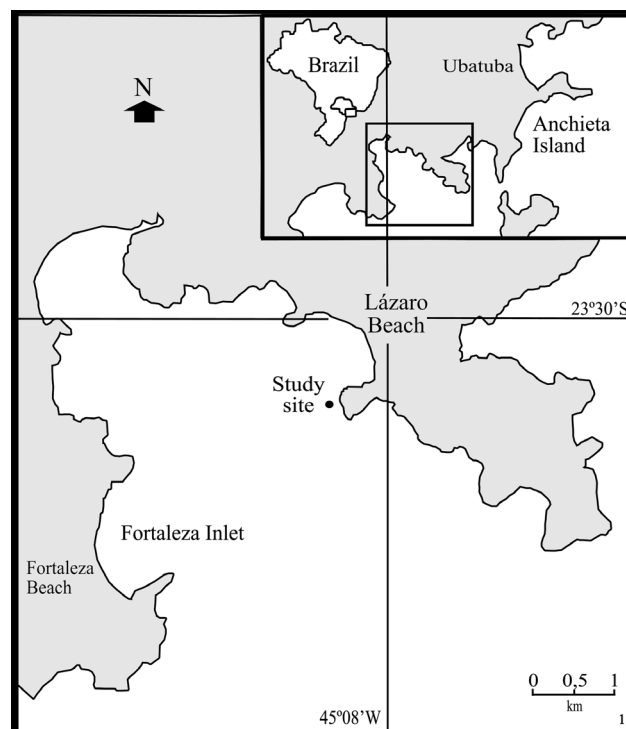


Figure 1. Map of the studied region indicating sampling site.

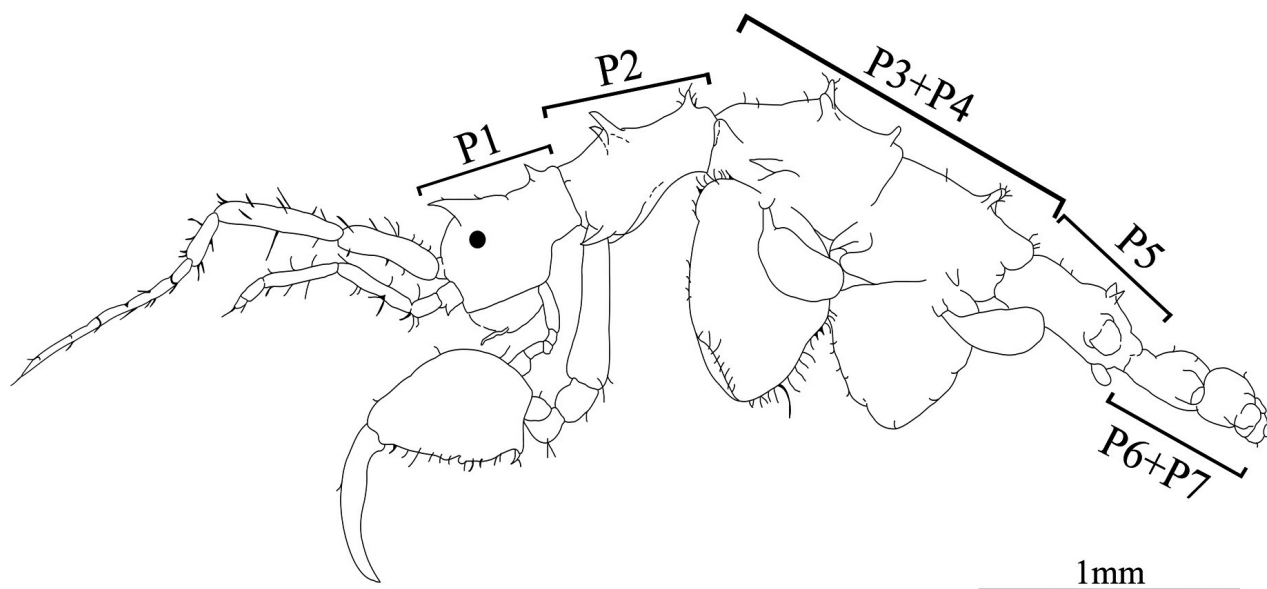


Figure 2. Indications of measurements in caprellids. Modified from Lacerda and Masunari (2011).

The females with intact brood pouches were separated for further analysis concerning the fecundity. The eggs were removed from the brood pouch of each female with a straight extra fine point tweezer, counted and their diameter measured. Egg volume was calculated with the sphere volume formula ( $V = (\pi/6) \cdot d^3$ ), where “d” is the diameter. *Sargassum cymosum* fronds collected were dried at room temperature ( $\sim 25^\circ\text{C}$ ) for one week. After this procedure, fronds were weighted with a precision balance (0.001 g) for obtaining their dry biomass. Density of caprellids in each frond was calculated as the number of individuals/dry *S. cymosum* biomass (g).

Algal dry biomass and density of the two caprellid species were compared among sampling periods by one-way ANOVA, followed by Tukey t test. Pearson's correlation coefficient analysis was applied to evaluate the relationship between caprellid species densities. Density of ovigerous females and juveniles were also compared throughout the year using ANOVA to determine the reproductive and recruitment periods. Mean fecundity and egg volume between species were compared using Student-t test. The relationship between fecundity (number of eggs) and total egg volume and female size were evaluated using linear regressions. Pearson correlation was used to test the relation between mean egg volume and fecundity of each species.

The number of size classes of the two caprellid species was calculated by means of the Sturges' formula but the population structure was not well described. So we grouped the caprellids of both species in size classes of 1 mm. The individual frequency distribution of size classes was analyzed every month, to evaluate possible temporal variations of the population frequency distribution and seasonal recruitment.

The sex ratio ( $\text{♂}/\text{♀}$ ) of each species was expressed as the total number of males divided by the total number of females (immature females were considered among females), every month. Qui-Square ( $\chi^2$ ) was used to test the sex ratio to the 1:1 proportion. The sizes of males and females were compared using Student-t test.

Normality was tested and when necessary data were log-transformed to fit statistical assumptions of the tests. A p value  $< 0.05$  was considered significant (Zar, 1999).

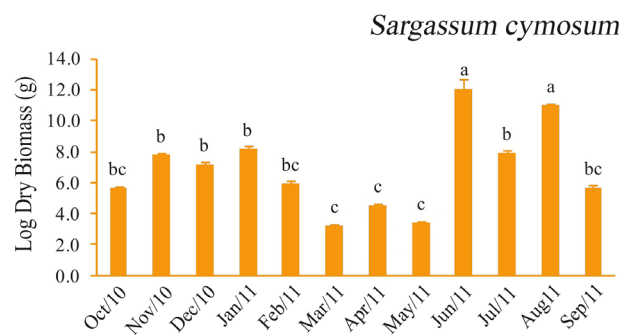
## RESULTS

A total of 486 individuals of *Pseudaeginella montoucheti* was obtained, of which 328 males, 38 immature females, 68 mature females, 22 ovigerous females and 30 juveniles; and 3069 individuals of *Paracaprella tenuis*, of which 2191 males, 408 immature females, 210 mature females, 78 ovigerous females and 182 juveniles.

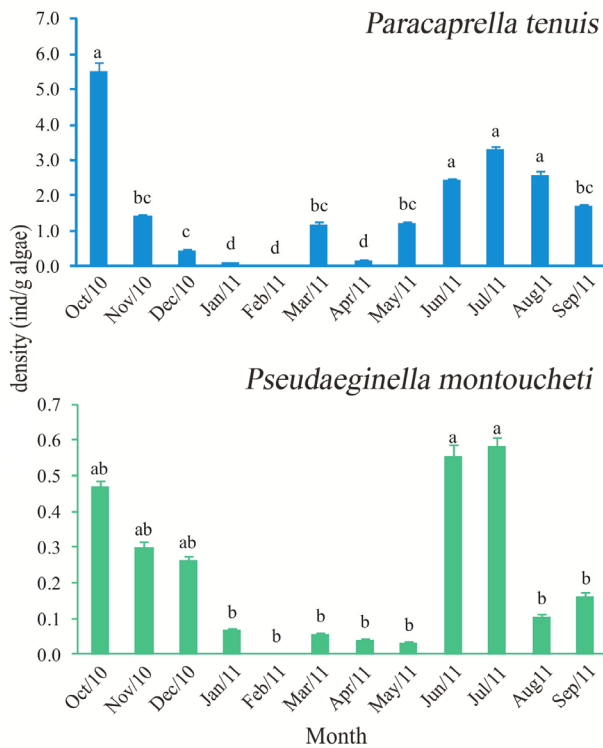
The *S. cymosum* fronds weight varied throughout the year ( $F_{11,288} = 12.826$ ;  $p < 0.001$ ). The lowest weight values were recorded between March and May, and the highest in June and August 2011 (Fig. 3).

*Paracaprella tenuis* population showed two density peaks during the study: October 2010 (spring) and June to August 2011 (winter); and it presented a decrease during summer and fall (December 2010 to May 2011) ( $F_{11,288} = 34.547$ ;  $p < 0.001$ ). *Pseudaeginella montoucheti* also presented substantial variations ( $F_{11,288} = 13.291$ ;  $p < 0.001$ ), with density peaks in winter (June and July 2011) and a population decrease mainly in summer and fall (January to May 2011) (Fig. 4). *Paracaprella tenuis* juveniles presented substantial oscillations throughout the year ( $F_{11,288} = 7.282$ ;  $p < 0.001$ ). According to the posteriori Tuckey test, October 2010, July and August 2011 had higher juvenile densities than the other months. Density of *P. montoucheti* juveniles was also variable ( $F_{11,288} = 3.817$ ;  $p < 0.001$ ), and June and July of 2011 had the highest density values (Fig. 5). Densities of the caprellid species were positively correlated ( $r = 0.8362$ ;  $p < 0.01$ ).

Ovigerous females of *P. tenuis* and *P. montoucheti* also showed substantial differences in densities



**Figure 3.** Monthly values of mean dry biomass ( $\pm$  standard error) of *Sargassum cymosum* fronds. Bars with the same letter show no statistical difference.

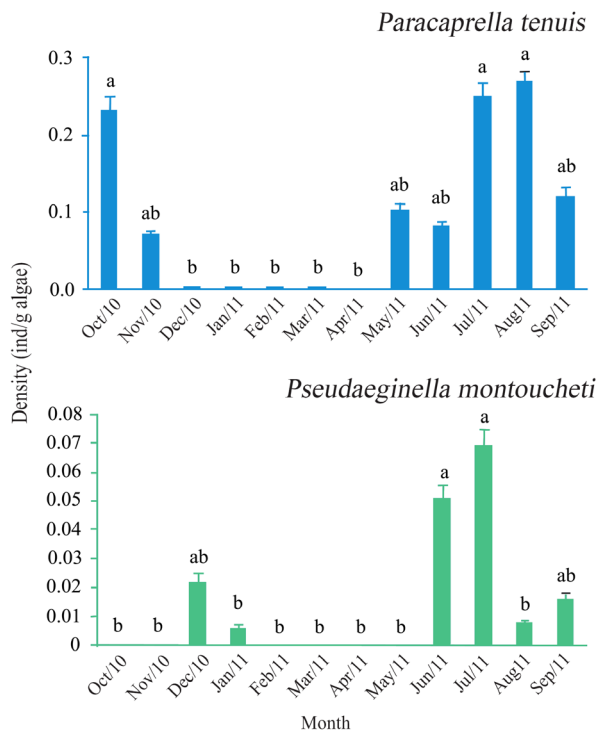


**Figure 4.** Monthly values of density (ind./g of algae) (mean ± standard error) of *Paracaprella tenuis* and *Pseudaeiginella montoucheti* from October 2010 to September 2011.

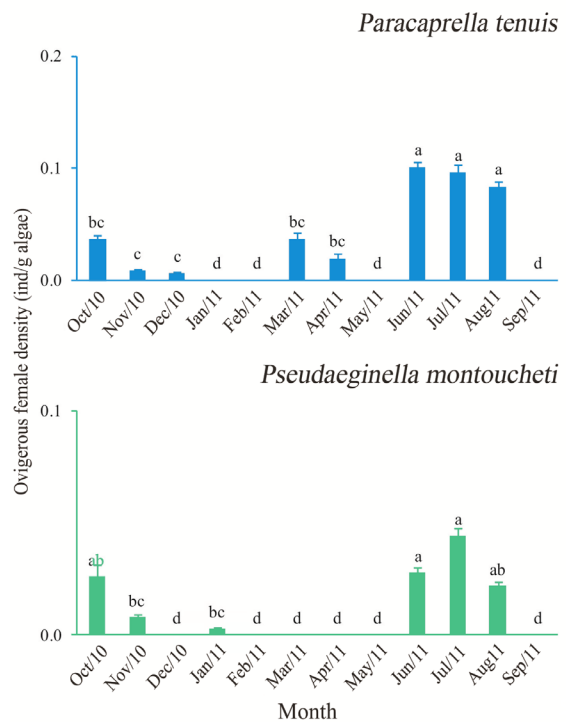
( $F_{11,288} = 2.108$ ;  $p = 0.02$  and  $F_{11,288} = 6.173$ ;  $p < 0.001$ , respectively). June, July and August 2011 recorded the highest densities of ovigerous females for *P. tenuis*. *Pseudaeiginella montoucheti* densities were higher in June and July (Fig. 6).

The fecundity expressed by the number of eggs varied a lot. *Pseudaeiginella montoucheti* presented a variation from 2 to 55 eggs, and *P. tenuis* from 2 to 13 eggs. However, the fecundity did not differ between the two species ( $t = 0.797$ ;  $df = 99$ ;  $p = 0.427$ ). It was observed a substantial difference between the egg volumes of the two species ( $t = 18.487$ ;  $df = 577$ ;  $p < 0.001$ ). *Pseudaeiginella montoucheti* eggs presented larger volumes ( $0.004 \pm 0.003 \text{ mm}^3$ ) than *P. tenuis* eggs ( $0.001 \pm 0.001 \text{ mm}^3$ ) (mean ±SD).

There was no relationship between fecundity and size for *P. tenuis* ( $F_{1,78} = 1.703$ ;  $p = 0.196$ ) ovigerous females and a weak relationship for *P. montoucheti* ( $F_{1,19} = 19.923$ ;  $p < 0.001$ ) (Tab. 1). However, size of ovigerous females and the mean egg volume showed a weak relationship for *P. tenuis* ( $F_{1,78} = 19.352$ ;  $p < 0.001$ ) and a strong relationship for *P. montoucheti* ( $F_{1,20} = 81.476$ ;  $p < 0.001$ ) (Tab. 1).



**Figure 5.** Monthly values of juvenile density (ind./g of algae) (mean ± standard error) of *Paracaprella tenuis* and *Pseudaeiginella montoucheti* from October 2010 to September 2011.



**Figure 6.** Monthly values of ovigerous female density (ind./g of algae) (mean ± standard error) of *Paracaprella tenuis* and *Pseudaeiginella montoucheti* from October 2010 to September 2011.

**Table 1.** Regression analyses based on the ovigerous female length (TL) as *x*-variable for *Paracaprella tenuis* and *Pseudaeginella montoucheti*.

Species	y-variable	Regression equation	R <sup>2</sup>
<i>Paracaprella tenuis</i>	Fecundity (F)	F = 0.9284x+3.0635	0.009
	Volume (V)	V = 0.0047x-0.0033	0.189
<i>Pseudaeginella montoucheti</i>	Fecundity (F)	F = 6.1557x-10.846	0.473
	Volume (V)	V = 0.0156x-0.0144	0.793

The mean volume of the eggs was inversely correlated to fecundity in *P. tenuis* ( $r = -0.304$ ;  $p = 0.006$ ;  $n = 80$ ), and there was no relationship for *P. montoucheti* ( $r = -0.007$ ;  $p = 0.976$ ;  $n = 21$ ).

The size class histograms of the two species are represented in the figures 7 and 8. During the study, no caprellids were sampled in February. Juveniles were not sampled only in two months and ovigerous females in four months. The size of males and females (Fig.7) differed significantly for *P. tenuis* ( $t = 10.123$ ;  $df = 2808$ ;  $p < 0.001$ ). The maximum size for males was 5.93 mm and for females 5.06 mm. The mean size of males was  $0.311 \pm 0.094$  mm (mean  $\pm$  SD), and female mean size was  $0.240 \pm 0.166$  mm.

For *P. montoucheti*, there were no juveniles and ovigerous females in six months. The mean size of males (Fig. 8) was  $0.370 \pm 0.119$  mm and of females  $0.312 \pm 0.127$  mm, with significant variation along the year ( $t = 4.131$ ;  $df = 433$ ;  $p < 0.001$ ). However, the largest male had 6.48 mm and the largest female 6.04 mm.

The sex ratio for *P. tenuis* showed a significant deviation towards males ( $1:0.32$ ;  $\chi^2 = 774.17$ ;  $p < 0.05$ ), except for March and April 2011 ( $1: 1.05$ ;  $\chi^2 = 0.049$ ;  $df = 1$ ;  $p = 0.8$  and  $1: 1.33$   $\chi^2 = 0.286$ ;  $df = 1$ ;  $p = 0.593$ , respectively), when there was a population decrease. For *P. montoucheti*, sex ratio was also deviated towards males ( $1: 0.39$ ;  $\chi^2 = 87.72$ ;  $p < 0.05$ ) in all sampling months.

## DISCUSSION

Our results showed density variation for both species through the year with higher densities mainly in winter and lower densities in fall and summer. Species densities of the two species were positively correlated. Both species presented continuous reproduction with reproductive peaks. Egg volume was different between caprellid species and it was directly related to female size. The number of eggs was weakly related to female size and the sex ratio was deviated for males in both species.

Density variation of the two analyzed species throughout the year was also recorded for many other amphipods associated to *Sargassum* (Jacobucci et al., 2009a) including caprellid species (Jacobucci et al., 2002; De Paula et al., 2016).

Local and large-scale environmental variation can be responsible for amphipod density patterns. The water temperature in Ubatuba can reach 30°C in summer, which does not favor *S. cymosum* growth reducing substrate availability which could negatively affect the associated epifauna. *Sargassum cymosum* biomass matched with other studies performed at same location, which indicated minimum biomass values and frond heights in summer and fall (Paula and Oliveira-Filho, 1980). Considering this situation, higher densities of caprellids would be expected in periods with higher biomass fronds and this pattern was recorded for *P. tenuis* and *P. montoucheti* at Lázaro beach.

Other factors could be also important to explain caprellid density variation since *P. tenuis* and *P. montoucheti* reached their highest densities in summer (Jacobucci et al., 2009a) when the host algae *Sargassum filipendula* presented the lowest biomass values, in a rocky shore at Fortaleza beach (Jacobucci et al., 2009b), just a few miles from the site of the present study. Epibiosis could be one of these factors since it increases habitat complexity (James and Heck, 1994). In the study at Fortaleza beach the densities of many amphipods including *P. tenuis* and *P. montoucheti* were positively related to epiphyte load. Detritus accumulation and colonization of bacteria and microalgae (Heck and Wetstone, 1977; Hacker and Steneck, 1990; Russo, 1990) are favored by epiphytes thus benefiting species that consume these food resources (Edgar, 1990). This may be the case of *P. tenuis* and probably of *P. montoucheti*, considering caprellids are mainly detritivores (Guerra-García and Figueroa, 2009).

Hydrozoan cover in *Sargassum* fronds is another factor that could explain caprellid density variation. Other studies indicate positive relationships between

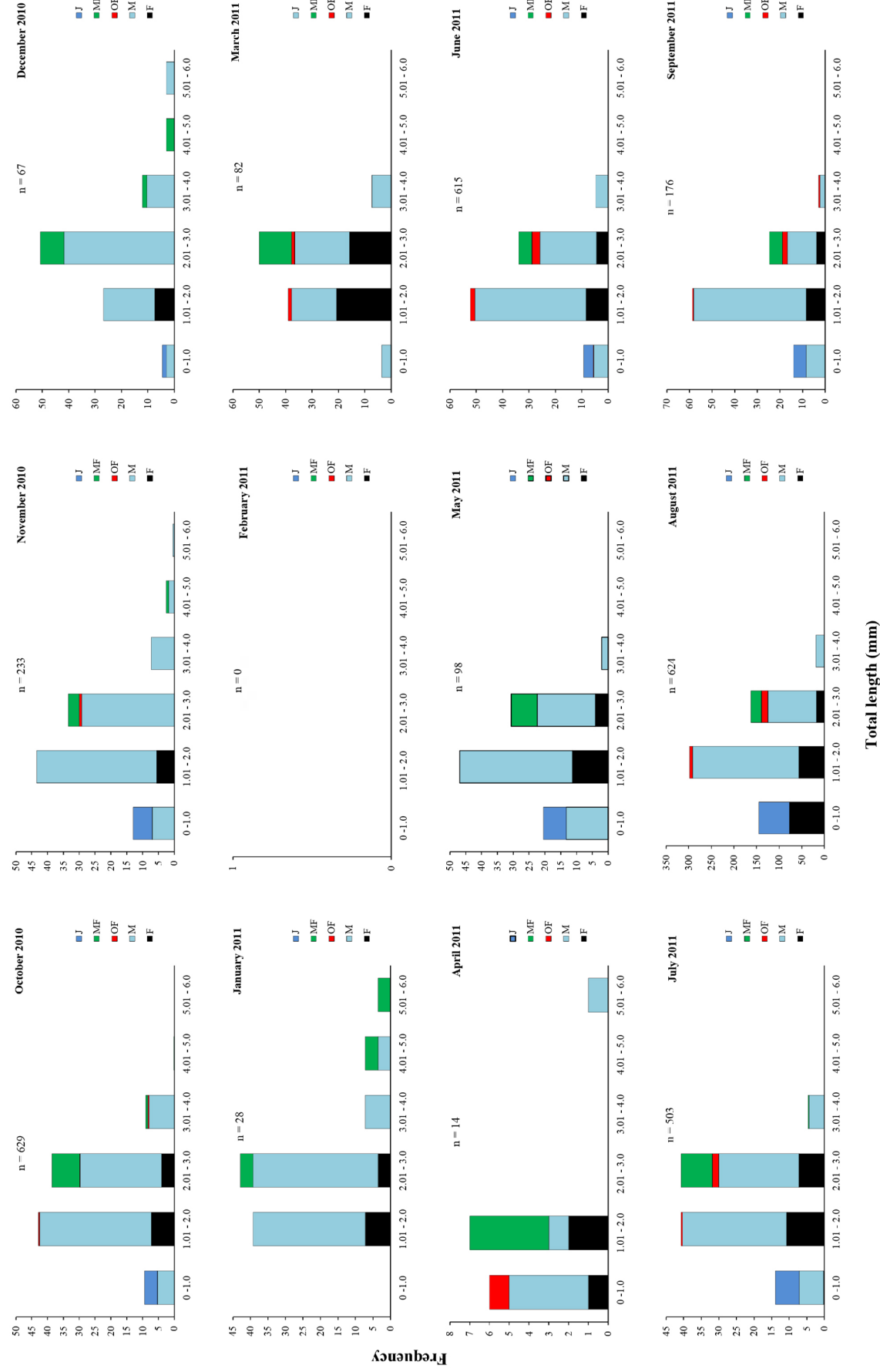
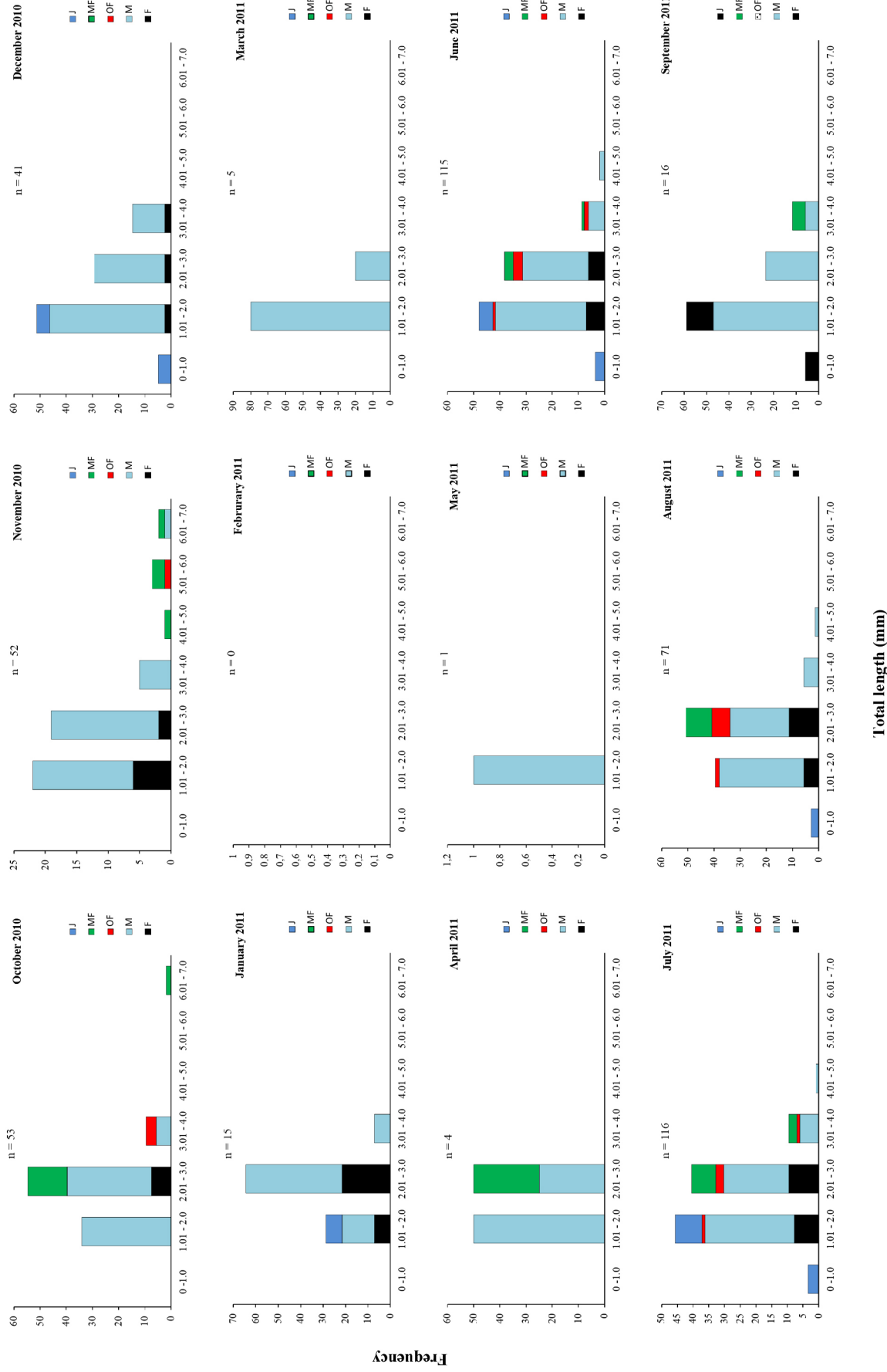


Figure 7. Frequency of females (F), males (M), ovigerous females (OF), mature females (MF) and juveniles (J) in size classes (total length in mm) of *Paracaprella tenuis* over the studied period.



**Figure 8.** Frequency of females (F), males (M), ovigerous females (OF), mature females (MF) and juveniles (J) in size classes (total length in mm) of *Pseudaeignella montoucheti* over the studied period.



hydrozoans and caprellids (*e.g.*, Leite *et al.*, 2007) thus *S. cymosum* fronds with higher hydrozoan cover could represent a more complex habitat directly or indirectly favoring the caprellid species studied. In a study conducted at Lázaro beach total density of caprellids and the density of *P. tenuis* and *P. montoucheti* were significantly related to total hydrozoan cover associated to *S. cymosum* fronds (Cunha *et al.*, 2018). However, hydrozoan cover had no variation along the year (Cunha and Jacobucci, 2010) and does not seem to be the main factor to explain seasonal density variation of caprellids.

Other factors often cited as responsible for regulation of caprellid populations include hydrodynamics, sedimentation and turbidity (Edgar, 1983; Tanaka and Leite, 2003; Castro *et al.*, 2008). Detritivores would be favored by higher supply of organic matter from sediments (Moore, 1978). Sediment dynamics in Ubatuba is related to passage of cold fronts in the area. From April to November mean wave action and turbidity are higher (Mahiques, 1995) thus increasing the input of water nutrients and re-suspended particulate organic matter from sediment to algal beds. This period approximately fits the period of higher mean densities of *P. tenuis* and *P. montoucheti* and higher *S. cymosum* biomass (Fig. 3).

Since density variation of the caprellid species is positively correlated it suggests habitat and environmental conditions affect *P. tenuis* and *P. montoucheti* in a similar way. However, one factor that could explain the much higher densities of *P. tenuis* is its opportunistic diet. *Paracaprella tenuis* probably presents a more varied diet than *P. montoucheti*. Although detritus is the main item found in gut content of *P. tenuis* it also feeds on diatoms, copepods and sponges. *Pseudaeginella* species, in turn, feed only on detritus (Guerra-García and Figueroa, 2009).

*Paracaprella tenuis* presented ovigerous females in eight months and juveniles in 10 months and ovigerous females and juveniles of *P. montoucheti* occurred in six months. This pattern indicates a tendency of reproductive peaks and continuous reproduction, a typical pattern for amphipods from tropical and subtropical regions (Sainte-Marie, 1991; Lopes and Masunari, 2004; Valério-Berardo and Flynn, 2004; Jacobucci and Leite, 2006).

The reproductive peaks in some periods may also represent a mechanism to minimize interspecific

competition (Jacobucci and Leite, 2006). Food availability could be a limiting resource for these caprellid species, considering the supply of organic matter by suspended sediments is reduced from December to March. The occurrence of higher densities of some *Caprella* species associated to *S. cymosum* in the sampling site during this period (De Paula *et al.*, 2016) would increase food and habitat competition since most *Caprella* species are also detritivores and larger than *P. tenuis* and *P. montoucheti*. Besides this situation, substrate competition by displacement was experimentally detected for caprellids (Shucksmith *et al.*, 2009).

The larger egg volumes of *P. montoucheti* probably indicate a difference in the incubation period between species, as egg size is directly proportional to the period of embryonic development (Steele and Steele, 1975; Cardoso and Veloso, 2001).

*Paracaprella tenuis* showed a similar pattern to Steele and Steele (1975) and Walter (1980) data, which indicates that the egg size is, in general, inversely proportional to crustacean fecundity. The egg size is related to the energy stored for posterior development (Giangrande *et al.*, 1994), which suggests that *P. tenuis* presents a differentiated pattern of directing energy for reproduction.

According to what was observed for both species, total egg volume and fecundity are directly related to female size, which could be influenced by the quantity of resources directed to reproduction (Moran and Mcalister, 2009). However, the relationship is weak for *P. tenuis* suggesting that other factors than female size could also be important. Weak relationship between size and fecundity was detected for other caprellid species (De Paula *et al.*, 2016). Valenti *et al.* (1989) indicate that the fecundity of crustaceans may vary with the physiological conditions of the females in different seasons. Considering the possible variability of resources in the area the metabolic status of females and consequently their fecundity would vary accordingly.

Males reached larger mean size than females. In many species of caprellids, males are usually relatively larger than the females (Guerra-García *et al.*, 2011; Lolas and Dimitris, 2013). This situation can be related to different energy allocation for growth and aggressive behavior between males before copulation (Caine, 1991).

The sex ratio of *P. tenuis* and *P. montoucheti* populations deviated for males was already observed for other amphipod species and may be associated to the species life cycles (Powell and Moore, 1991; Maranhão *et al.*, 2001). Caine (1979) mentioned that sex ratio is usually anomalous for caprellids, with the same proportion of males and females for smaller individuals, dominance of females at intermediate size classes and dominance of males at larger size classes. According to Emmerson (1994) the predominance of males indicates a higher longevity of the males and suggests an intraspecific competition for females that can guarantee the fertilization of all the females (Powell and Moore, 1991). The sex ratio disparity found may be also explained by the high energetic investment with reproduction by the females (Cardoso and Veloso, 1996), which can limit growth and reduce survival (Thiel, 2003).

The results of the present study highlighted basic data on dynamics and reproductive biology of two species of caprellids that occur in algal beds of different regions. However, the biology of caprellids is still poorly known compared with other crustaceans and additional studies of other species are essential to increase our knowledge about this group.

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