

Effect of temporal variation and size of herbivorous amphipods on consumption levels of *Sargassum filipendula* (Phaeophyta, Fucales) and their main epiphyte, *Hypnea musciformis*

Efeito da variação temporal e do tamanho de anfípodas herbívoros nos níveis de consumo de *Sargassum filipendula* (Phaeophyta, Fucales) e sua principal epífita, *Hypnea musciformis*

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Abstract

The impact of herbivorous amphipods on a community of macroalgae does not depend only on the species present. Two equally important factors are the relative abundance and potential consumption of herbivorous species. The aim of this study was to determine the role of temporal and size variation of herbivorous amphipods in the consumption of *Sargassum filipendula* and their main algal epiphyte *Hypnea musciformis*. Monthly collections of 15 fronds of *S. filipendula* were carried out between June 2000 and May 2001 at Fortaleza beach, north coast of the state of São Paulo, Brazil, to evaluate the size structure of the herbivorous amphipods of the families Hyalidae and Ampithoidae and the occurrence of epiphytic algae associated with *S. filipendula*. Ampithoidae and Hyalidae amphipods were identified, separated in size classes and counted. Choice consumption assays were performed to estimate the grazing rates of amphipods of different size classes on *S. filipendula* and *Hypnea musciformis*. The amphipods showed temporal variation in abundance and recruitment in all sampling periods. Algal consumption varied among species and size of amphipods with a tendency for increased consumption with size (from a mean daily value of 0.143 g/frond for 0.75 mm *Hyale nigra* to 6.757 g/frond for 4.0 mm *Cymadusa filosa*). Consequently, the contributions of each species for the removal of the algae were different along the year. Our results indicate that amphipod algal herbivory should be evaluated at fine taxonomic resolution considering the individual contribution of different size classes.

Key words: Amphipoda, herbivory, phytal.

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Resumo

O impacto de anfípodas herbívoras em uma comunidade de macroalgas não depende somente das espécies presentes. Dois fatores igualmente importantes são a abundância

relativa e o consumo potencial de espécies herbívoras. O objetivo deste estudo foi determinar o papel da variação temporal e de tamanho de anfípodes herbívoros no consumo de *Sargassum filipendula* e sua principal alga epífita *Hypnea musciformis*. Coletas mensais de 15 frondes de *S. filipendula* foram realizadas entre junho de 2000 e maio 2001 na praia da Fortaleza, litoral norte do estado de São Paulo, Brasil, para avaliar a estrutura de tamanho de anfípodes herbívoros das famílias Hyalidae e Ampithoidae e a ocorrência de algas epifíticas associadas a *S. filipendula*. Anfípodes ampitoídeos e hialídeos foram identificados, separados em classes de tamanho e contados. Ensaios de consumo com escolha foram realizados para estimar as taxas de herbivoria de anfípodes de diferentes classes de tamanho em *S. filipendula* e *Hypnea musciformis*. Os anfípodes mostraram variação temporal na abundância e recrutamento em todos os períodos de amostragem. O consumo das algas variou entre espécies e tamanho dos anfípodes com uma tendência de aumento de consumo com o tamanho (de um valor médio diário de 0,143 g/fronde para *Hyale nigra* com 0,75 mm a 6,757 g/fronde para *Cymadusa filosa* com 4,0 mm). Conseqüentemente, as contribuições de cada espécie para a remoção das algas foi diferente ao longo do ano. Nossos resultados indicam que a herbivoria por anfípodes deve ser avaliada com elevada resolução taxonômica, considerando-se a contribuição individual das diferentes classes de tamanho.

Palavras-chave: Amphipoda, herbivoria, fital.

Introduction

Marine macrophytes of coastal regions include a large diversity of invertebrates (Masunari, 1987), many of which utilize their hosts not only as substrate for attachment and cover, but also as a food source (Brawley, 1992). These meso-herbivores, represented mainly by amphipods, isopods and small gastropods, are primary consumers that play a fundamental role in marine grass systems (Orth and van Montfrans, 1984), because they are the main ones responsible for the transfer of energy to higher trophic levels (Edgar and Shaw, 1995; Taylor, 1998). In addition, they constitute important structuring elements in these communities (Jernakoff *et al.*, 1996), since they do not consume indiscriminately the macrophytes present in the environment (Duffy and Harvilicz, 2001). The effect of meso-herbivores on marine grasses is basically indirect, because these are generally overlooked as a food item compared to epiphytic algae (Nicotri, 1980). The consumption of epiphytes favors the development of marine grasses (Robertson and Mann, 1982), because algae increase shading and compete with plants for nutrients (van Montfrans *et al.*, 1984; D'Antonio, 1985).

The effects of meso-herbivores on macroalgal communities appear to be more complex since these invertebrates prey on epiphytic microalgae (Norton and Benson, 1983) up to laminaria algae (Tegner and Dayton, 1987). When there is preferential consumption of epiphytes, the effects are similar to those reported for marine grass communities, with reduced deleterious effects on substratum macroalgae (Brawley and Adey, 1981; Shacklock and Doyle, 1983; D'Antonio, 1985). However, there are cases of consumption of substratum macroalgae resulting in substantial modifications in the biomass as well as in the composition of species in the algal community (Duffy and Hay, 2000).

This picture is probably due to the large taxonomic diversity of meso-herbivores (Brawley, 1992) and consequent variation in the extent of their diets (Duffy, 1990; Poore, 1994). Gastropods, for example, are herbivores that are more efficient in consuming epiphytic algae when compared to amphipods, but because the latter ones are more selective and show greater mobility and abundance they can have more substantial effects on the structure of the algal community (Jernakoff and Nielsen, 1997). Even in more restricted taxonomic groups, there can be an enormous difference in the effects of herbivory on the same algal community (Duffy and Hay, 2000). This situation

seems to be particularly applicable to amphipods, where representatives of one family (Ampithoidae) and even a whole genus (*Ampithoe*), can show feeding preferences by different species of algae that occur in a given environment (Duffy and Hay, 1991, 1994; Duffy and Harvilicz, 2001).

The impact of herbivorous amphipods on a community of macroalgae does not depend only on the species present. Two equally important factors are the relative abundance and consumption potential of herbivorous species. Since the number of amphipods varies considerably at different spatial and temporal scales (Edgar, 1983a, b; Martin-Smith, 1993; Jacobucci and Leite, 2002; Tanaka and Leite, 2003), true estimates of herbivory should take these aspects into account. In addition, the same species can vary based on the size of the organisms (Tararam *et al.*, 1985, 1990; Ruesink, 2000), such that assays to determine levels of herbivory should utilize from juveniles up to adult individuals and consider the temporal variation in the size structure of the populations involved.

The banks of algae that occur along the coast of the states of São Paulo and Rio de Janeiro in Brazil are dominated by species of *Sargassum* which show substantial variations in biomass in different locations and periods during

the year (Paula and Oliveira Filho, 1980; Széchy and Paula, 2000; Leite and Turra, 2003). In these environments, various species of amphipods can be found, including gammarids amphithoids and hyalids (Tararam and Wakabara, 1981; Wakabara *et al.*, 1983; Leite *et al.*, 2000) whose diet includes macroalgae (Barnard and Karaman, 1991). *Ampithoe ramondi*, *Cymadusa filosa*, *Sunampithoe pelagica* (Ampithoidae) and *Hyale nigra* (Hyalidae) are the species that consume *Sargassum* spp. as well as epiphytes.

The aim of this study was to determine the role of temporal and size variation of herbivorous amphipods in the consumption of *S. filipendula* and their main algal epiphyte to answer the following questions: (i) How does size structure of herbivorous amphipods of the families Hyalidae and Ampithoidae vary during the course of the year? (ii) Is there a difference in the consumption of *Sargassum* and their main epiphyte for herbivorous amphipods of different sizes? (iii) What is the mean estimated consumption of *Sargassum* and of their main epiphyte during the course of the year?

Material and methods

Study area

Samples were collected in the lower shore region of the beach of Fortaleza (23°32' S, 45° 10' W) located in Fortaleza inlet, municipality of Ubatuba, north coast of the state of São Paulo. This location is formed by a narrow rocky stretch running in the southeast-northeast direction, showing two sides with different degrees of exposure to wave action. The rock shore where samples were collected is about 2.5 m in depth, which can be considered moderately protected from wave action, according to the criterion used by Széchy and Paula (2000). *S. filipendula* is dominant in terms of cover, representing about 90% of the total algae and *Hypnea musciformis* is the most abundant epiphyte, occurring

mainly in the upper portion of the fronds of *S. filipendula* (personal observation).

Sampling and processing

Monthly collections of 15 fronds of *S. filipendula* were carried out between June 2000 and May 2001 to evaluate the size structure of the herbivorous amphipods of the families Hyalidae and Ampithoidae and the occurrence of epiphytic algae associated with *S. filipendula*. A section transect 50 m wide was marked in the region of the lower shore of the embayment to be sampled. The fronds were wrapped in cloth bags with a mesh size of 200 µm and the substrate was scraped off with the help of a spatula. These bags were placed in containers with seawater and transported to the laboratory. The collections were carried out using scuba diving equipment. Each frond was placed separately in a tray with a solution of 4% formaldehyde in seawater and submitted to four successive washings to remove fauna. The washes from this process were filtered through a screen with a mesh size of 200 µm for retention of the amphipods which were fixed in 70% alcohol. The amphipods were identified and counted under a stereomicroscope. The amphipods of the families Ampithoidae and Hyalidae were passed through a series of nylon screens of decreasing mesh (4.0 mm, 2.8 mm, 2.0 mm, 1.4 mm, 1.0 mm, 0.75 mm, 0.5 mm and 0.2 mm) to obtain a separation of individuals of different size classes (adapted from Edgar, 1990). The epiphytes adhering to the fronds of *Sargassum* were removed manually. The species visually most abundant and present in all the months of the collection was *H. musciformis* which was separated and placed on absorbent paper for 5 min and weighed. The same weighing procedure was used to obtain the wet weight of *S. filipendula*.

Consumption by individuals of different sizes

Individuals of the species *Cymadusa filosa*, *Ampithoe ramondi*, *Sunampithoe*

pelagica and *Hyale nigra* belonging to the size classes of 0.75, 1.0, 1.4, 2.0, 2.8 and 4.0 mm, were identified and placed individually in 500 ml containers for consumption assays with *S. filipendula* and the epiphyte *H. musciformis*. For each species of amphipod, 20 replicates were utilized with animals of each size class, along with 10 replicates without amphipods to determine variations in weight independent of the consumption of algae, during the course of the experiments. The containers were kept in the laboratory at a controlled temperature of 23°C, under artificial light and a 16/8h photoperiod. To standardize the measure of weight, the fragments of algae were kept on absorbent paper for 2 min before weighing. After 48 h, the fragments of algae were again placed on absorbent paper and weighed. Consumption by the amphipods was determined for each alga by subtracting the mean weight of replicates with amphipods (n=20) from the mean weight of algae incubated without amphipods (n = 10). The standard error of each mean was determined from the weighted variance of the replicates with and without amphipods (Zar, 1999). Individuals of size classes 0.2 and 0.5 mm were not used because of the difficulty in their manipulation and identification.

Amphipod herbivory estimates

The daily estimates of herbivory per frond in each month were obtained using the formula:

$$C_{\text{month}} = \frac{(C_{\text{class}} \times A_{\text{class}})}{F_{\text{month}}}$$

where:

C_{month} is an estimate of daily consumption of the species (g/frond) per month; $\sum (C_{\text{class}} \times A_{\text{class}})$ represents the summed estimates of consumption (g)

of each size class (C_{class}) multiplied by the abundance of individuals of the size class collected in the month (A_{class}); and F_{month} is the number of fronds collected per month (= 15 fronds)

Results

The species of amphipods evaluated showed temporal variation in abundance. In addition, in all the periods when

species were recorded, individuals of small dimensions were detected, indicating recruitment. Considering the whole collection period, *H. nigra* was the second most abundant species ($n = 1289$), occurring during practically the entire year, but mainly in winter. The large number of young individuals indicates a reproductive peak in this period. *Ampithoe ramondi* was the most abundant species ($n = 1676$) and showed a tendency for an increased abundance

at the end of spring with maximum numbers in the month of January, while there were very few individuals of this species in December. *Cyamadusa filosa* was more abundant at the end of spring and during summer, when it was the dominant species especially in December. The species *S. pelagica* showed a greater number of individuals in spring, with juveniles mainly in November, and was absent from samples as of February (Figure 1).

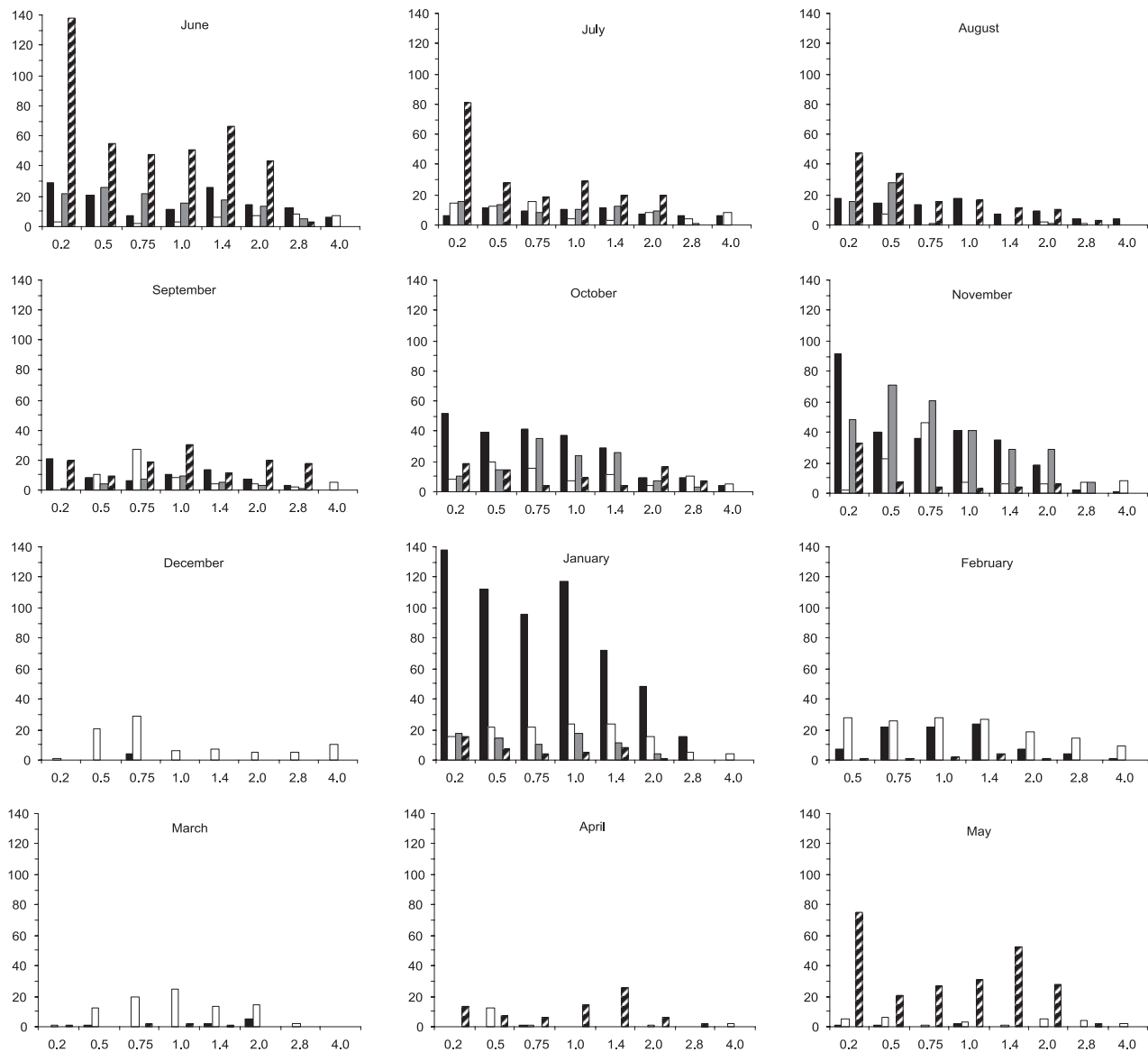


Figure 1. Distribution of size classes of *Ampithoe ramondi* ■, *Cyamadusa filosa* □, *Sunampithoe pelagica* ■ and *Hyale nigra* ▨ between June, 2000 and May, 2001. Vertical axis: number of individuals; horizontal axis: size classes (mm).

There was a tendency for increased consumption of algae with the size of the amphipods. Although the preference of each species for the algae was not explicitly tested, *H. nigra* appeared to consume primarily *H. musciformis*, whereas the amphipods utilized proportionally more *S. filipendula* (Figure 2).

The formula for daily consumption for the month (C_{month}) was used to obtain estimates of herbivory of *S. filipendula* and *H. musciformis*, per frond, for each amphipod species. The summed consumption of the species was also calculated for each month (Figure 3). The contributions of each species for the removal of the algae were different. *Ampithoe ramondi* showed a mean daily consumption that varied greatly over the course of the year. In January it was responsible for more than half of the consumption of *S. filipendula* (Figure 3). Although this amphipod species shows mean values for consumption

of *H. musciformis* per size class similar to those for *H. nigra* (Figure 2), its large abundance in January (Figure 1) accounted for it being the species showing the greatest removal of the epiphyte in this month (Figure 3). *Cymadusa filosa*, in turn, showed a relatively uniform contribution throughout the year and was the only species removing both algae in the month of December (Figure 3). The consumption of *S. pelagica* was concentrated especially in the first six months of the sampling, because the species was absent as of February. The elevated abundance of *H. nigra* between June and September and again in April and May, (Figure 1) made this species the principal consumer of *H. musciformis* in these periods (Figure 3).

Discussion

The effect of meso-herbivores on the structure of macrophyte communities

appears to be as important as physical-chemical factors (Jernakoff and Nielsen, 1997; Duffy and Hay, 2000), because many of these organisms besides feeding selectively can vary their level of consumption depending on the availability of the food (Schaffelke *et al.*, 1995; Cruz-Rivera and Hay, 2001). This appears to be the case for the amphipods studied, which consume *S. filipendula* as well as the epiphyte *H. musciformis*.

The results obtained indicate that the impact of herbivory caused by these amphipods varies with regard to the taxonomic level examined. Both qualitative and quantitative differences in consumption were observed among the representatives of the families Hyalidae and Ampithoidae.

Ampithoids were seen to consume proportionally greater quantities of *S. filipendula* in relation to *H. musciformis* (Figure 2). The utilization of brown

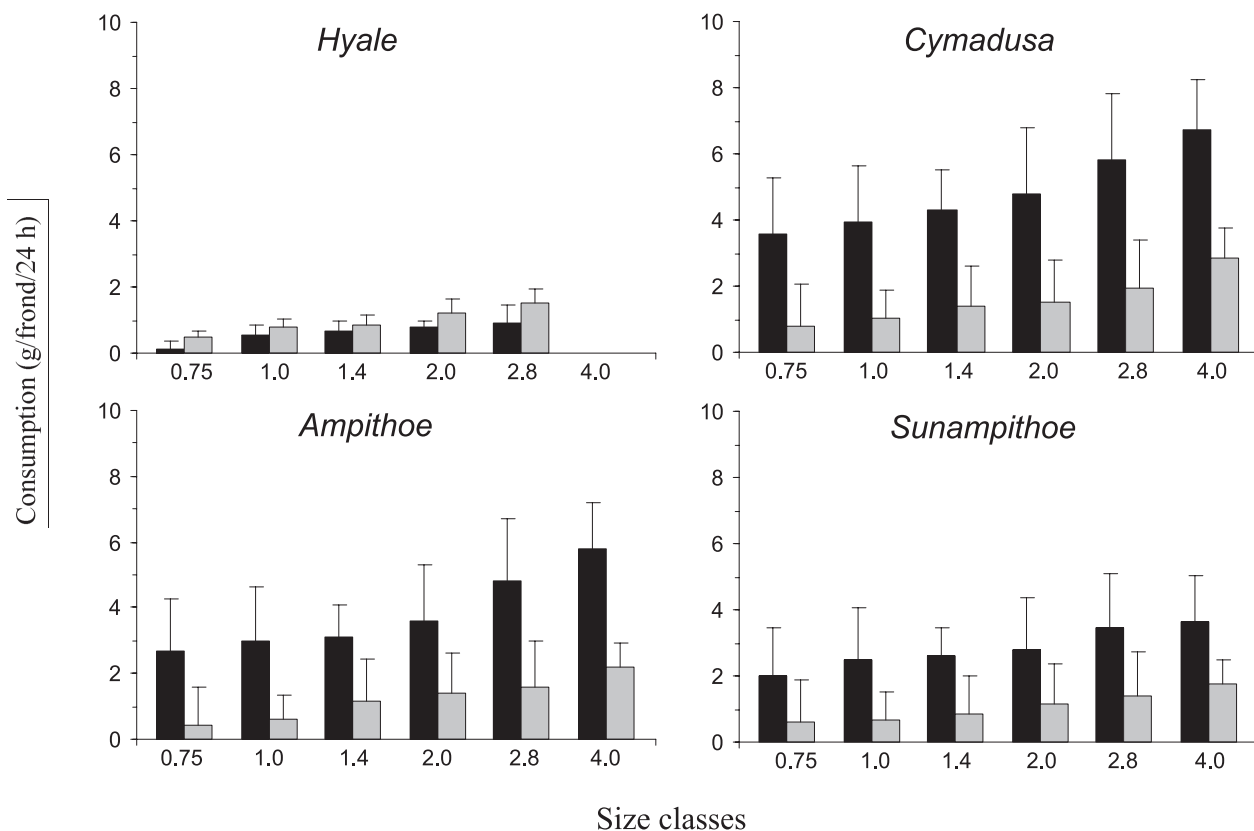


Figure 2. Consumption (mean + standard error) of *S. filipendula* ■ and *H. musciformis* ■ by amphipods in choice experiments.

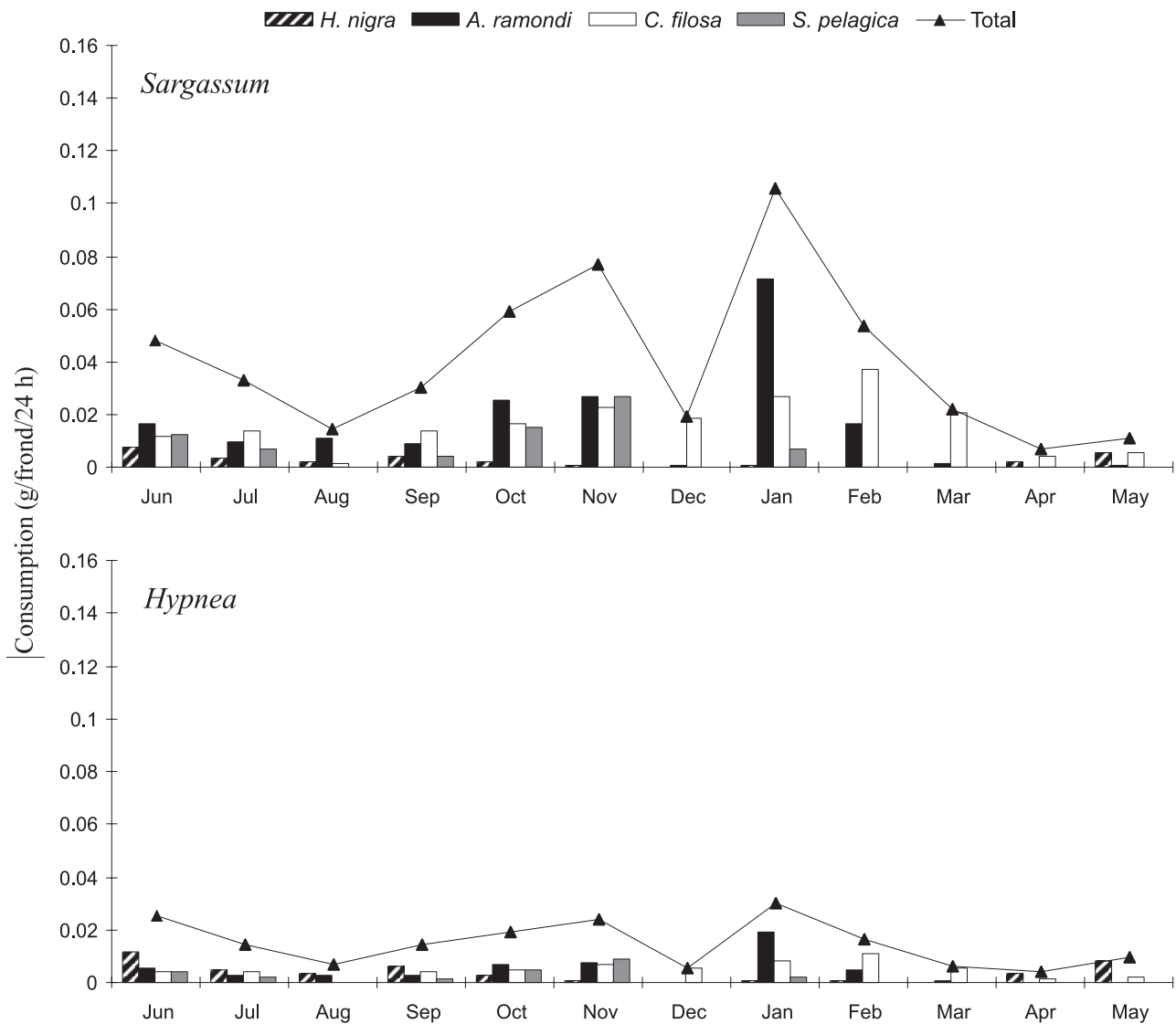


Figure 3. Daily estimates of herbivory per frond in each month for *Sargassum filipendula* and *Hypnea musciformis* with regard to each of the amphipod species *Hyale nigra*, *Ampithoe ramondi*, *Cymadusa filosa* and *Sunampithoe pelagica*, separately and all together.

macroalgae as a preferred habitat and for food has been reported for various species of amphipods (Hay *et al.*, 1990; Duffy and Hay, 1991; Cruz-Rivera and Hay, 2001). This finding can be explained by the presence of polyphenolic compounds in these algae, which confers protection against predation, mainly from omnivorous fishes, for which these algae are a deterrent (Hay, 1986; Hay *et al.*, 1987, 1990). In addition, it has been demonstrated that the food preference for these amphipods can vary between genera (Zimmerman *et*

al., 1979) and even between species of the same genus (Duffy and Hay, 1994). For the species *A. ramondi*, *C. filosa* and *S. pelagica*, there appears to be a quantitative difference in relation to the consumption of the algae (Figure 2). Species of the Hyalidae family also include algae in their diet (Buschmann and Santelices, 1987; Hay *et al.*, 1987; Pereira and Yoneshigue-Valentin, 1999; Ruesink, 2000), although items of animal origin and detritus can also be utilized (Tararam *et al.*, 1985). Preferences for distinct species of

algae have been reported for species of the genus *Hyale* (Buschmann, 1990). The consumption of species of the genera *Sargassum* and *Hypnea* by amphipods and hyalids is not a new finding, since it has already been determined from studies of the contents of their digestive tract, in food preference experiments and in mesocosms (Norton and Benson, 1983; Duffy, 1990; Tararam *et al.*, 1985, 1990; Duffy and Hay, 1991, 2000; Viejo, 1999). However, studies that have quantified the relative

impact of herbivorous amphipods of different sizes are rare and limited with respect to time (Brawley and Fei, 1987; Ruesink, 2000).

Despite the limitations of laboratory experiments with limited offering of items to choose (Brawley, 1992), the results obtained in the present study can be considered robust. Factors such as water temperature and photoperiod were adjusted as closely as possible to natural conditions and the organisms were maintained in aquariums with fronds of *Sargassum* obtained in the field, avoiding excessive handling before the experiments. Besides, this approach has been widely used with very consistent results (Norton and Benson, 1983; Duffy, 1990; Tararam *et al.*, 1985, 1990; Duffy and Hay, 1991, 2000; Poore, 1994; Pavia *et al.*, 1999; Viejo, 1999).

The consumption levels of the amphipods studied are similar to those determined for other species of Ampithoidae and Hyalidae (Duffy, 1990; Duffy and Hay, 1994, 2000; Ruesink, 2000) and apparently do not differ when the organisms have a greater extent of algae available as observed in experiments carried out with other species of epiphytes. However, the latter finding cannot be generalized because the life style of the species involved and the availability of food in nature must be considered.

Tube-dwelling species, such as *A. ramondi*, *C. filosa* and *S. pelagica*, can show reduced mobility (Brawley and Adey, 1981; Duffy and Hay, 1994) in relation to free-living species such as *H. nigra* (personal observation). This can signify that due to the large variation in composition and relative abundance of epiphytes among the fronds of *S. filipendula* and also to the occurrence of other species of substratum algae in the study area (personal observation), the consumption of *H. nigra* could have been overestimated because of the limited access to only two alga species in these experiments. Even for the ampithoids, there could have been compensatory feeding; that is,

in the absence of other food items with higher nutritional quality, the consumption of available items would be increased to meet metabolic needs (Cruz-Rivera and Hay, 2000, 2001).

It was evident that consumption depended on not only the total abundance of organisms but also the relative frequency of the size classes of the amphipods, since there was an increase in consumption with body size (Figure 2). This relationship has been reported for macro-herbivores such as sea urchins (Klumpp *et al.*, 1993). This means that factors that alter the abundance of amphipods, indirectly affect their impact on algae. Factors that can be considered the most significant are predation, particularly by fish (Nelson, 1979; Martin-Smith, 1993), competition (Edgar and Aoki, 1993; Brawley and Adey, 1981) and recruitment (Edgar, 1983b, 1990).

Understanding of the consumption of amphipods and other meso-herbivores can be of great importance for determining effects on productivity in the exploitation and cultivation of algae of commercial interest such as in the case of *Sargassum* spp., utilized for extraction of alginate, production of medicines and animal feed (Széchy and Paula, 2000), and of *Hypnea* spp., which is a source of carrageenan, a substance utilized industrially as a stabilizer, thickener or emulsifier (Reis *et al.*, 2003).

The present work demonstrated the importance of studying meso-herbivores at specific levels with regard to their impact on algal communities, because there is qualitative and quantitative variation at the different levels. This indicates that studies combining different species from large taxonomic groups or even functional groups are not recommended because they can mask the true role of amphipods in the organization of algal communities.

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