Habitat and food selection by herbivorous amphipods associated with macroalgal beds on the southeast coast of Brazil

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Abstract - The factors that influence the selection of marine macrophytes by meso-herbivores are complex, and may include the nutritional quality of algae, the value of the habitat as a shelter, and the availability of algae in the environment. Here we investigated the existence of differential use of *Sargassum filipendula* C. Agardh, 1824 (Phaeophyta) and *Galaxaura stupocaulon* Kjellman, 1900 (Rhodophyta) as habitats and feeding resources by species of Hyalidae and Ampithoidae, in laboratory manipulation experiments and in an algal bed on the northern coast of the state of São Paulo, Brazil. In the field, 19 fronds were collected from each alga and the associated amphipods were identified and counted. To evaluate food preference and habitat selection by amphipods, we conducted laboratory experiments using containers containing fragments of algae and individuals of *Cymadusa filosa* Savigny, 1816 or *Hyale nigra* (Haswell, 1879). In natural conditions, the density of *C. filosa* was significantly higher on *G. stupocaulon*, while in the feeding and habitat preference experiment we found a higher density on *S. filipendula*. The densities of *H. nigra* did not differ between the algae in both experiments, probably as a result of the variety of food items in its diet, and its high mobility and wide distribution on different substrates. The different results for *C. filosa* suggest that the pattern of feeding and habitat selection can be affected by external characteristics of the algae; probably, refuge from predation is an important selective force acting on the use of algae by these animals.

Key words: Amphipods, food choice, habitat choice, predation refuge

Introduction

The term phytal has been used to designate a marine biotype where there are interrelationships between marine animals and macrophytes (Masunari and Forneris, 1981). These macroalgae can occur in dense banks, forming patches that provide substrate for diverse faunistic groups, mainly the amphipods, the most important group of peracarid crustaceans in terms of richness and abundance in benthic communities (Thomas, 1993; Jacobucci and Leite, 2002).

The effects of amphipods and other meso-herbivores on the banks of aquatic macrophytes are fundamental in the dynamics of these ecosystems, promoting the cycling of nutrients (Klumpp *et al.,* 1992), influencing the transfer of energy between trophic levels

(Brawley, 1992), and affecting the productivity of benthic communities (Van Montfrans *et al.,* 1982).

The factors that influence the selection of algae by meso-herbivores are complex and may include, for example, the nutritional quality of algae, the value of the habitat as a shelter against environmental stress (Jormalainen *et al.,* 2001), and the availability of algae (Nicotri, 1980; Lubchenco and Gaines, 1981; Arrontes, 1990).

It is expected that food will be selected according to its palatability, energy content, digestibility and efficiency in algae absorption (Jernakoff *et al.,* 1996). However, the feeding preference of meso-herbivores may not necessarily be related to the algal nutritional qualities (Nicotri, 1980). The value of the algae as a habitat can affect the feeding patterns on the potential algal hosts (Hay, 1992; Arrontes, 1999); in such a situation, protection from predators may override feeding preferences (Hay *et al.,* 1987; Hay *et al.,* 1989). According to Duffy and Hay (1991) and Duffy *et al.* (2001), predation could be the most important factor in regulating the densities of phytal invertebrates.

The effects of meso-herbivores can be equally as important as physical and chemical factors in structuring macrophyte communities (Duffy and Hay, 2000). Nevertheless, little is known about the feeding and habitat preferences of amphipods from the families Ampithoidae and Hyalidae. Of the five species of Hyalidae and three of Ampithoidae found on the coast of São Paulo (Leite *et al.,* 2000), the diets of only *Apohyale media* (Dana, 1853) and *Parhyale hawaiensis* (Dana, 1853) have been investigated in Brazil (Tararam *et al.,* 1985; Perreira and Yoneshigue-Valentin, 1999).

This study sought to determine the existence of differential utilization of *Sargassum filipendula* C. Agardh, 1824 (Phaeophyta) and *Galaxaura stupocaulon* Kjellman, 1900 (Rhodophyta) as habitats and feeding resources by species of Hyalidae and Ampithoidae, in laboratory manipulation experiments and in a bank of macroalgae on the northern coast of the state of São Paulo, Brazil. Specifically, we posed the following questions: Do the species of Hyalidae and Ampithoidae occur in different densities on the macroalgae? Do the most abundant species of Hyalidae and Ampithoidae prefer different habitats (macroalgal species)? Do the most abundant species of Hyalidae and Ampithoidae show feeding preferences for different macroalgal species?

Material and Methods

Study area

The samples were collected on the northern coast of the state of São Paulo, Brazil (Fig. 1), in the infralittoral zone of Fortaleza Beach (23°31'S/45°09'W) in the Municipality of Ubatuba. Much of this part of the coast is rocky, affording a wide variety of substrates (Perreira and Jacobucci, 2008). The rocky shore where the samples were collected has an average depth of 2.5 m and is moderately protected from wave action, according to the criteria used by Széchy and Paula (2000). The brown alga *Sargassum filipendula* is dominant in the area, and *Galaxaura stupocaulon* (Rhodophyta), *Padina gymnospora* (Kützing) Sonder (Phaeophyta), and *Caulerpa racemosa* (Forsskal) J.Agardh, 1872 (Chlorophyta) also occur at the sampling site.

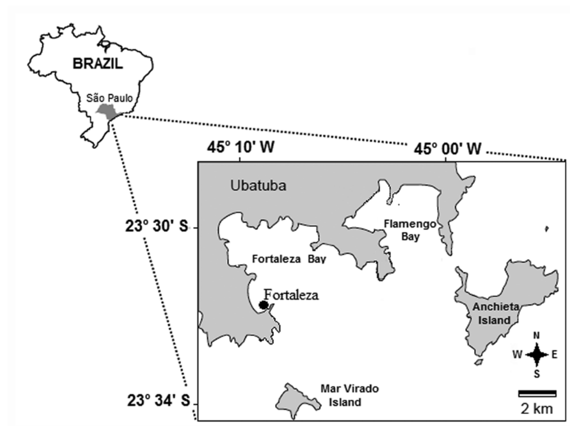

Figure 1. Location of the study area, Fortaleza Beach (23°32'S, 45°06'W), Ubatuba, state of São Paulo, Brazil.

Collection and treatment of samples

We collected 19 fronds from each of the dominant species of algae (*S. filipendula* and *G. stupocaulon*) in an area in the infralittoral zone of Fortaleza Beach where beds of *S.*

filipendula are approximately 50 m distant from beds of *G. stupocaulon*. Using snorkeling, we enclosed the fronds in a cloth bag with a 0.2 mm mesh size and removed them from the holdfast with the aid of a spatula (Jacobucci *et al.,* 2009).

In the laboratory, each frond was placed in a separate dish with a solution of 4% formaldehyde in sea water, and was washed four times to remove the macrofauna. The wash water was filtered through a 0.2 mm cloth bag to retain the organisms, which were then placed in a 70% ethanol solution. This process removes around 99% of the vagile epifauna from the fronds (Taylor and Cole, 1994). The amphipods of the families Ampithoidae and Hyalidae were counted and identified to species level with a stereoscopic microscope. The species were identified according to Conlan (1982) and Serejo (2004). Voucher specimens were preserved in 70% ethanol and deposited in the reference collection of the Laboratory of Aquatic Ecosystems Ecology in the Institute of Biology at the Federal University of Uberlândia, Brazil. The dry mass of the *Sargassum* fronds was obtained after drying at 60° C for 48 h (Jacobucci *et al.,* 2009).

Food preference and habitat selection experiments

To evaluate food preference and habitat selection, the two most abundant amphipod species recorded in the sampling location, *Hyale nigra* (Haswell, 1879) and *Cymadusa filosa* Savigny, 1816, were used. In the feeding-preference experiment, we used 10 individuals of *C. filosa* and 10 of *H. nigra*, taken from 10 fronds of *S. filipendula* and 10 of *G. stupocaulon*. The amphipods were removed by dipping and rinsing the fronds for a few minutes in seawater. From these fronds, small fragments of algae were removed, standardized by their volume as measured in a pipette, and subsequently dried on paper towels for 30 s and weighed on an analytical balance.

The fragments were placed in pairs, one in each end of a glass container, with a volume of 155 ml. Then, one amphipod was introduced. Ten replicates were used for each species of amphipod. Ten controls (without amphipods) for each amphipod species were kept in the same conditions for the same period as for the replicates, with the objective of evaluating possible losses of algal biomass, independently of consumption by the amphipods (Szlávecz, 1985). After 24 h, the fragments of macroalgae were removed from the system, dried on paper towels for 30 s, and weighed again on an analytical balance. The estimated consumption of each alga by the amphipods was calculated by subtracting the mean value for algal mass remaining in the replicates with the amphipods, from the mass in the control replicates without amphipods.

In the habitat-selection experiment, ten plastic containers 30 cm in length, 20 cm in width and 10 cm tall and provided with aerators were used. Fragments of macroalga were added, with a different species in each end of the container. Ten amphipods of similar sizes were placed in each container with the two fragments of macroalgae. Ten replicates were used for each species of amphipod. The amphipods were allowed to acclimate for 24 h, in a 12 h light/dark cycle in an ambient temperature of 25°C. In order to check to which fragments of algae the individuals moved, and thus observe which substrate the species prefers, each fragment of algae was washed separately and then the individuals present were identified and counted. Because the experiments were conducted in a controlled environment and over a short period, no mortality of the amphipods was observed.

Data analyses

The taxonomic groups were expressed as number of individuals per gram of dry mass of *Sargassum* or *Galaxaura,* to standardize the abundance data. To compare the natural densities of individuals per algal species, the Mann-Whitney test for independent samples was used.

The feeding preference of each species was evaluated by comparing the amount of algae consumed, through the T test for paired samples. To test the selection of substrate, a chi-square test (χ^2) was used to compare the proportions found in the experiment on substrate selection.

Results

Characterization of phytal macrofauna

A total of 1,240 individual amphipods were collected, 476 on *Sargassum filipendula* and 764 on *Galaxaura stupocaulon*. The most abundant species on *S. filipendula* was *Hyale nigra*, which comprised 52% of the total of amphipods encountered. On *G. stupocaulon* the most abundant species was *Cymadusa filosa*, which comprised 66% of the total organisms. The less-numerous species on *S. filipendula* were *Ampithoe ramondi* Audouin, 1826, *Sunampithoe pelagica* (Milne-Edwards, 1830), and *C. filosa*. On *G. stupocaulon*, *H. nigra*, *S. pelagica,* and *A. ramondi* were less abundant (Table 1).

Table 1. Amphipods recorded on fronds of the macroalgae *Sargassum filipendula* and *Galaxaura stupocaulon*, with their total and relative (%) abundances. Ind = number of individuals.

Family/Species	*Sargassum filipendula*		*Galaxaura stupocaulon*	
	Total (Ind)	%	Total (Ind)	%
Hyalidae				
Hyale nigra	247	52	41	6
Ampithoidae				
Cymadusa filosa	84	18	506	66
Ampithoe ramondi	69	14	170	22
Sunampithoe pelagica	76	16	47	6
Total	476	100	764	100

Comparison of natural densities

The Mann-Whitney test indicated significantly higher densities of *C. filosa* ($U = 46$; $p = 0.0001$) and *A. ramondi* ($U = 86$; $p = 0.0061$) on *Galaxaura* in relation to *Sargassum. Hyale nigra* ($U = 139$; $p = 0.2257$) and *S. pelagica* ($U = 160.5$; $p = 0.5593$) did not show significant differences in their densities between the two algae (Fig. 2).

Habitat selection and feeding preference

In the habitat-selection experiment, when fragments of both algae were offered, *C. filosa* showed a preference for fragments of *S. filipendula* as a substrate ($\chi^2 = 16$; g.L = 1; $p < 0.05$), with 70% of the individuals associated with *S. filipendula* and 30% with *G. stupocaulon* (Fig. 3). Likewise, *C. filosa* showed a significantly greater feeding preference for *S. filipendula* over *G. stupocaulon* ($t = 1.93$; g.L = 9; $p < 0.05$) (Fig. 4).

Hyale nigra showed no significant preference for either of the algae offered as a substrate ($\chi^2 = 0.64$; g.L = 1; $p > 0.05$): at the end of the experiment 46% of the individuals were associated with *S. filipendula* and the remainder with *G. stupocaulon* (Fig. 3). In relation to feeding preference, no significant differences were noted in the consumption of *S. filipendula* and *G. stupocaulon* ($t = -1.19$; g.L = 9; $p > 0.05$) (Fig. 4).

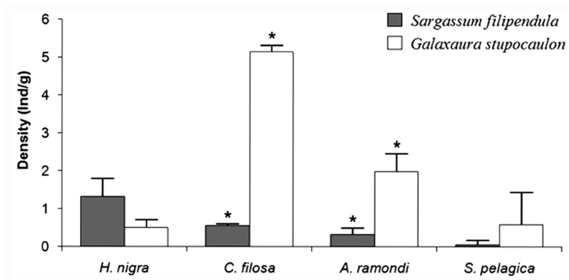

Figure 2. Mean density (+SE) of amphipod species on the macroalgae *Sargassum filipendula* and *Galaxaura stupocaulon*. *Indicates significant differences among macroalgae.

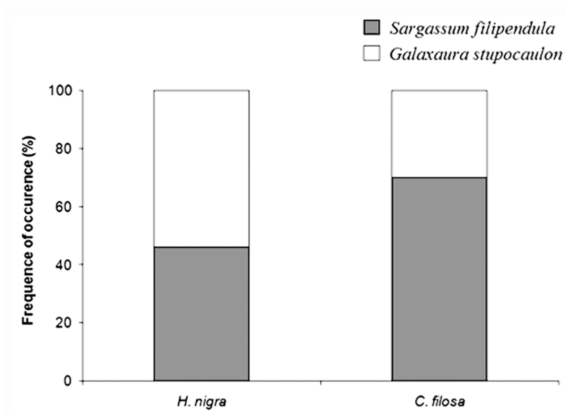

Figure 3. Frequency of occurrence of *Hyale nigra* and *Cymadusa filosa* on fragments of the macroalgae *S. filipendula* and *G. stupocaulon* at the end of the preference experiment.

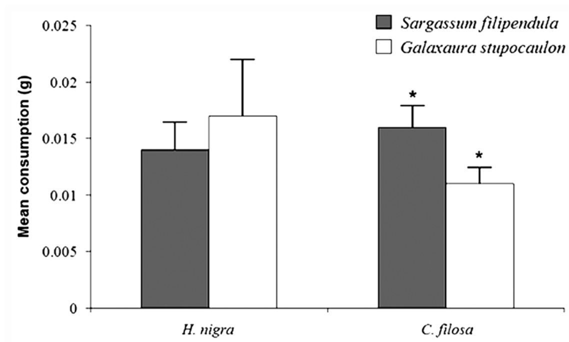

Figure 4. Mean consumption (+ SE) of *Sargassum filipendula* and *Galaxaura stupocaulon* by the amphipods *Cymadusa filosa* and *Hyale nigra*. *Indicates significant differences among macroalgae.

Discussion

Our results indicate that the ampithoid *Cymadusa filosa* showed a preference for certain types of macrophytes as food or habitat. However, habitat selection by *C. filosa* differed in the laboratory and in the field. The hyalid *Hyale nigra* showed no preference for either alga as a feeding resource or substrate.

In the field, *C. filosa* and *Ampithoe ramondi* showed significantly higher densities on *Galaxaura stupocaulon*. However, the laboratory experiments indicated a preference for food and habitat on *Sargassum filipendula*. Many experiments have established that the nutritional quality and chemical content of algae, in addition to the morphological characteristics and size of the amphipods, can determine feeding preferences (Nicotri, 1980; Brawley, 1992). However, the divergence between the results from the field observations and from the laboratory experiments suggests that for *C. filosa*, the feeding pattern and habitat selection could be affected by external characteristics of the algae. This implies that the feeding preference and the capacity to use the habitat for growth could have evolved in conjunction.

Therefore, the dominance of *C. filosa* on *G. stupocaulon* in natural conditions could be related to the use of algae as a refuge against predation. According to Hay *et al.* (1990), the value of algae as a refuge or shelter against predation can be especially important for the evolution of the use of host algae by herbivorous amphipods. The presence of predators frequently restricts the aquatic prey to the refuge that offers the most protection, even though it may have a low foraging value (Mattingly and Butler, 1994).

The regulation of amphipod populations through predation is an important factor for selection in a phytal community (Nelson, 1979), responsible for molding the characteristics of prey such as morphology, physiology, behavior and life cycle (Mattingly and Butler, 1994). According to Wakabara *et al.* (1996), the density of amphipod predators is higher in the colder months, as in the period of sample collection, which would increase the predation pressure on the amphipods. This characteristic, together with the low mobility and relatively larger size of *C. filosa* and *A. ramondi* in relation to other species of amphipods, makes them more susceptible to visual predators such as fish (Mattila, 1992; Isaksson *et al.,* 1994).

The more-compact structure of *G. stupocaulon* retains large amounts of sediments and nutrients (Iribarne, 1996), which may better protect the associated animals by hindering visual detection by predators (Stoner, 1980), favoring suspension-feeding and detritivorous species and providing raw materials for tubiculous species such as ampithoids to construct their homes (Norton and Benson, 1983).

The preference for *G. stupocaulon* may also be associated with the availability of the algae in the natural environment. According to Hughes (1980), the availability and abundance of a food supply affects the amount of time and energy necessary for the herbivore to locate its food. The banks of seaweed of Fortaleza Beach are not distributed homogeneously, with patches of other species of algae (unpublished data). The bank of *G. stupocaulon* sampled was relatively isolated by a sandbar, around 50 m from the bank of *S. filipendula*. The low mobility of the tubiculous species *C. filosa* and *A. ramondi* could have caused an aggregation effect due to the isolation of the bank of *G. stupocaulon*, resulting in a higher density of these species at that location.

In the experiment, the supply of *S. filipendula* as a substrate and feeding resource without the pressures in the natural environment could have influenced the preference for this alga by *C. filosa*, such that the nutritional quality of *S. filipendula* could have been a determining factor in the choice of algae. Jernakoff *et al.* (1996) showed that *S. filipendula* has good nutritional quality and palatability, which could favor the choice of this alga by herbivorous amphipods. The use as a preferential habitat and the consumption of brown algae has been reported for many ampithoid species (Hay *et al.,* 1990; Duffy and Hay, 1991; Cruz-Rivera and Hay, 2001).

Sunampithoe pelagica showed a different pattern from the other ampithoids, with low density on *G. stupocaulon*. This may be associated with the presence of *C. filosa* and *A. ramondi*, which are more aggressive and larger (Brawley and Adey, 1981) and might competitively exclude *S. pelagica*.

For *Hyale nigra*, the lack of feeding preferences and habitat selection in both the field and the laboratory may be related to the omnivorous habit of the species. Other studies recorded the highly mobility and wide distribution of *H. nigra* on different substrates, and also the use of a variety of food items (Tararam *et al.,* 1985; Ruffo, 1998).

We conclude that in natural conditions, the choice of habitat and the feeding preference of ampithoids, especially *C. filosa*, are mainly influenced by local environmental characteristics. It is probable that the search for food and the selection of habitat are determined by structural characterisitics of the algae, which offer shelter and protection from predators. For *H. nigra*, apparently environmental pressures were not the principal factors that influenced its feeding preference and habitat selection, which were possibly more related to its high mobility and varied diet.

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