

Caprellid amphipods on *Sargassum cymosum* (Phaeophyta): Depth distribution and population biology.

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Abstract

Depth distribution and population structure of 5 caprellid species associated with *Sargassum cymosum* were evaluated in a sublittoral zone of Lazaro Beach, Ubatuba, São Paulo State, southeastern Brazil. Four seasonal samples were obtained during one year period at three depth intervals. Twenty seven fronds were sampled from October, 1997 to July, 1998. Seven caprellid species were recorded but only those of the genus *Caprella* were numerically abundant in all sampling periods. *Fallotritella montoucheti* occurred in all sampling periods but at low densities. Two *Caprella* species showed significant depth distribution patterns: *Caprella scaura* was more abundant at deeper sites, while *Caprella dilatata* occurred mainly in shallower sites. Distribution of *Caprella danilevskii*, *C. equilibra* and *F. montoucheti* showed variable trends over the year. Sex ratio was skewed for males for all species excepting *F. montoucheti*. Ovigerous females and juveniles were more frequently in October, 1997 and July, 1998, suggesting a discontinuous reproductive activity. Caprellid recruitment are necessarily involved in seasonal population structure variation and tolerance to particular hydrodynamic conditions over the depth gradient together with substrate and food partitioning probably play a major role in caprellid amphipod depth distribution.

Key words: Caprellidea, epifauna, population structure, depth distribution, *Sargassum*

Introduction

The vagile epifauna associated with marine macrophytes is highly diverse and some taxonomic groups are especially well represented. A great proportion of the algal and seagrass bed associated macrofauna are composed by gastropods (Montouchet, 1979) and crustaceans (Tararam and Wakabara, 1981; Edgar, 1983a; Edgar & Robertson, 1992). Richness and abundance of peracarid crustaceans, particularly amphipods, are frequently high in shallow water environments dominated by brown seaweeds (Wakabara *et al.*, 1983; Taylor and Cole, 1994; Jacobucci and Leite, 2002).

The suborder Caprellidea is one of the main epifaunal peracarid crustaceans in phytal communities, occupying a diverse range of rocky shore macrophytes and epiphytic algae, but their morphology favors strong attachment to other sessile organisms such Hydrozoa, Porifera and Bryozoa (Bynum, 1978; Aoki, 1999).

Although studies on caprellids are not uncommon in the literature, descriptions of new species and systematic revisions (Krapp-Schickel, 1998; Guerra-Garcia *et al.*, 2001) are much more common than investigations on some important biological traits such as spatial distribution and population biology. The early studies by Caine (1974, 1977) dealing with feeding behavior and functional morphology are still important contributions to the basic biology of the group. Recent papers on development and maternal care performed under laboratory conditions (Takeuchi & Hirano, 1991; 1992; Aoki, 1999) help to understand some important reproductive patterns of caprellids. However, population studies are still rare (Caine, 1979, 1980) and, although some authors have evaluated the relationships between abiotic variables, such as hydrodynamics and suspended organic matter (Takeuchi *et al.*, 1987; Guerra-Garcia and Garcia-Gomez, 2001), and species composition in phytal communities, the role of depth in caprellid distribution (Krapp-Schickel, 1993) is still not clear.

Sargassum spp are very common brown macroalgae in southeastern Brazil algal beds, representing over than 80% of algae biomass in some shallow hard bottom substrates of São Paulo and Rio de Janeiro states (Paula and Oliveira-Filho, 1980). Caprellid amphipods are very frequent inhabitants of these *Sargassum* beds but their biology is still poorly known. In order to obtain more information about these peracarids, we investigated the species composition, depth distribution and population biology of caprellid amphipods associated with *Sargassum* in an algal bed of São Paulo state.

Materials and Methods

Study Area

This study was carried out at Lazaro Beach (23°30'S, 45°08'W), situated at Fortaleza inlet, Ubatuba, southeastern Brazil (Fig. 1). The sampled rocky shore is moderately exposed to wave action (Jacobucci and Leite, 2002). The adjacent soft bottom was demonstrated to have high contents of gravel and organic matter (Negreiros-Fransozo *et. al.*, 1991). The study area has a diverse macrophyte community dominated by the brown seaweed *Sargassum cymosum* that formed a homogeneous bed of about 30 m long that covers the hard bottom from the sublittoral fringe to 4 m depth. Other algae such as *Dictyopteris delicatula*, *D. plagiogramma*, *Bryothamnion seaforthii* and *Gracilaria* aff. *verrucosa* occurs in very low densities within *Sargassum* fronds in this area (Eston, 1987).

Sampling Procedure

A 20 m sampling sector was defined parallel to the shore line where three perpendicular transects were sorted seasonally from October 1997 to July 1998. In each transect 3 samples of *Sargassum cymosum* were randomly collected at each of 3 depth intervals: upper (0.5 - 1.5 m), middle (1.5 - 2.5 m) and lower (2.5 - 3 m), summing up 9 samples per transect and 27 per season. Each sample, comprising an individual *Sargassum* frond, including the holdfast, was carefully enclosed in a 0.2 mm mesh bag. All samples were collected by SCUBA.

Processing

At the laboratory each frond was washed successively in 4 buckets containing freshwater with formalin to detach animals from plants. Epifauna remaining in the buckets was carefully washed onto a 0.2 mm mesh sieve. Caprellid amphipods were preserved in 70% alcohol for further identification and quantification. The wet weight of *Sargassum* fronds was determined after spinning for 2 minutes to remove water excess.

Sub-samples of 6 fronds from the middle depth interval, for each season, were sorted to evaluate the population structure of numerically dominant caprellid species. For these fronds, the cephalon and first pereonite lengths of all caprellids were measured. This size criterion was adopted not only for handling convenience and accuracy of measure but also to evaluate the occurrence of sexual dimorphism. Elongation of the first pereonite has already been reported for males of some caprellid species (Takeda, 1981). Individuals were then separated in size groups and classified into sexually mature, immature and juveniles according to Bynum (1978). Females could be distinguished from males by the presence of oostegites wich appeared as small buds near the gills on the pereonites at the onset of sexual maturity. The smallest individual having these buds, considering all sampling periods, was used as a reference for each species. All specimens smaller than the reference individual were classified as juveniles. Individuals of equal or larger size than the reference caprellid and without oostegites were considered males. Females were separated into three categories. Those with oostegites without setae were considered immature. Females with setous oostegites were classified as mature and those carrying eggs or embryos as ovigerous. The total number of males and females of the more abundant species was determined summing individuals of all sampling periods for each species.

Data analysis

To access depth distribution, the density of caprellid amphipods was expressed as the number of individuals per unit wet weight of *Sargassum* fronds. The occurrence of vertical distribution patterns in depth gradient was evaluated comparing mean caprellid densities among depth levels for each sampling period through one-way ANOVA followed by Tukey test for *a posteriori* pair-wise comparisons. Mean size comparisons between males and females for each species were done with Student t-test and sex proportions were evaluated by Log-Likelihood G-test. Data normality and homocedasticity were verified and suitable transformations were performed when necessary prior to analyses of variance (Zar, 1999).

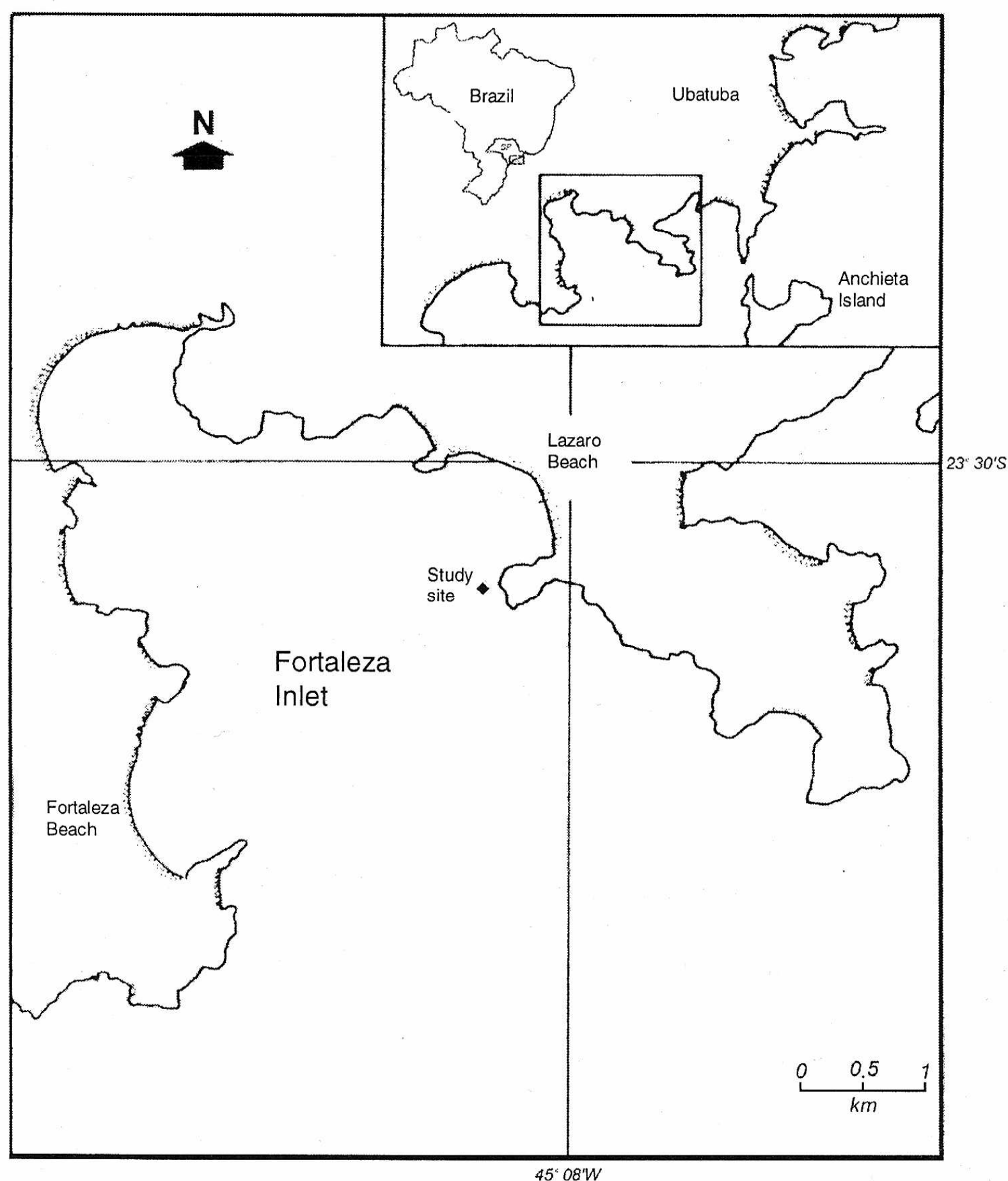


Figure 1: Map of the study area at Lazaro Beach, in Fortaleza Inlet, Ubatuba, southeastern Brazil.

Results

Composition

Seven species of caprellid amphipods were found in association with *Sargassum cymosum* fronds. From the 6 species belonging to the family Caprellidae Leach, 1814, those of the genus *Caprella* (*Caprella scaura* Templeton, 1836, *C. dilatata* Krøyer, 1843, *C. equilibra* Say, 1818 and *C. danilevskii* Czerniavski, 1868) were very abundant (mean densities over 5 ind. g⁻¹ wet weight of *Sargassum*) and were present in all sampling periods. *Fallotritella montoucheti* Quitete, 1971 and, particularly, *Hemiaegina minuta* Mayer, 1890 were much less frequent. The family Pariambidae Laubitz, 1993 was only represented by *Paracaprella tenuis* Mayer, 1903 in very small densities.

Depth distribution

Analyses of variance showed that only two species have a seasonal consistent trend in its depth patterns of distribution. Density differences among depth intervals were detected for *C. scaura* and for *C. dilatata* (Table I). *C. scaura* was significantly more abundant in lower and middle levels in all sampling periods while *C. dilatata* occurred at higher densities in the upper and middle levels for three sampling periods. Density varied considerably for the other species at each depth level from one sampling period to another (Fig. 2). *Caprella danilevskii* occurred at higher densities in upper and middle levels in April and July 1998 but in January and October 1997 this species did not show any density difference among levels. Density of *C. equilibra* was higher in middle and lower levels in January and in upper and middle levels in April. *Fallotritella montoucheti* showed no significant differences among levels.

Population structure

Seasonal variation in size structure of the caprellids was evident for all species. Small individuals of *C. danilevskii* occurred at higher numbers in October 1997, January and July 1998 indicating intense recruitment in these periods. Higher frequencies of *Caprella dilatata* and *C. equilibra* juveniles were recorded in July and small specimens of *C. scaura* mainly occurred in January. For *F. montoucheti* the frequency of juveniles was basically the same during the sampling periods excepting for April (Fig. 3). Size differences between male and female were observed for three species. First pereonite elongation in males of *C. scaura*, *C. equilibra* and *C. danilevskii* (Fig. 3) made them larger than females. For the other two caprellid species size dimorphism were not registered (Table II).

Ovigerous females and juveniles were recorded in all periods indicating a tendency of continuous reproduction with variable peaks for each caprellid species, except for *C. dilatata* that was absent in April (Fig. 3). Higher densities of females with eggs were, often observed in the same periods of higher numbers of juveniles (Fig. 4) indicating reproduction and recruitment of caprellid populations.

Sex ratio was skewed for males in *C. scaura* (917 vs 571 females; $G = 81.96$; $df = 1$; $p < 0.001$), *C. equilibra* (562 vs 434 females; $G = 16.50$; $df = 1$; $p < 0.001$), *C. dilatata* (214 vs 167 females; $G = 5.81$; $df = 1$; $p < 0.025$) and *C. danilevskii* (253 vs 166 females; $G = 3.50$; $df = 1$; n.s.) while males and females occurred in similar proportions in *F. montoucheti* (35 vs 46 females; $G = 1.50$; $df = 1$; n.s.).

Table I: One-way ANOVA followed by Tukey test comparing caprellid densities among depth levels (1 - upper: 0.5-1.5 m, 2 - middle: 1.5-2.5 m, 3 - lower: 2.5-3.5 m) for each sampling period.

	October			January			April			July		
	df	F	Tukey	df	F	Tukey	df	F	Tukey	df	F	Tukey
<i>Caprella danilevskii</i>												
Depth	2	0.6456 ns	<u>1 2 3</u>	2	3.565 ns	<u>1 2 3</u>	2	3.857 *	<u>1 2 3</u>	2	17.267 ***	<u>1 2 3</u>
Residual	24			24			24			24		
<i>Caprella dilatata</i>												
Depth	2	6.545 **	<u>1 2 3</u>	2	6.374 **	<u>1 2 3</u>	2	0.519 ns	<u>1 2 3</u>	2	14.263 ***	<u>1 2 3</u>
Residual	24			24			24			24		
<i>Caprella equilibra</i>												
Depth	2	0.493 ns	<u>1 2 3</u>	2	5.204 *	<u>2 3 1</u>	2	4.699 *	<u>2 3 1</u>	2	1.098 ns	<u>1 2 3</u>
Residual	24			24			24			24		
<i>Caprella scaura</i>												
Depth	2	3.957 *	<u>1 2 3</u>	2	24.870 ***	<u>1 2 3</u>	2	15.172 ***	<u>1 2 3</u>	2	8.007 **	<u>1 2 3</u>
Residual	24			24			24			24		
<i>Fallotritella montoucheti</i>												
Depth	2	2.224 ns	<u>1 2 3</u>	2	1.242 ns	<u>1 2 3</u>	2	0.860 ns	<u>1 2 3</u>	2	1.086 ns	<u>1 2 3</u>
Residual	24			24			24			24		

ns non significant, * p < 0.05; ** p < 0.01; *** p < 0.001;
Depth levels linked by horizontal bars indicate absence of significant difference in caprellid densities.

Nauplius

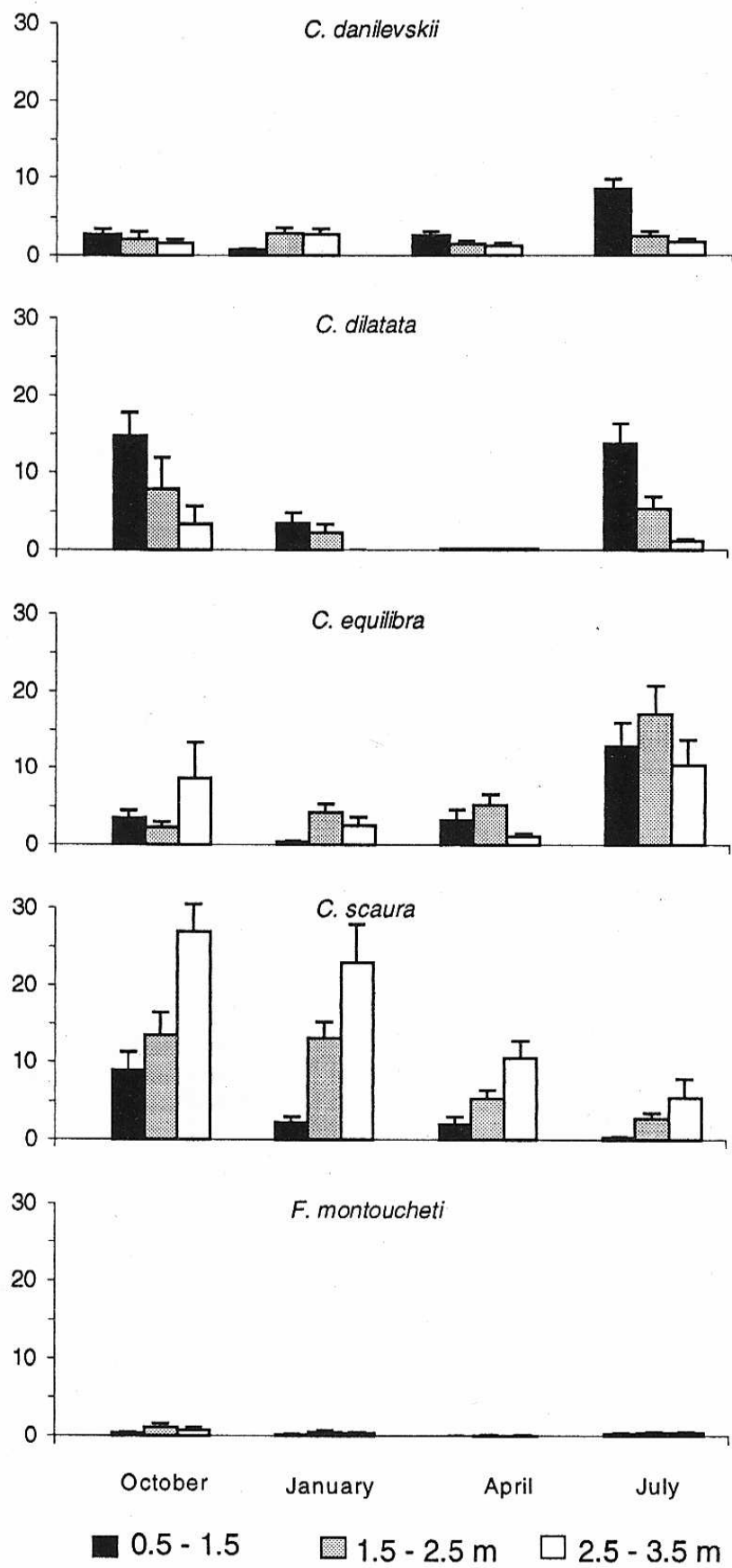


Figure 2: Mean densities (+ SE) of caprellid amphipods associated with *Sargassum cymosum* fronds at 0.5-1.5 m, 1.5-2.5 m and 2.5-3.5 m depth levels in October 1997, January 1998, April 1998 and July 1998.

Table II: Results of Student t-test comparing male and female cephalon + pereonite 1 (C + P1) and pereonite 1 (P1) lengths for caprellid species. Values are mean lengths \pm standard deviations in mm.

SPECIES	SEX	C+P1 \pm SD	P1 \pm SD	t (C+P1) t (P1) df
<i>Caprella scaura</i>	F	0.734 \pm 0.149	0.257 \pm 0.086	-3.322 **
	M	0.811 \pm 0.515	0.379 \pm 0.103	-6.818 *** 1486
<i>Caprella dilatata</i>	F	0.568 \pm 0.084	0.124 \pm 0.028	2.380 ns
	M	0.529 \pm 0.166	0.130 \pm 0.059	-0.979 ns 379
<i>Caprella equilibra</i>	F	0.693 \pm 0.146	0.233 \pm 0.075	-3.406 ***
	M	0.780 \pm 0.484	0.350 \pm 0.292	-5.781 *** 994
<i>Caprella danilevskii</i>	F	0.690 \pm 0.128	0.159 \pm 0.059	-2.015 *
	M	0.764 \pm 0.463	0.294 \pm 0.260	-3.541 *** 419
<i>Fallotritella montoucheti</i>	F	0.427 \pm 0.089	0.144 \pm 0.053	-0.461 ns
	M	0.444 \pm 0.219	0.164 \pm 0.158	-0.799 ns 79

ns non significant, * p < 0.05; ** p < 0.01; *** p < 0.001; F = female; M = male

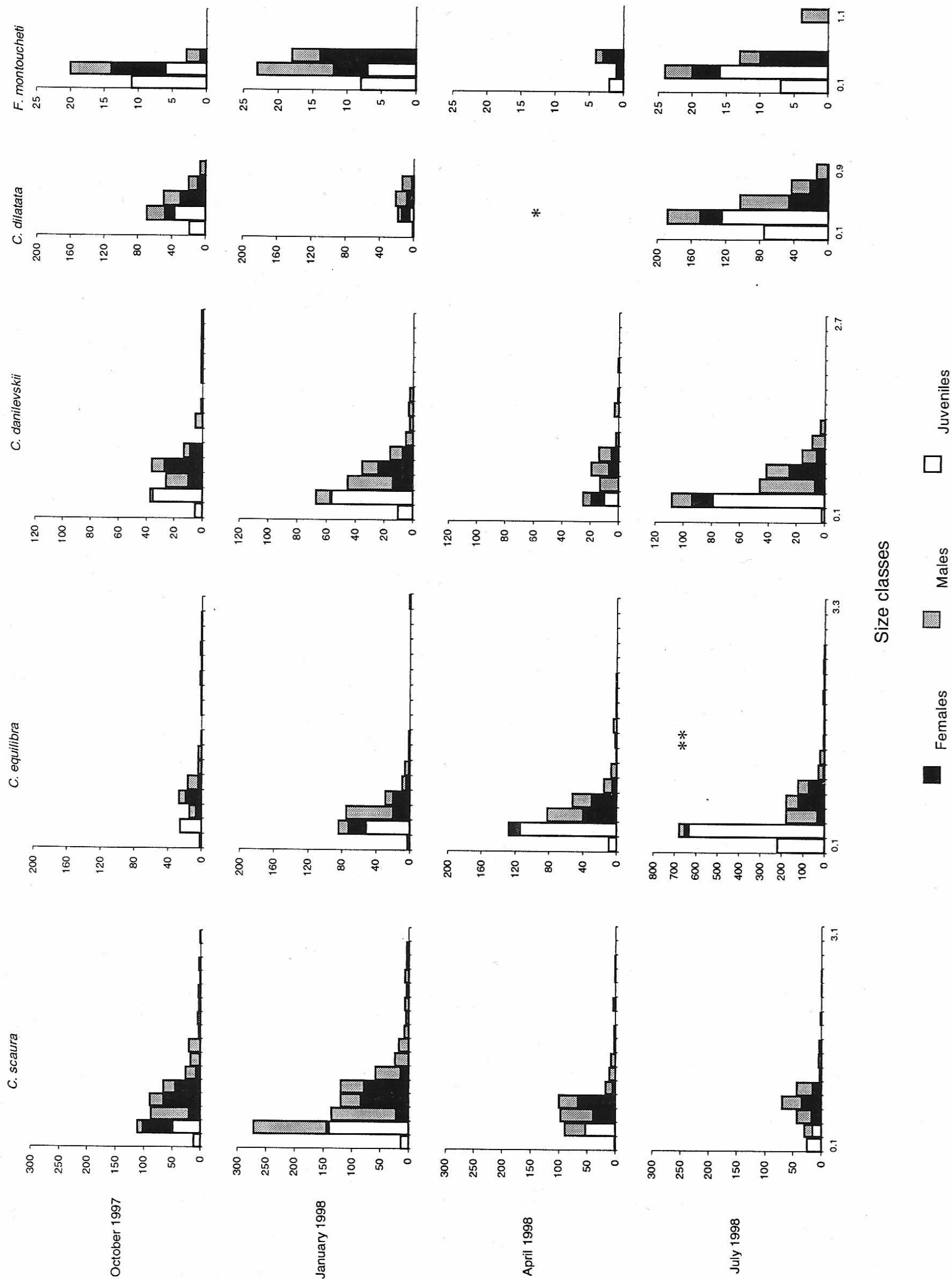


Figure 3: Seasonal size frequency distribution of males, females and juveniles of *C. danilevskii*, *C. equilibra*, *C. dilatata*, *C. scaura* and *F. montoucheti* associated with *Sargassum cymosum* fronds of Lazaro Beach, Ubatuba, southeastern Brazil.

C. dilatata* absent in April 1998; *C. equilibra* y-axis 0 - 800 individuals

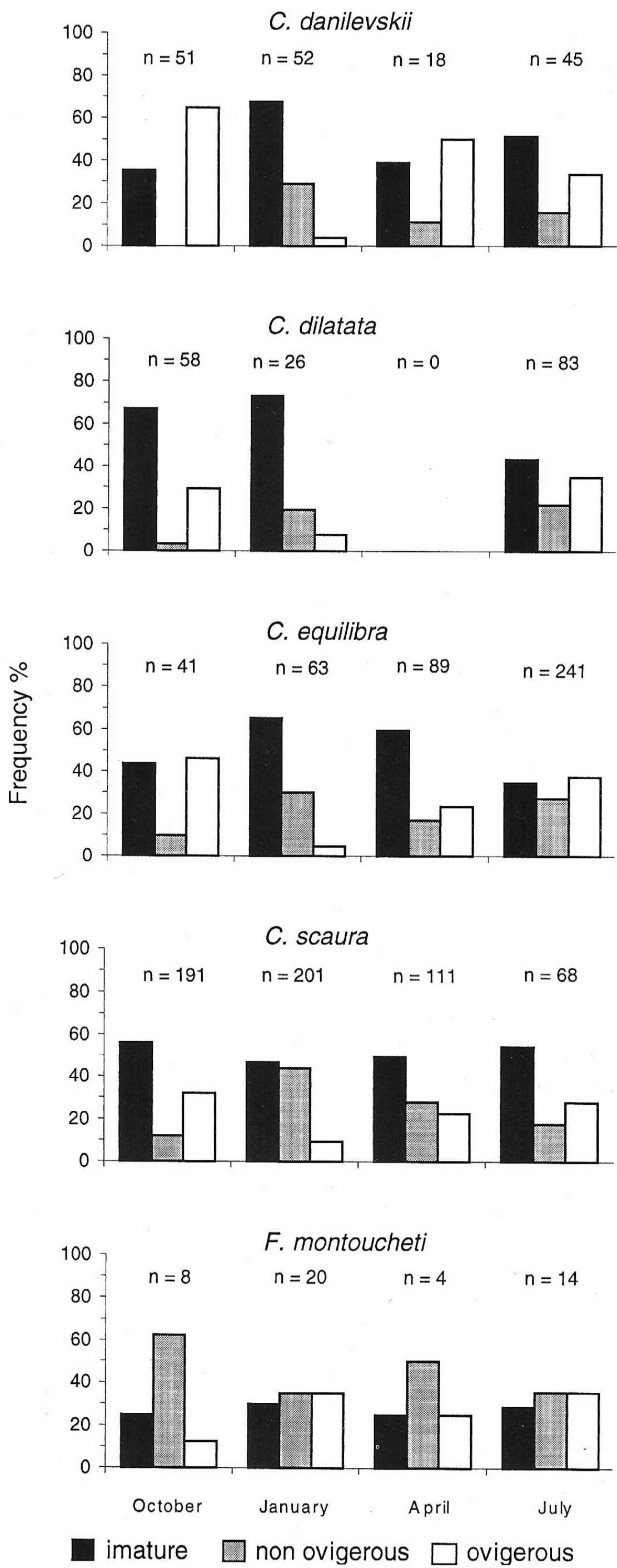


Figure 4: Frequency of immature, non-ovigerous and ovigerous females of *C. danilevskii*, *C. dilatata*, *C. equilibra*, *C. scaura* and *F. montoucheti* associated with *Sargassum cymosum* fronds at Lazaro Beach, Ubatuba, southeastern Brazil.

Discussion

Depth distribution of the caprellids studied could be related to various factors that are not necessarily working alone. Hydrodynamic differences among sampled depth levels could select species according to their substrate fixation ability and may be responsible for the patterns of density variation in *C. scaura* and *C. dilatata*. Higher densities of *C. scaura* in the deepest level would mean smaller resistance to water movement (Takeuchi *et al.*, 1987) that could be due to the slender and relatively longer body of this species. By the other side, *C. dilatata* with its stout and short segmented body and pereopods seems to be adapted to clinging tightly in the shallower turbulent level.

The species without clear patterns of zonation could have their distribution determined by other variables than depth such as substrate features. According to Caine (1978), the caprellids have pereopods adapted to maximize their feeding effectiveness. Filter-feeders, such as *C. equilibra*, capable of passively filtering water currents with their second antennae would be favored by highly branched substrata which permits grasping (Caine, 1974; Guerra-Garcia *et al.*, 2002). This kind of habitat is represented in the study site by *Sargassum* fronds with heavy load of epiphytic hydroids (personal observation). Some species could also be dependent on substrate food value. *Caprella danilevskii*, a primarily scraping feeder caprellid, that feeds upon diatom colonies (Takeuchi and Hirano, 1991; Guerra-Garcia *et al.*, 2002), would select fronds with a rich cover of periphyton and other epiphytic algae.

Finally, although caprellids show high tolerance against overcrowding, interspecific dominance through aggressive behavior (Lim and Alexander, 1986) could determine spatial segregation. Aggressive caprellids might reach high densities at substrates with greater food and shelter value preventing other species from settling or colonizing amongst these *Sargassum* fronds (Edgar and Aoki, 1993).

Seasonal fluctuations in population densities is a general feature of agile phial species including gamma rid and capriole amphipods living in tropical and subtropical areas. They could be related to seasonal availability of food resources, variable predation pressure and physical factors such as water temperature (Edgar, 1983a).

The caprellids have short term reproductive cycles, high fecundity and frequently continuous breeding seasons with reproductive peaks (Caine, 1980) being able to quickly exploit favorable environmental conditions. Although continuous reproduction could not be extrapolated for Lazaro Beach caprellids because our data were seasonally sampled, the occurrence of ovigerous females and juveniles indicates at least four seasonal reproductive cycles for all species but *C. dilatata*, that was not registered in April.

Different abundance peaks and reproductive output of caprellid species are probably determined by availability of specific food and habitat requirements although different life strategies (such as generation time and fecundity) and competitive interactions could also be involved (Edgar, 1983b).

The dimorphism in size observed for some species could be related to differential growth rates between sexes. *Caprella scaura*, *C. equilibra* and *C. danilevskii* males reach larger sizes than females. This pattern results from pereonite 1 elongation in males. For *C. scaura* the pereonite 1 growth rate changes in the later stages of development becoming exponential in males and linear in females (Takeda, 1981). Absence of molting during egg incubation is another factor that could limit female growth (Carefoot, 1973). Also, for some species with maternal care such as *C. scaura* studied by Aoki (1997), the young protection could mean high energetic costs for females and consequently lower growth rates.

Lower growth rates and higher mortality of females are potential contributors to male skewed sex ratio for some *Caprella* species studied. Moreover, according to Caine (1979), caprellid amphipods generally present an anomalous sex ratio, with equal proportions of males and females for smaller individuals, dominance of females in intermediate sizes and a majority of males at larger size classes. This trend is evident for *C. scaura*, *C. equilibra* and *C. danilevskii* (Fig. 2).

In conclusion, results obtained indicate great variability in depth distribution and population dynamics for caprellid amphipods, even for congeneric species, and encourage additional studies focusing the ecology and population biology of the caprellid fauna.

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