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***Research Article***

# The role of epiphytic algae and different species of *Sargassum* in the distribution and feeding of herbivorous amphipods

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**ABSTRACT.** The presence of particular algal species can directly influence the distribution and abundance of mesoherbivores. The aim of this study was to answer the following questions: Do *Sargassum* beds of different localities show variation in the load of epiphytic algae? Do *Sargassum* beds of different localities show variation in the density of herbivore amphipods? Does the density of these amphipods in the same algal bed vary with epiphyte load? Are species of *Sargassum* and their epiphytes equally consumed by amphipods? The collections were carried out in three infralitoral algal beds in southeastern Brazil. Fronds of *Sargassum* were collected at each algal bed and the associated ampithoid and hyalid amphipods were separated, identified and counted. *Sargassum* fronds and epiphytes were identified, dryed and weighted. Experiments were carried out to determine the consumption of *Sargassum* species and epiphytes by amphipods. The weight of the epiphytes *Hypnea musciformis* and *Dyctiopteris delicatula* and the density of amphipods were different among sampling sites. There was a relationship between amphipod density and epiphyte weight at two sampling sites. The four amphipod species tested consumed algae, but showed different patterns of consumption. Despite consuming the epiphytes, the ampithoids preferentially feed on the three species of *Sargassum*, while *Hyale nigra* had a preference for *Hypnea musciformis*.

**Keywords:** amphipods, *Sargassum*, epiphytes, herbivory, feeding, distribution.

# El papel de las algas epífitas y diferentes especies de *Sargassum* en la distribución y alimentación de anfípodos herbívoros

**RESUMEN.** La presencia de determinadas especies de algas puede influir directamente en la distribución y abundancia de mesoherbívoros. El objetivo de este estudio fue responder a las siguientes preguntas: ¿Los bancos de *Sargassum* de diferentes localidades muestran una variación en la carga de las algas epífitas? ¿Los bancos de *Sargassum* de diferentes localidades muestran una variación en la densidad de anfípodos herbívoros? ¿La densidad de estos anfípodos varía en un mismo banco de algas con la carga epífita? ¿Son las especies de *Sargassum* y sus epífitas igualmente consumidas por anfípodos? El muestreo se realizó en tres bancos de algas del infralitoral en el sureste de Brasil. Las frondas de *Sargassum* se recogieron en cada banco de algas y los anfípodos ampithoides y hyalidos asociados fueron separados, identificados y contados. Las frondas de *Sargassum* y epífitas fueron identificadas, secadas y pesadas. Los experimentos se efectuaron para determinar el consumo de especies de *Sargassum* y epífitas por los anfípodos. El peso de las epífitas *Hypnea musciformis* y *Dyctiopteris delicatula* y la densidad de anfípodos fueron diferentes entre los sitios de muestreo. Se observó una relación entre la densidad de anfípodos y el peso de las epífitas en dos sitios de muestreo. Las cuatro especies de anfípodos analizados consumieron algas, pero mostraron diferentes patrones de consumo. A pesar de consumir epífitas, los amphitoídeos se alimentaron preferentemente de las tres especies de *Sargassum*, mientras que *Hyale nigra* mostró preferencia por *Hypnea musciformis*.

**Palabras clave:** anfípodos, *Sargassum*, epífitas, herbivoría, alimentación, distribución.

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## INTRODUCTION

Phytal communities are influenced by environmental conditions, whose relative contribution can vary spatially and temporally (Edgar, 1983a, 1983b). Factors such as water movement (Fenwick, 1976; Gibbons, 1988), depth (Krapp-Schickel, 1993; Jacobucci & Leite, 2002), accumulation of detritus (Moore, 1973), and pollution (Smith & Simpson, 1993) can have a direct effect on the distribution and abundance of the fauna associated with macrophytes. However, as these factors can modify the morphological characters (Paula, 1988) and growth and mortality rates of the macrophytes (Jernakoff *et al*., 1996), the effects on associated animals can occur in an indirect manner (Dommasnes, 1968).

There is a strong correlation between density (Coull & Wells, 1983; Dean & Connel, 1987) and size of the animals (McKenzie & Moore, 1981) and the physical characters of the algae such as biomass, volume, shape and texture (Smith *et al*., 1996). These characters, according to Hicks (1986), determine the habitat complexity for the phytal organisms.

The increase in the habitat complexity has been seen as an intensifier of the density and diversity of organisms in marine systems (Heck & Orth, 1980; Stoner & Lewis III, 1985). It provides a greater amount of space available for settlement and colonization (Jacobi & Langevin, 1996), increasing the probability of more individuals and species being present. It also furnishes additional habitats, permitting the coexistence of more species in a given area. It increases the availability of refuges, making prey chemically and visually less distinguishable to predators (Holmlund *et al*., 1990; Edgar & Robertson, 1992; James & Heck, 1994) providing a greater quantity and diversity of food, due to the increase in the availability of prey in relation to lower rates of predation and competitive interactions, thereby a greater retention of organic matter (Iribarne, 1996). Finally it also favors the maintenance of a more stable microenvironment, particularly in the intertidal zone, where the mechanical action of waves and desiccation are intense (Jacobi & Langevin, 1996).

Sessile epibiont organisms such as hydrozoans, sponges and particularly epiphytic algae influence the abundance and diversity of phytal fauna (Kangas, 1978; Leite & Turra, 2003), because they increase the complexity of the macrophytes on which they develop (Bell *et al*., 1984; Hall & Bell, 1988).

A large part of the epifauna associated with algae is composed by peracarid crustaceans, mainly amphipods (Dean & Connell, 1987; Taylor & Cole, 1994; Jacobucci & Leite, 2002). The amphipods show a great variety of feeding habits, which can be suspensivorous, detritivorous, predatory or herbivorous; they may even feed on different items, characterizing them as omnivorous (Duffy, 1990). Herbivorous amphipods can consume macroalgal substrate or associated epiphytic algae indiscriminately or they can show feeding preference for some species (Duffy & Hay, 1994; Viejo, 1999; Goeckera & Kåll, 2003). Therefore, the presence of particular species of algae in the environment can directly influence the distribution and abundance of these mesoherbivores (Edgar, 1992; Martin-Smith, 1993; Jernakoff & Nielsen, 1998).

*Sargassum* beds (Phaeophyta) are particularly conspicuous in the mid- and infralittoral zones on the southeast coast of Brazil. In many coastal areas of the states of São Paulo and Rio of Janeiro, *Sargassum* fronds are dominant in terms of cover and biomass (Paula & Oliveira-Filho, 1980). These states harbor seven species of *Sargassum* which occur in monospecific algal beds or with some dominant species (Széchy & Paula, 2000). These species can show distinct frond dimensions and degree of branching depending on water movement (Paula, 1988; Széchy & Cordeiro-Marino, 1991). This structural variation can determine differences in the composition and relative abundance of epiphytic algae and of the associated epifauna (Jacobucci *et al*., 2009). Among the organisms of the macro-epifauna whose occurrence can be influenced by the presence of epiphytes in *Sargassum* fronds, there are various species of amphipods (Norton & Benson, 1983; Martin-Smith, 1993; Viejo, 1999; Leite & Turra, 2003), some of which utilize algae not only as refuge, but also as a food resource. This is the case with gammarid amphipods of the families Ampithoidae and Hyalidae, for which there are reports of the utilization of epiphytes and *Sargassum* (Zimmerman *et al*., 1979; Duffy, 1990; Duffy & Hay, 1994). For the *Sargassum* beds on São Paulo coast, there are five hyalid and three ampithoid species of amphipods reported (Tararam & Wakabara, 1981; Wakabara *et al*., 1983; Leite *et al*. 2000; Jacobucci & Leite, 2006).

Some of these species had its feeding habits evaluated. For example, Brawley & Adey (1981) showed that *Ampithoe ramondi* consumed filamentous algae and shifted the community towards one dominated by *Hypnea spinella*, which was unpalatable to it. Hay *et al*. (1994) showed that *Cymadusa filosa* was abundant in some green algae from the Florida Keys but was deterred by chemical defenses and/or calcification from *Udotea, Penicillus* and *Rhipocephalus*. Paul *et al*. (2006) studied the consumption of filamentous algae with and without cellular inclusions by *Hyale* *nigra*. Alhtough these studies pointed out important aspects of herbivory by ampithoid and hyalid amphipods, the role of *Sargassum* and its epiphytic algae in the distribution and feeding of herbivorous amphipods in tropical algal beds are still poorly known. The hyalids *Hyale media* (Dana, 1853), *Parhyale hawaiensis* (Dana, 1853) and *Hyale nigra* (Haswell, 1879) had some aspects of their diet investigated in Brazil (Tararam *et al*., 1985; Fleury *et al*., 1994; Pereira & Yoneshigue-Valentin, 1999; Tavares *et al*., 2013). Feeding preference between *Sargassum filipendula* (Phaeophyta) and *Galaxaura supocaulon* (Rodophyta) was evaluated for *Cymadusa filosa* Savigny, 1816 in algal beds of southeast Brazil (Tavares *et al*., 2013).

Therefore, the aim of this study was to answer the following questions: 1) Do *Sargassum* beds of different localities show variation in the load of epiphytic algae on their fronds? 2) Do *Sargassum* beds of different localities show variation in the density of ampithoid and hyalid amphipods? 3) Does the density of these amphipods vary with the load of epiphytes on the fronds? 4) Are species of *Sargassum* and their epiphytes equally utilized as a food resource by these amphipods?

## MATERIALS AND METHODS

### Study area

The collections were carried out in the infralitoral zone of the rocky shores of Fortaleza (23°32’S, 45° 10’W), Lázaro (23°31’S, 45°08’W) and Perequê-Mirim (23°31’S, 45°02’W) beaches, located in the municipality of Ubatuba, north coast of the state of São Paulo, Brazil, in December 2003. The locations where the collections were made had a depth of about 2.5 m. Fortaleza and Lázaro beaches can be considered moderately protected from wave action, and Perequê-Mirim beach is more sheltered (Széchy & Paula, 2000).

Perequê-Mirim beach is subject to the constant movement of fishing and recreational boats and pollution by fuel oil is a constant impact (Jacobucci, unpublished data). The water quality data of the region indicate that Perequê-Mirim beach showed a higher coliform concentration than that of Lázaro beach in the sampling period (CETESB, 2004). Although there was no systematic collection of samples for water quality evaluation on Fortaleza beach, this beach should show, on average, better water quality than the others, since human influence is less intense (Tavares *et al*., 2013).

The infralittoral zone of the rockshores of the sampling sites is dominated by different species of *Sargassum*. *Sargassum filipendula* C. Agardh occurs for the most part on Fortaleza beach. *Sargassum cymosum* C. Agardh is the dominant species on Lázaro beach, while on Perequê-Mirim *S. stenophyllum* J. Agardh dominates. The brown algae *Dictyopteris delicatula* J.V. Lamouroux and *Dictyota cervicornis* Kützing and the red alga *Hypnea musciformis* (Wulfen) J.V. Lamouroux were the most abundant and most frequent epiphytes on the fronds in the sampling period. Other epiphytic algae were recorded but were not identified, due to their sporadic occurrence and small biomass.

### Epiphytic load and amphipod density

Fifteen fronds of the dominant species of *Sargassum* were randomly collected at each algal bed. For such, a 50 m wide transect was outlined parallel to the rockshores, in the infralittoral zone. The fronds were placed in fabric bags with 200 μm mesh size and the substrate scraped off with the help of a spatula. These bags were placed in containers with sea water and taken to the laboratory. The sampling was performed with scuba diving equipment. Each frond was separately placed in a tray with 4% formaldehyde prepared with sea water and submitted to four successive washings to remove the fauna. The resulting water of this process was filtered using a net with a 200 μm mesh for the retention of the amphipods which were fixed in 70% alcohol. The ampithoid and hyalid amphipods were identified and counted under a stereomicroscope.

The epiphytes adhering to the fronds of *Sargassum* were manually removed, and the most abundant species were identified. Next, they were placed in an oven at 60°C for 48 h and weighted. The same drying procedure was utilized to obtain the dry weight of *Sargassum* spp.

One-way ANOVA was used to evaluate the differences in weight of *Sargassum* and of its epiphytes between sampling sites. The same was done to compare the density (expressed as the number of individuals/dry weight of *Sargassum*) of the amphipods. When there were significant differences, analysis of variance was followed by Tukey’s test for multiple comparisons. The data were evaluated with respect to normality and homogeneity of variances and, when necessary, $^{2}\sqrt{x}$ and log (1+x) transformations were performed (Zar, 1999).

Linear regression analysis of dry weight of epiphytes on amphipods density was carried out to determine the influence of epiphyte load on the occurrence of the amphipods. The variables were log transformed and the dry weight of the epiphytes was divided by the weight of *Sargassum* to avoid possible effects of frond size on the density of the amphipods. To determine if there were significant differences in the density of amphipods and weight of epiphytes relations between beaches, regressions were compared utilizing analysis of covariance (ANCOVA).

### Use of algae as food resource

To evaluate if the ampithoid and hyalid amphipods equally use *Sargassum* species and epiphytic algae as a food resource, experiments were carried out to determine the consumption of these algae. Forty fronds of *Sargassum* were collected in each sampling site, and they were immediately placed in a bucket with sea water. Next, the fronds were individually placed in a tray to separate the amphipods for the experiment. Investigating the branches of the algae, the ampithoid and hyalid amphipods were separated. A stereomicroscope was used to identify the amphipods belonging to the species *Ampithoe ramondi* Audouin, 1826, *Cymadusa filosa* Savigny, 1816, *Sunampithoe pelagica* H. Milne Edwards, 1830 (Ampithoidae) and *Hyale nigra* Haswell, 1879 (Hyalidae). The amphipod species indicated were utilized, because in pilot experiments they consumed *Sargassum* and their epiphytes.

The amphipods were maintained in aquaria with circulating water. Twenty adult individuals of each species were selected from each sampling site; they were of similar size to minimize possible variations in consumption due to size. Each amphipod was individually placed in a container of about 250 mL with sea water and similar-sized pieces of the algae *Sargassum* sp., *Dictyopteris delicatula*, *Dicyiota cervicornis* and *Hypnea musciformis*. The dominant species of *Sargassum* was utilized for each sampling site. The algae were placed in 20 containers without amphipods to determine variations in weight independent of the consumption of algae, during the period in which the experiment was conducted. The containers were maintained at a controlled temperature of 23$^{o}$C, under artificial light and a photoperiod of 16/8 h. To standardize the measurement of weight, the fragments of algae were placed on absorbent paper for 2 min, before weighting. After 48 h, the algal fragments were again placed on absorbent paper and weigthed. Consumption of each algal species by the amphipods was calculated by subtracting the mean variation in weight of the algae in replicates with amphipods (n = 20) from the mean variation in weight in replicates without amphipods (n = 20). The standard error of each mean was obtained based on the weighted variance of the replicates with and without amphipods (Zar, 1999).

For logistical reasons, the experiments on consumption for each sampling site were carried out on different days. Differences in biomass reduction between treatments and control were compared for each algal species, utilizing the *t*-test for independent observations.

Due to the non-independence of the treatments, differences in consumption at the same sampling site, for each amphipod species, were tested utilizing the consumption data of only one algal species in each container. These data were obtained by sorting the containers that would be utilized for each algal species. Therefore, there was an effective reduction in the sample size (n = 5), but it was possible to evaluate the preference of each amphipod species, utilizing unifactorial ANOVA and Tukey's test for multiple comparisons, in case of a significant difference (Peterson & Renaud, 1989). When necessary, data were transformed to guarantee the assumptions of the tests (Zar, 1999).

## RESULTS

### Epiphytic load and density of ampithoid and hyalid amphipods

Although the species of *Sargassum* sampled at each beach were different (Perequê-Mirim: *Sargassum stenophylum*; Lázaro: *Sargassum cymosum*; Fortaleza: *Sargassum filipendula*), there was no significant difference observed in the dry weight of the fronds. The weight of *H. musciformis* on Lázaro was significantly greater in relation to the other beaches. For *D. delicatula* and the other epiphytes, the dry weight on Fortaleza beach was significantly greater, but *D. cervicornis* did not show a difference in weight among beaches (Table 1).

Differences in density of the amphipods *Ampithoe ramondi* ($F_{2,42}$ = 14.55; $P < 0.001$), *Cymadusa filosa* ($F_{2,42}$ = 3.61; $P < 0.05$), *Sunampithoe pelagica* ($F_{2,42}$ = 11.91; $P < 0.001$) and *Hyale nigra* ($F_{2,42}$ = 17.47; $P < 0.001$) were observed between the sampling sites, with significantly lower values for Perequê-Mirim beach (Fig. 1).

### Relationship between amphipod density and epihyte load

The linear regressions indicated that the variation in density of *A. ramondi* and *H. nigra* is due, in part, to the weight of the epiphytes associated with *Sargassum* on Lázaro beach. The same dependence was found for all the species of amphipods on Fortaleza beach (Fig. 2). On Perequê-Mirim beach, due to the absence of the

**Table 1.** Mean ( ± standard error) and results of unifactorial ANOVA and Tukey's test for dry weight (g) of *Sargassum* spp. and their epiphytes on the beaches studied. F: Fortaleza, L: Lázaro, P: Perequê-Mirim. Underlined letters indicate the lack of significant difference. ns: not significant; **P* < 0.05; *** *P* < 0.001.

| | Lázaro | Fortaleza | Perequê-Mirim | | |
|---|---|---|---|---|---|
| *Sargassum* spp. | 7.49 ± 0.90 | 8.66 ± 1.84 | 6.93 ± 0.79 | $F_{2,42} = 2.41^{ns}$ | L F P |
| *Hypnea musciformis* | 2.10 ± 0.29 | 0.31 ± 0.14 | 0.64 ± 0.12 | $F_{2,42} =$ 22.59*** | L F P |
| *Dictyopteris delicatula* | 0.02 ± 0.01 | 0.28 ± 0.11 | 0.04 ± 0.01 | $F_{2,42} =$ 5.28* | F L P |
| *Dictyota cervicornis* | 0.04 ± 0.04 | 0.05 ± 0.04 | 0.04 ± 0.02 | $F_{2,42} = 0.06^{ns}$ | L F P |
| Other epiphytes | 0.01 ± 0.001 | 0.18 ± 0.07 | 0.03 ± 0.02 | $F_{2,42} =$ 5.61* | F L P |

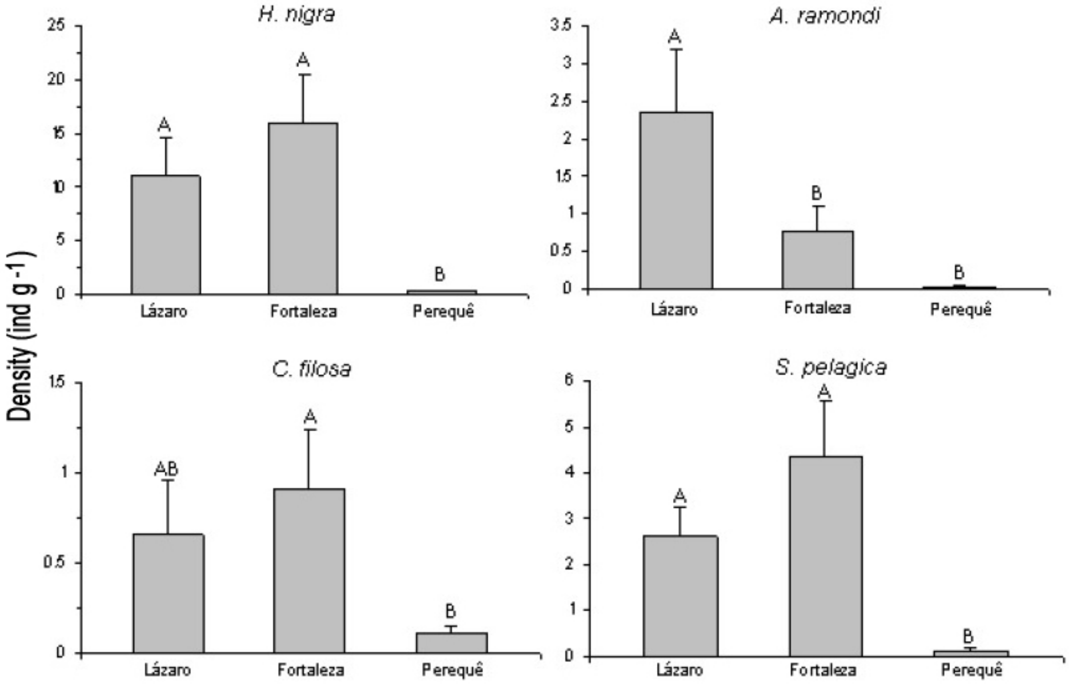

**Figure 1.** Mean density (+ standard error) of herbivorous amphipods associated with *Sargassum* spp. Bars with the same letters indicate the lack of significant difference.

species of amphipods tested on various fronds, no regressions were performed.

In comparing the regression lines of Lázaro and Fortaleza for *A. ramondi* and *H. nigra*, it was found that the relation between density of amphipods and dry weight of epiphytes depends on the beach considered (ANCOVA for *A. ramondi*: intercepts F = 33.69 ; df = 1; *P* < 0.001; slope F = 11.94; df = 1; *P* < 0.005; ANCOVA for *H. nigra*: intercepts F = 12.63; df = 1; *P* < 0.005; slope F = 0.29; df = 1; *P* > 0.05).

### *Sargassum* and their epiphytes as food resource for amphipods

The four species tested consumed algae, but showed different patterns of consumption. A significant difference was found for weight between treatments with ampithoid amphipods and without amphipods for *Sargassum* spp. and *H. musciformis* (*P* < 0.01 for all cases). There are indications of the utilization of *D. delicatula* and *D. cervicornis* by the three species of ampithoids, because of the herbivory marks detected in these algae, but without significant differences in relation to the controls without amphipods (*P* > 0.05) (Fig. 3).

There was a significant difference in consumption among algal species on Lázaro beach by *A. ramondi* ($F_{3,16}$ = 138.17; *P* < 0.001), *C. filosa* ($F_{3,16}$ = 310.35; *P* < 0.001) and *S. pelagica* ($F_{3,16}$ = 130.59; *P* < 0.001). On Fortaleza beach, significant differences in consumption were also found for *A. ramondi* ($F_{3,16}$ = 218.79; *P* < 0.001), *C. filosa* ($F_{3,16}$ =184.18; *P* < 0.001) and *S. pelagica* ($F_{3,16}$ = 115.35; *P* < 0.001).

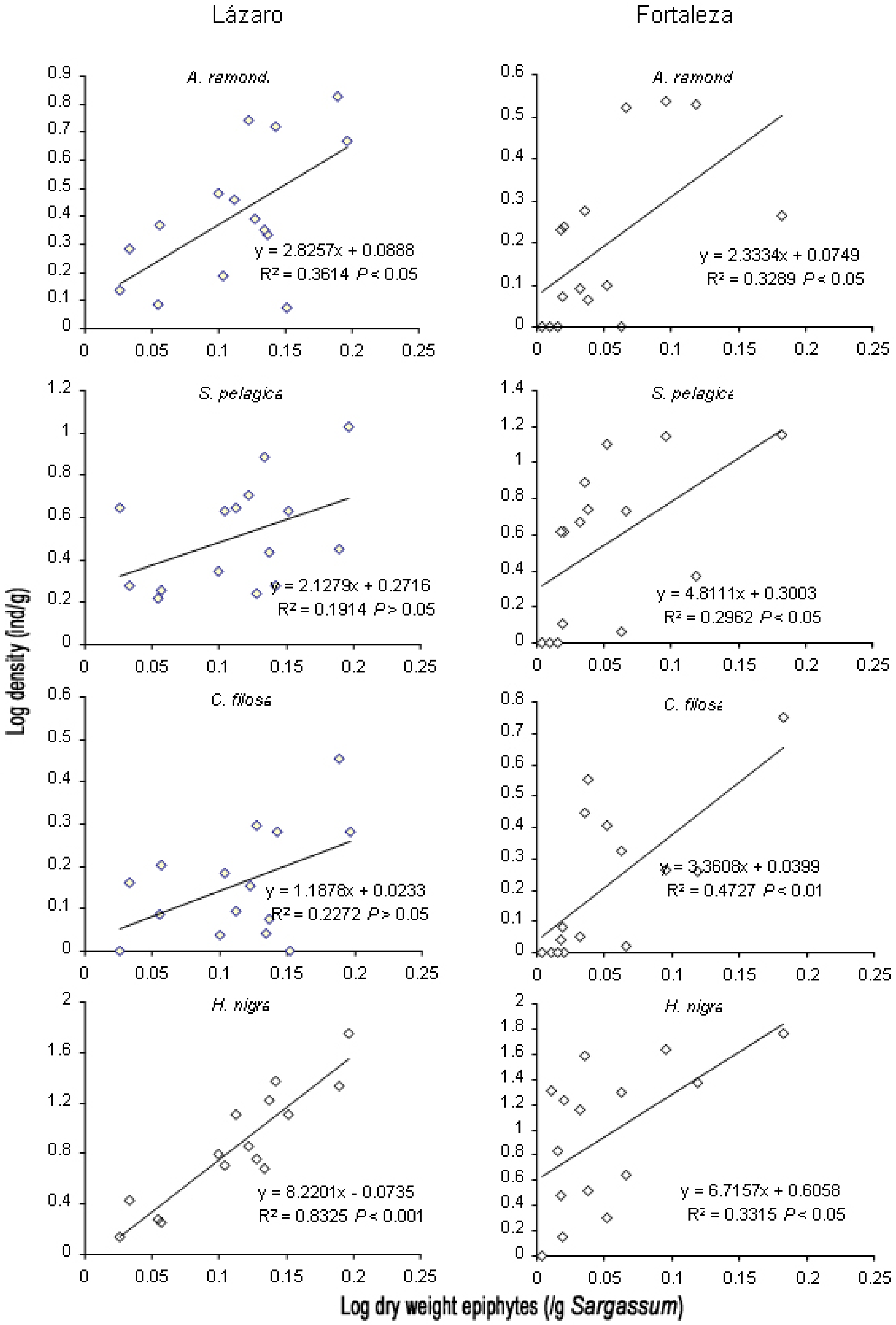

**Figure 2.** Linear regressions of the relationship between the densities of amphipods and dry weight of epiphytes on *Sargassum cymosum*, on Lázaro and Fortaleza beaches (both variables $\log_{10}$ transformed).

The same pattern was observed on Perequê-Mirim beach (*A. ramondi*: $F_{3,\ 16} = 275.39$; $P < 0.001$, *C. filosa*: $F_{3,\ 16} = 334.30$; $P < 0.001$ and *S. pelagica* $F_{3,\ 16} = 208.14$; $P < 0.001$) (Fig. 3).

*Hyale nigra* consumed significant quantities of *Sargassum* ($P < 0.01$) and the epiphytes *Hypnea musciformis*, *Dictyopteris delicatula* and *Dictyota cervicornis* ($P < 0.01$ in all cases). Differences in consumption between algae were found on all beaches (Lázaro: $F_{3,\ 16} = 167.41$; $P < 0.001$, Fortaleza: $F_{3,\ 16} = 215.55$; $P < 0.001$ and Perequê-Mirim: $F_{3,\ 16} = 27.88$; $P < 0.001$) (Fig. 3).

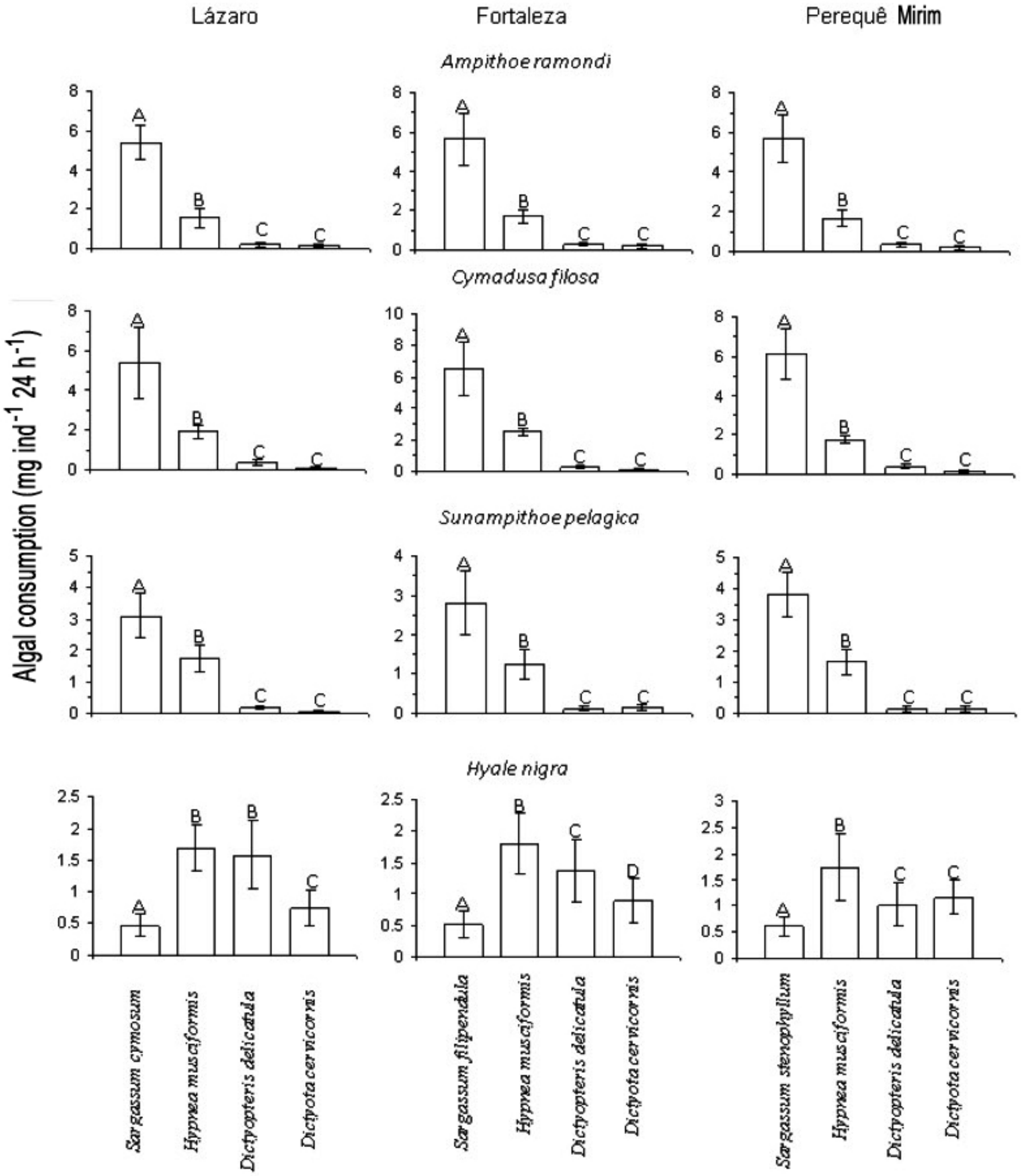

**Figure 3.** Consumption of *Sargassum* spp. and their epiphytes by amphipods in selected experiments. Bars with the same letters indicate the absence of significant difference in consumption.

## DISCUSSION

The distribution and abundance of benthic organisms, including marine macrophytes and their associated epifauna, are dependent on environmental factors which act on different scales (Edgar, 1983a; Tanaka & Leite, 2003). In the present study, the local conditions of the beaches sampled could have been partially responsible for the differences observed in the weight of epiphytic algae and in the density of the amphipods studied.

The fact that the hydrodynamic characteristics of the beaches are similar (Széchy & Paula, 2000) probably determined the lack of difference in the mean weight of the species of *Sargassum* (Table 1). These results concur with the observations of Paula (1988), according to whom the morphologic characteristics of the *Sargassum* species on São Paulo coast are highly dependent on the local hydrodynamic conditions. Different species can show the same morphological type (size and branching) if the wave action conditions are equivalent.

In relation to the epiphytic algae, variation in availability of nutrients could have resulted in a different *Sargassum* load on the three beaches (Table 1). A different input of nutrients, coming from the resuspended sediment adjacent to the algal beds or from the patterns of water circulation can significantly influence the growth rates of some species of epiphytes. An increase in growth rates of *Hypnea musciformis* was detected in experimental studies with nitrate enrichment (Berchez & Oliveira, 1989). There does not appear to be, however, a simple relation between the quantity of nitrogenous compounds and the growth of epiphytes, since Perequê-Mirim beach, considerably richer in exogenous organic matter (CETESB, 2004), did not show higher values of weight for these algae.

The occurrence of the amphipods investigated in all the sampling locations confirm these species are common on the north coast of São Paulo as detected in other studies (Tanaka & Leite, 2003; Jacobucci *et al*., 2009). Both ampithoids and *Hyale nigra* occur in these areas with greater hydrodynamism as well as at highly impacted locations (Leite *et al*., 2000). However, the density of the amphipods is dependent on local conditions. The species occurred at significantly lower densities on Perequê-Mirim beach (Table 1). Pollution due to the presence of boats can be responsible for the lower densities of amphipods on Perequê-Mirim. Compounds from antifouling paint used in boats, particularly TBT (tributyltin) had been recently detected in a nearby area (Jacobucci *et al*., unpublished data) and can cause increased mortality and decreased fecundity in amphipod populations (Ohji *et al*., 2003). Although the general hydrodynamic conditions of the beaches studied are similar, the sampling site on the Lázaro beach has a little higher water movement compared to the others. This could explain the greater density of *A. ramondi* on Lázaro beach. The preference of this species for areas with greater hydrodynamism had already been detected by Sánchez-Moyano & García-Gómez (1998).

Confirming the results of other studies (Norton & Benson, 1983; Hall & Bell, 1988; Martin-Smith, 1993), the presence of epiphytes appears to be an important structuration factor, particularly on a small spatial scale, since on the two beaches evaluated a direct relation was noted between the density of the amphipods and the load of epiphytes on the fronds of *Sargassum* (Fig. 2). Considering that the amphipods studied are herbivorous, it would be expected that the density related to epiphytes could be due to the greater feeding value of fronds with higher epiphyte load. The consumption experiments favours this hypothesis, since the three ampithoid species consumed substantial quantities of *H. musciformis* and left marks of herbivory on *D. delicatula* and *D. cervicornis*, although the variation in weight of the latter was not different from that obtained in controls without amphipods (Fig. 3). The consumption of *H. musciformis* has already been reported for other species of ampithoids in algal beds of temperate (Duffy, 1990; Duffy & Hay, 2000) and tropical regions (Jacobucci *et al*., 2008).

However, the low values for most of the determination coefficients obtained in the regression analyses (Fig. 2) and the differences between regression lines of the same species of amphipod in different beaches indicate that other factors influence amphipod densities on *Sargassum* spp.

Despite consuming the epiphytes, the ampithoids preferentially consumed the three species of *Sargassum*. The consumption of species of this genus by ampithoids (Duffy, 1990; Cruz-Rivera & Hay, 2000) and its use for the construction of tubes (Norton & Benson, 1983; Schneider & Mann, 1991; Appadoo & Myers, 2003) has also been reported. This suggests that the load of epiphytes, at least as a food resource, is not the main factor to explain density variation of the ampithoids.

On the other hand, the presence of epiphytes can increase the habitat complexity, making it more attractive as providing food resources indirectly, making environments available for the development of the periphyton and favoring the accumulation of sediments (Hicks, 1980). Taking into account that the diet of some species of the genera *Ampithoe* and *Cymadusa* includes microalgae (Brawley & Adey, 1981; Norton & Benson, 1983) and detritus (Zimmerman *et al*., 1979), it would be possible that these amphipods are indirectly related to epiphytic algae.

The lower consumption of Dyctiotales by ampithoids could be related to the lower quality of these algae as a food resource, when compared with the *Sargassum* species evaluated. Our results differ from Hay *et al*. (1988) study that showed an opposite pattern. *Dictiopteris delicatula* and *Dictyota dichotoma* were more consumed than *Sargassum hystrix* both by hyalid and ampithoid amphipods. Considering that many species of amphipods are resistant to the secondary metabolites of Dyctiotales, other compounds from algae, seems to be more important in determining food selection by the amphipod species we tested.

The higher densities of *H. nigra* on fronds showing abundant cover for epiphytes should be related to the utilization of these algae as food (Fig. 3). Herbivorous feeding habits were already reported for the genus

*Hyale* (Tararam *et al.*, 1985; Buschmann & Santelices, 1987; Hay *et al.*, 1988; Poore, 1994), and the dependence on the density of a species in relation to the quantity of epiphytes was experimentally demonstrated (Edgar & Robertson, 1992). Although the presence of epiphytes is an important factor for explaining the distribution of *H. nigra* on Lázaro beach ($R^2 = 0.832$), the same pattern was not observed on Fortaleza (Fig. 2), which indicates the dependence of this species on other local factors. The results of the consumption experiments (Fig. 3) and the greater representativity of this species on fronds of *Sargassum* with greater number of reproductive structures (Jacobucci, unpublished data) indicate that other characteristics of this alga can also influence the occurrence of *H. nigra*.

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