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# Amphipods on seaweeds: partners or pests?

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**Summary.** Herbivorous marine amphipods have been implicated as important grazers on filamentous and ephemeral algae, and thus as beneficial to macrophytes in reducing overgrowth by epiphytic competitors. In North Carolina, USA, amphipods comprise 97% of all macroscopic animals inhabiting the abundant brown seaweed *Sargassum filipendula*, and peak in abundance between late winter and early summer. I used outdoor tank experiments to test the species-specific impact of common phytal amphipods on the growth of *Sargassum* and its epiphytes. The results show that seaweed-associated amphipods are a trophically diverse group that could either increase or decrease host fitness depending on their feeding preferences. The amphipods *Ampithoe marcuzii, Caprella penantis*, and *Jassa falcata* each significantly reduced growth of epiphytes on *Sargassum* plants relative to amphipod-free controls, while *Ericthonius brasiliensis* had no significant effect on *Sargassum* or its epiphytes. However, amphipod grazing was not necessarily beneficial to *Sargassum*. *A. marcuzii* consumed *Sargassum* in one outdoor tank experiment, reducing its mass by 11%, while *Sargassum* plants without amphipods grew by 81%. Epiphytes (mostly diatoms and the filamentous brown alga *Ectocarpus siliculosus*) and detritus remained abundant on these plants suggesting that *A. marcuzii* preferred the host to its epiphytes. Similarly, when given simultaneous access to *Sargassum* and to several common foliose and filamentous epiphytes in the lab, *A. marcuzii* ate *Sargassum* almost exclusively. The other three amphipods ate no macroalgae. In contrast to *A. marcuzii, C. penantis* consistently reduced epiphytes with no negative effect on *Sargassum*. Thus the species composition of the amphipod fauna can determine whether these animals increase or decrease seaweed fitness.

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Many seaweed communities are structured in part by the interplay between interspecific competition and grazing (Dayton 1971; Lubchenco 1978; Sousa 1979; Hay 1981, 1985; Lewis 1986). When grazers are absent from temperate rocky intertidal habitats, fast-growing ephemeral or filamentous algae often overgrow larger slow-growing seaweeds; when grazers are present, their preferential feeding on the ephemeral algae favors the establishment of perennial seaweeds (Lubchenco 1978, 1983; Sousa 1979). Conversely, in some (Carpenter 1986; Lewis 1986) but not all (Brawley and Adey 1981a) coral reef communities, macroalgae appear competitively superior to filamentous turfs and exclusion of larger grazers results in macroalgal dominance.

Overgrowth by epiphytes can reduce a macrophyte's growth and persistence through shading, interference with nutrient uptake, and increased susceptibility to breakage and tissue loss (Sand-Jensen 1977; Sousa 1979; Orth and van Montfrans 1984; D'Antonio 1985). If unchecked by grazers, ephemeral and "epiphytic" species may even dominate primary substrate to the exclusion of macroalgae and sessile animals, at least early in succession (Lubchenco 1978; Sousa 1979; Brawley and Adey 1981a; Dethier 1981).

The importance of grazing fishes (Hay 1985; Carpenter 1986; Lewis 1986; Horn 1989), sea urchins (Carpenter 1986; Morrison 1988), mollusks (Dayton 1971; Hawkins and Hartnoll 1983) and crabs (Sousa 1979) in structuring some seaweed communities is well documented. In addition to these conspicuous herbivores, seaweeds characteristically support faunas of small invertebrates that may achieve high densities. These phytal faunas are often dominated by amphipod crustaceans (Mukai 1971; Edgar 1983; Norton and Benson 1983; Gunnill 1985).

Despite extensive data on the species composition and abundance of these animals, details of their feeding biology are poorly known, and their potential impact on their host plants remains controversial (Schiel and Choat 1980; Brawley and Adey 1981b; Hay et al. 1987; Bell 1991).

Several studies indicate that amphipods and other mesograzers (small herbivorous invertebrates) can significantly reduce epiphyte growth on macroalgae and seagrasses (Howard 1982; Robertson and Mann 1982; D'Antonio 1985; Hootsmans and Vermaat 1985; Howard and Short 1986; Brawley and Fei 1987). In some cases removal of epiphytes by mesograzers stimulates macrophyte growth (Hootsmans and Vermaat 1985; Howard and Short 1986), thus mitigating the competitive supression of macrophytes by epiphytes (Brawley and Adey 1981a). These beneficial effects of mesograzers have been widely cited (Shacklock and Doyle 1983; Orth and van Montfrans 1984; D'Antonio 1985; Brawley and Fei 1987). However, in some circumstances, amphipods directly consume macroalgae and have catastrophic effects on seaweed communities, reducing both biomass and species richness (Jones 1965; Tegner and Dayton 1987). These conflicting results and the great diversity of amphipods (over 5500 species, Barnes 1980) suggest potentially important differences in feeding patterns between species. This diversity in the effects of amphipod feeding does not appear to be generally appreciated.

The large brown seaweed *Sargassum filipendula* is one of the most abundant algae on hard substrates in North Carolina, USA (Hay 1986), and supports dense populations of amphipods. In this paper I examine the feeding biology and potential impact of amphipods on *Sargassum*, asking: 1) What effects, if any, do common phytal amphipods have on the growth of this macroalga? 2) Are effects primarily positive, through reduction of epiphytes, or negative, through grazing on macroalgal tissue? 3) Do amphipod species differ significantly in their effects on the seaweed/epiphyte system?

## Methods

### *Field sampling*

Amphipods living on *Sargassum filipendula* were sampled bimonthly at Radio Island Jetty near Morehead City, North Carolina, USA (34°42′ N, 76°41′ W) between February 1987 and June 1988. Radio Island jetty is exposed to moderate wave action, and supports a diverse algal flora similar to that of natural hard substrates offshore at depths of 20–30 m (Richardson 1978; Peckol 1982). On each date I sampled 5 *Sargassum* plants, each consisting of a discrete individual attached to the rock by a holdfast (occasionally the plant was severed just above the holdfast). Plants were pulled from the substrate at depths of 0.5–1.5 m and immediately (within a few seconds) sealed underwater in individual plastic bags. I attempted to collect plants that were relatively free of epiphytes but this was impossible during some sampling periods. The samples were fixed in formalin and associated animals were removed by repeatedly washing the plant with tapwater and pouring the water through a 163 μm sieve. All amphipods retained by the sieve were counted and identified to species. Each plant was weighed after being spun in a salad spinner to remove excess water. Amphipod densities were expressed as a function of plant wet mass.

### *Amphipod feeding preferences*

Feeding studies were conducted with 4 of the 6 most abundant amphipod species (see Results), *Caprella penantis*, *Jassa falcata*, *Ericthonius brasiliensis*, and *Ampithoe marcuzii*. Abundant species that were not studied were *Corophium* spp., which are detritus/deposit feeders (Shillaker and Moore 1987), and *Stenothoe* sp., which is reported to feed on sessile animals (Barnard 1969).

To assess whether the four amphipod species studied could eat macroalgae, I offered each amphipod a choice of three algae that appeared to be commonly accessible to the animals in the field, and measured their grazing rates. The algae were *Sargassum filipendula* and two foliose species, *Punctaria latifolia* (Phaeophyta) and *Enteromorpha* sp. (Chlorophyta), that commonly grow as epiphytes on *Sargassum*. The latter two species are soft, bladed forms that I assumed would be easy for amphipods to eat. Amphipods were placed individually in 5-cm diameter plastic cups ($N = 11$ cups for *A. marcuzii*, $N = 20$ for each of the other 3 species) with about 50 ml of seawater and given one 7-mm diameter disk, cut with a cork borer, from the thallus of each of the three algal species. All algal pieces were free of visible epiphytes and detritus. After 45 h, the remaining area of each disk was measured by counting the number of points that fell on the remaining portion when looking through an ocular grid mounted in a Wild M-5 stereoscope (intact discs = 13 points each). In many cases, *A. marcuzii* grazed only partially through the *Sargassum* thallus, leaving some cell layers intact. Points falling over these areas were counted as half a point each. As the area of the discs did not change visibly in the absence of grazing, controls were unnecessary.

A second choice assay measured preferences of *A. marcuzii* among a wider range of algae. Individual *A. marcuzii* were placed in 12.5-cm diameter plastic bowls with about 400 ml of seawater, and were offered preweighed pieces of *Sargassum filipendula*, the common green macroalga *Codium fragile*, the foliose epiphytes *Punctaria latifolia* and *Enteromorpha* sp., and the filamentous brown epiphyte *Ectocarpus siliculosus*. All algal pieces were free of visible epiphytes and detritus. Pieces of the different algal species varied considerably in mass (17–45 mg for *Ectocarpus*, 143–316 mg for the dense *Codium*, other species were between these extremes) but were intended to be similar in volume to equalize their probability of being encountered by the amphipod in the bowl. Eighteen replicate bowls received amphipods, which were allowed to graze for 73 h. Seven controls, containing algae but no amphipods, were used to estimate algal mass changes caused by factors other than amphipod grazing.

### *Grazing experiments in outdoor tanks*

Experimental field studies of small invertebrates such as amphipods have been plagued by difficulties, stemming primarily from indirect effects of cage structures on the physical environment and predator access (Young et al. 1976; Virnstein 1978; Nelson 1979). As a compromise between minimizing these problems and still approximating natural conditions, I conducted experiments in outdoor tanks to assess the effects of the four common phytal amphipods on *Sargassum* and its epiphytic flora.

The tanks were trough-shaped, fashioned from a length of PVC pipe (28 cm inside diameter), cut in half longitudinally. Flat PVC plates cemented into the trough divided it into separate tanks, each 28 cm wide, 28 cm long, 19 cm deep, and 20 L in volume. Though physically connected, the tanks were independent, each with its own seawater source and drain. Natural seawater was pumped from adjacent Bogue Sound, passed through a sand filter where much of the coarser suspended material was removed, and flowed continuously through separate spigots positioned above each tank. Water exited each tank through a mesh-covered drain hole near the top of one wall. Turnover time of water in the tanks, estimated as filling rate in 10 tanks several months after the experiments, ranged from 5.8–18.8 min (mean $\pm$ SE = 10.0 $\pm$ 1.5). Tanks were covered with 5-mm plastic mesh which excluded larger debris

such as leaves, and reduced irradiance by 50% (P.E. Renaud, personal communication) to approximate more closely the situation in the turbid waters of coastal North Carolina. The tanks were thus exposed to ambient light and weather conditions and to sand-filtered seawater drawn directly from nearby (approximately 30 m) Bogue Sound. Assuming that amphipods are most likely to affect macroalgae when amphipod abundance is high and plant growth rates are relatively low (Norton and Benson 1983), the mesocosm experiments tested whether four amphipods could significantly affect the growth of *Sargassum* and its epiphytes at the amphipods' natural winter densities, as determined by sampling amphipods living on *Sargassum* in February and April 1987.

*Initially epiphyte-free plants.* The first experiment examined amphipod effects on *Sargassum* plants that had been cleaned of epiphytes. On 17 March 1988, *Sargassum* plants were collected from Radio Island jetty and cleaned of epiphytes and adherent detritus with a stiff-bristled paintbrush. This technique effectively removed all visible epiphytes without damaging the *Sargassum*. Plants were then defaunated by dipping in freshwater for a few minutes. Holmlund et al. (1990) showed that 3 one-minute treatments with freshwater remove 93–97% of the amphipods on *Sargassum* with no significant detrimental effects on the plants. Pieces (3.50–4.47 g) of these cleaned plants were spun in a salad spinner to remove excess water, weighed, and a 28-g lead weight was attached to the base of each plant piece (hereafter "plant") with a small cable-tie. The plants were then stored in the outdoor tanks overnight without amphipods. The next morning, these plants were transferred to 12.5-cm diameter plastic bowls filled with about 400 ml of seawater, and assigned haphazardly to one of five treatments, receiving: i) no amphipods (controls), ii) 8 *Ampithoe marcuzii* (2 amphipods/g wet *Sargassum*), iii) 80 *Jassa falcata* (20/g), iv) 80 *Caprella penantis* (20/g), or v) 16 *Ericthonius brasiliensis* (4/g). These amphipod densities corresponded to field densities measured on *Sargassum* in February–April 1987 (see Results). Amphipods were allowed to settle on the *Sargassum* plants in the bowls for 30–90 minutes before each plant, with its associated amphipods, was transferred to a separate outdoor tank. In general, large amphipods were used for ease in retrieving the animals at the end of the experiment. Six replicate plants in separate tanks were subjected to each treatment.

After five days the plants and amphipods were removed from the tanks, and tanks were searched carefully for amphipods clinging to the bottom and sides. In the lab, amphipods were removed from the plants by dipping in freshwater, and all live amphipods from both the plant and the tank were counted and identified. Epiphytes and detritus were removed by placing the plant in a bowl of water and carefully cleaning it of all adhering material with a stiff-bristled paintbrush. The cleaned plant was spun-dry in a salad spinner and weighed. The bowl of water containing epiphytes and detritus was poured through a 63 μm mesh sieve. The sieve contents were washed onto a preweighed filter paper, suction-filtered, dried overnight at 60° C, and weighed.

Since epiphytes were removed in freshwater, we assumed that most salt was removed from the plants and would not contribute significantly to the mass of dried epiphyes. To control for mass changes in the filter paper caused by the filtration and drying steps, five replicate "procedural controls" were performed. Five filters were weighed, placed in a Buchner funnel, and a few ml of tap water, containing no plant material or detritus, were filtered through each. The filters were then dried at 60° C overnight and reweighed. Mean mass change in these procedural controls was subtracted from the final mass of each experimental filter. The mass of epiphytes and detritus was obtained by subtracting the filter paper mass (measured at the beginning of the experiment) from this final mass. Epiphyte/detritus load was thus expressed as a dry mass.

*Initially fouled plants.* Many seaweeds are moderately to heavily fouled by epiphytes in the field. To determine whether amphipods could affect the growth of naturally-fouled *Sargassum* or its epiphytes, I conducted a second outdoor tank experiment. *Sargassum* plants were collected on 29 March 1988, defaunated, cleaned, and weighed (3.50–4.45 g) as before. They were then left in the outdoor tanks without amphipods for eight days. These plants developed a lush growth of epiphytes that appeared relatively uniform in species composition and coverage on all plants; epiphytes were not quantified at this stage to avoid damaging them. Homogeneity of epiphyte cover was intended to reduce the risk that final differences in epiphyte and *Sargassum* mass were due to initial differences in abundance or composition of the epiphytes. After the 8 d of epiphyte accumulation, amphipods were introduced to the plants ($N=6$ of each treatment) at the same densities used in the first experiment. Three replicate plants of each treatment were removed from the tanks after 7 d of grazing, and the other 3 replicates of each treatment were removed the following day. All amphipods in each tank were counted and identified. Epiphytes were removed as described above and epiphyte mass and *Sargassum* mass were measured.

*Distinguishing species effects from density effects.* Because the amphipods were stocked on the plants at their natural winter densities in the first two experiments, *Caprella penantis* and *Jassa falcata* were an order of magnitude more abundant than *Amphithoe marcuzii*. To distinguish the effects of different species from the effects of amphipod density, I set up a third outdoor tank experiment which compared the effects of *C. penantis* with those of *A. marcuzii* at initially equal densities (approximately 8/g wet *Sargassum*).

On 3 May 1988, a group of *Sargassum* plants was defaunated, cleaned, and weighed (2.76–3.48 h) as described above. They were then allowed to grow epiphytes in the outdoor tanks for ten days, after which each plant was assigned haphazardly to one of three treatments: i) control (no amphipods, $N=6$), ii) *C. penantis* (8 amphipods/g wet *Sargassum*, $N=6$), and iii) *A. marcuzii* (also 8/g, $N=5$). The plants were left in the tanks with amphipods for another ten days, then removed, and all amphipods in each tank were counted and identified. Epiphytes were removed as described above and epiphyte mass and *Sargassum* mass were measured.

## Results

### *Amphipod abundance*

Twenty-three species of amphipods were found on *Sargassum* plants from the field, comprising 97% of all macroscopic animals collected. *Caprella penantis* and *Jassa falcata* together made up 79% of the total amphipods (Table 1). These two species, along with *Ericthonius brasiliensis, Stenothoe* sp., *Corophium* spp., *Ampithoe marcuzii, Ampithoe longimana*, and *Gammaropsis sutherlandi* accounted for 98% of the total amphipods. Fifteen other amphipods each accounted for less than 1% of the total (Table 1).

*C. penantis, J. falcata, E. brasiliensis*, and *A. marcuzii* peaked in abundance between February and April in 1987, and declined to relatively low numbers during the summer (Fig. 1). The seasonal pattern in 1988 was more erratic; abundances peaked later than in the previous year, but as in 1987, *C. penantis, J. falcata*, and *A. marcuzii* had declined by late summer (Fig. 1).

### *Amphipod feeding biology*

Known or likely feeding modes for most of the amphipods found in this study are summarized in Table 1.

**Table 1.** Total abundances of amphipods found in this study, and their probable feeding modes. Feeding modes are listed in hypothesized decreasing order of importance for each species, and are based on gut content analysis, experiments, and/or observations of feeding by live animals. Superscript numbers refer to references describing feeding modes (see foot of Table). References in parentheses refer to other species in the same genus as the species listed here. For species with no entry under feeding mode, I was unable to find any reference for the genus. *C* = commensal/parasite with sessile invertebrates, *D* = detritivore (feeding from substrate), *F* = filter-feeder (feeding from water column), *H* = herbivore (macroalgae), *Hm* = herbivore (microalgae), *L* = "lignivore" (feeding on woody stipes of algae), *P* = predator

| Species | Feeding Mode | Total # found | % of total |
|---|---|---|---|
| *Caprella penantis* | D/Hm[a,d], F[d] | 30,006 | 45.2 |
| *Jassa falcata* | F[j], Hm[a,c] | 22,589 | 34.0 |
| *Ericthonius brasiliensis* | | 4,063 | 6.1 |
| *Stenothoe* sp. | C?[(b,i)] | 2,617 | 4.0 |
| *Corophium* spp. | F[(m)], D[(m)] | 2,296 | 3.5 |
| *Ampithoe marcuzii* | H[a] | 1,339 | 2.0 |
| *Ampithoe longimana* | H[e,f,g,k] | 946 | 1.4 |
| *Gammaropsis sutherlandi* | | 836 | 1.3 |
| *Gammarus mucronatus* | D[n,o], Hm[o], H[e,o] | 366 | <1 |
| *Elasmopus levis* | D[k], P[k] | 349 | <1 |
| *Amphilochus* sp. | C?[(b)] | 305 | <1 |
| *Paracaprella tenuis* | F[d], D/Hm[d], P[d] | 237 | <1 |
| *Batea catharinensis* | | 120 | <1 |
| *Caprella equilibra* | F/D[h], Hm[h], P[h] | 38 | <1 |
| *Heterophlias seclusus* | L[(i)] | 35 | <1 |
| *Ampithoe valida* | H[e,l] | 16 | <1 |
| *Dulichiella appendiculata* | D[n] | 15 | <1 |
| *Caprella* spp. (juveniles) | | 14 | <1 |
| *Cerapus tubularis* | | 13 | <1 |
| *Microdeutopus* sp. | | 9 | <1 |
| *Microprotopus raineyi* | | 7 | <1 |
| *Biancolina* sp. | L[i] | 4 | <1 |
| *Lembos smithi* | F/D[(m)], Hm[(m)], P[(m)] | 3 | <1 |
| *Atylus* sp. | | 3 | <1 |
| Unidentified juveniles | | 102 | <1 |
| Total | | 66,333 | |

[a] This study, [b] Barnard 1969, [c] Brawley and Fei 1987, [d] Caine 1974, [e] Duffy 1989, [f] Hay et al. 1987, [g] Holmes 1901, [h] Keith 1969, [i] Myers 1985, [j] Nair and Anger 1979, [k] Nelson 1979, [l] Nicotri 1977, [m] Shillaker and Moore 1987, [n] Smith et al. 1982, [o] Zimmerman et al. 1979

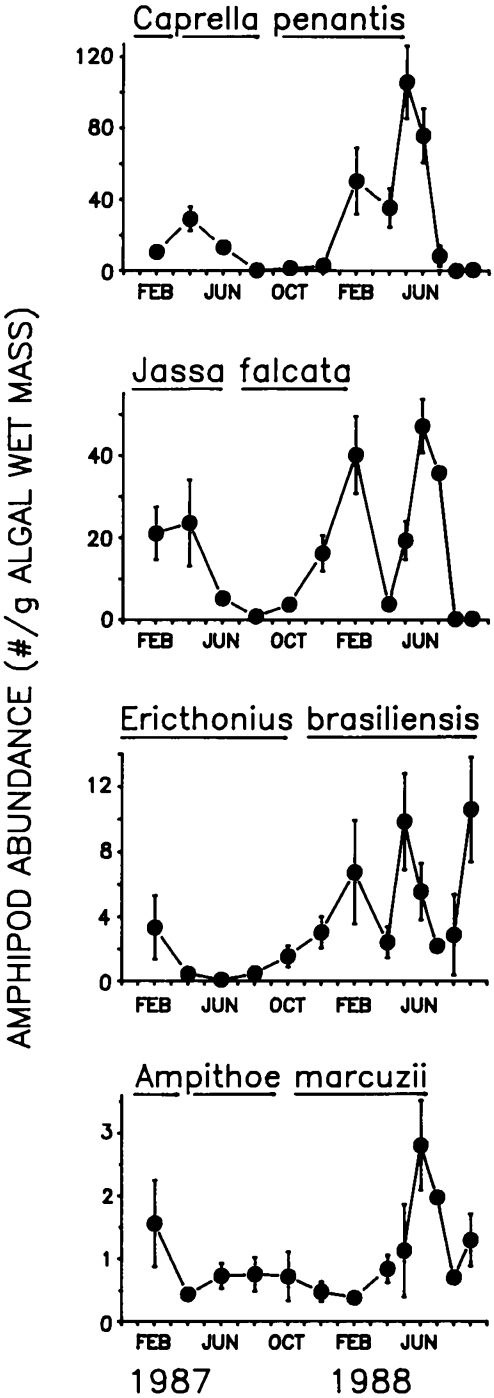


**Fig. 1.** Seasonal abundance patterns of four common amphipod species associated with the brown seaweed *Sargassum filipendula* in North Carolina, USA. Each point represents the mean (±1 SE) of 5 plants

Of the four amphipod species assayed here (*Caprella penantis, Jassa falcata, Ericthonius brasiliensis*, and *Amphithoe marcuzii*), only *A. marcuzii* ate significant amounts of *Sargassum* or its macroscopic epiphytes (Fig. 2); mean loss in area of algal discs was significantly different from zero for *Sargassum* ($P<0.001$, t-test) and *Punctaria* ($P<0.002$, t-test) exposed to *A. marcuzii*. Feeding preference of *A. marcuzii* among the 3 algae could not be directly tested with ANOVA since the 3 treatments (algal species) were simultaneously available in each replicate and were therefore not independent (Peterson and Renaud 1989). Grazing losses were not significantly different from zero ($P>0.05$, t-test) for any alga exposed to the other 3 amphipod species (Fig. 2).

When offered a wider range of algae, including the abundant filamentous epiphyte *Ectocarpus siliculosus* and the green macroalga *Codium fragile*, *A. marcuzii* again grazed *Sargassum* (Fig. 3). *Sargassum* was the only species in which mass loss in replicates exposed to amphipods ($N=18$) was significantly greater ($P=0.0004$, Mann-Whitney U-test, after an F max test showed unequal variances) than in amphipod-free controls ($N=7$). The estimated mass of *Sargassum* eaten (i.e. mean mass change in replicates exposed to amphipods minus mean

mass change in amphipod-free control replicates) was approximately five times that of any other algal species, though relative preference could not be tested rigorously (see above). Small amounts of grazing damage were visible on the foliose epiphytes Punctaria and *Enteromorpha*. The filamentous epiphyte *Ectocarpus* and the macroalga *Codium* appeared untouched.

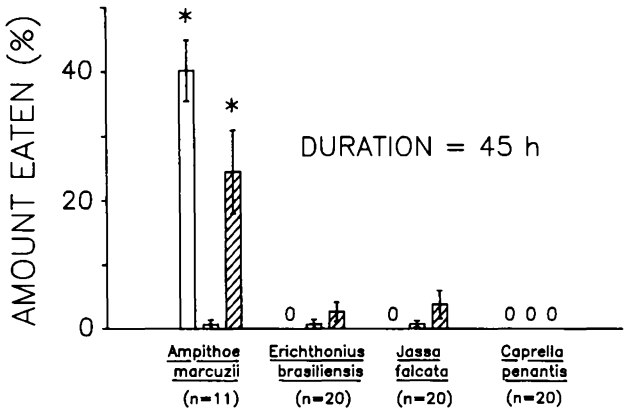


**Fig. 2.** Grazing by four *Sargassum*-associated amphipods on *Sargassum filipendula* and two common foliose epiphytes, *Enteromorpha* sp. and *Punctaria latifolia*, when offered together in a choice assay. Grazing was measured as change in surface area of algal discs. Bars represent means (±1 SE). A zero above the x-axis indicates that none of that alga was eaten. An asterisk above a bar indicates that the mean is significantly different from zero ($P<0.05$, t-test). Differences among algal species in estimated amount eaten were not tested explicitly due to non-independence of treatments (Peterson and Renaud 1989). □ *Sargassum*; ▨ *Enteromerpha*; ▨ *Punctaria*

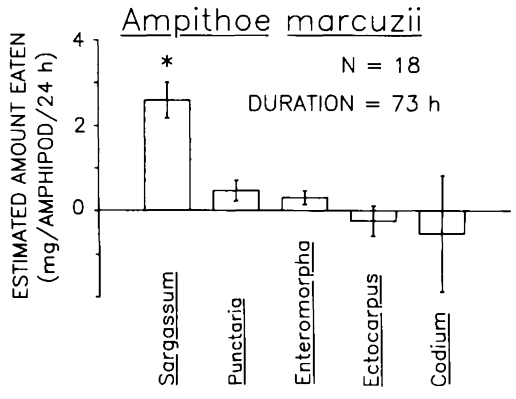


**Fig. 3.** Grazing by the amphipod *Ampithoe marcuzii* on five common algae, when offered together in a choice assay. Estimated amount eaten = mean mass change in replicates with amphipods ($N=18$) minus mean mass change in amphipod-free replicates ($N=7$); SE of each mean is calculated from the pooled variance [$(SS_1+SS_2)/(DF_1+DF_2)$, Zar 1974] of amphipod and control replicates. An asterisk above a bar indicates that mean mass loss in replicates with amphipods is significantly different from mean mass loss in replicates without amphipods ($P<0.05$, t-test, or Mann-Whitney U-test where an F test indicated unequal variances). Differences among algal species in estimated amount eaten were not explicitly tested due to non-independence of treatments (Peterson and Renaud 1989)

*Grazing experiments in outdoor tanks*

*Initially epiphyte-free plants.* When stocked at natural densities on cleaned *Sargassum* plants in the outdoor tanks, three of the four amphipod species significantly reduced accumulation of epiphytes ($P<0.05$, Kruskal-Wallis and non-parametric SNK tests, after an F max test showed unequal variances, Fig. 4). After five days in the tanks, control *Sargassum* plants (without amphipods) had accumulated a noticable load of epiphytes and associated detritus. Microscopic examination of several of these plants suggested that the most common epiphytes, in decreasing order of abundance (volume),

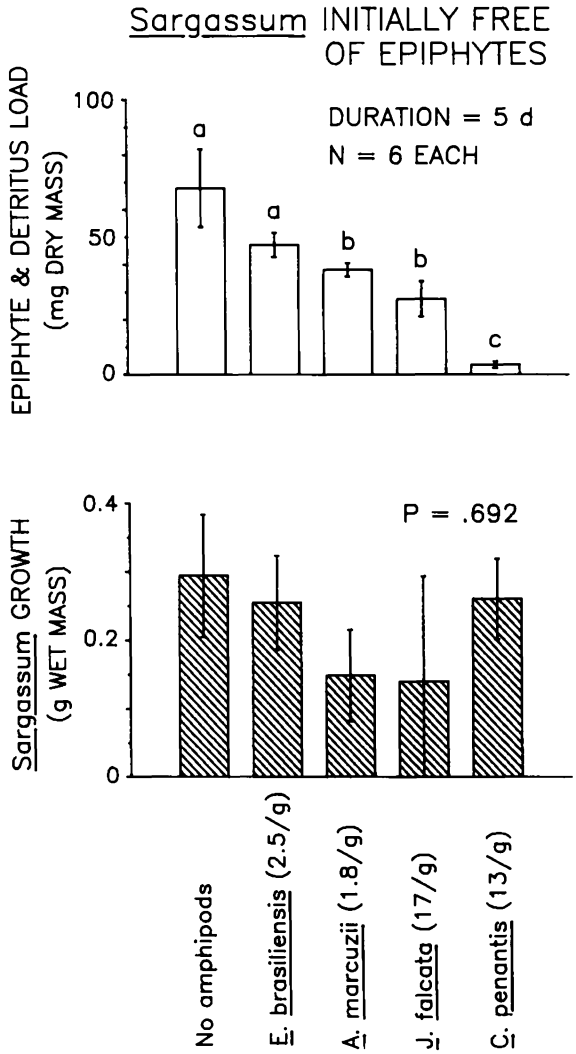


**Fig. 4.** Change in mass (mean ± 1 SE) of initially epiphyte-free *Sargassum* plants and net accumulation of epiphytes after 5 d in outdoor tanks, either exposed to one of four amphipod species at natural densities (measured in February–April 1987) or in the absence of amphipods ($N=6$ each). Effective densities (mean of initial number and final number/initial mass of *Sargassum*, see Table 2) of amphipods during the experiment appear in parentheses after each species. Initial masses of *Sargassum* plants ranged from 3.50–4.47 g wet mass. Bars with the same letter above them do not differ significantly at $\alpha=0.05$ (Kruskal-Wallis and nonparametric SNK tests). *P*-value in the lower graph is from ANOVA

were the filamentous brown alga *Ectocarpus siliculosus*, the diatom *Licmophora* sp., and the filamentous red alga *Polysiphonia harveyi*. In contrast, *Sargassum* plants stocked with *Caprella penantis* supported only 6% of the epiphyte/detritus mass of controls at the end of the experiment (Fig. 4). *Ampithoe marcuzii* and *Jassa falcata* had significant but less drastic effects on the epiphytes of *Sargassum*, with epiphyte/detritus masses 41% and 56% of control values respectively (Fig. 4). *Ericthonius brasiliensis* had no significant effect on the epiphyte/detritus load of *Sargassum*.

Mortality was high for *C. penantis* and *E. brasiliensis* during this experiment (Table 2), possibly because the initially epiphyte-free plants and sand-filtered seawater contained little detrital and microalgal food. Because amphipod density changed during the experiment, the effective density of amphipods (#/g wet *Sargassum*) in each replicate was defined as the mean of the initial and final amphipod abundances, divided by the initial *Sargassum* wet mass. Water occasionally flooded over the dividers separating adjacent tanks, allowing some movement of amphipods between tanks (contamination). These were less than 25% of the amphipods in any treatment (Table 2). No amphipods of species other than those stocked in the experiment recruited to the tanks, and the large sizes of all amphipods retrieved at the end of the experiment suggested that there had been no recruitment of stocked species either, with the exception of two juvenile *A. marcuzii* presumably released by one of the stocked females.

There was no significant difference in *Sargassum* growth among the different treatments ($P = 0.692$, ANOVA, Fig. 4).

*Initially fouled plants.* After 8 d in the mesocosm tanks without amphipods, *Sargassum* plants had developed a lush growth of epiphytes, dominated in volume (estimated visually) by the diatom *Tabellaria* sp. After a subsequent 7–8 d with natural densities of amphipods, only *Caprella penantis* and *Jassa falcata* had significantly decreased epiphyte load on the plants relative to amphipod-free controls ($P < 0.05$, Kruskal-Wallis and non-parametric SNK tests, after an F max test showed unequal variances, Fig. 5). Mean mass of epiphytes on *C. penantis*-stocked plants was 25%, and on plants with *J. falcata* was 69%, of controls. Epiphyte loads on plants stocked with *Ericthonius brasiliensis* or *Ampithoe marcuzii* were indistinguishable from controls.

Survival of *C. penantis* and *E. brasiliensis* was substantially better than in the previous experiment (Table 2), though still low for *E. brasiliensis*. Again there was some movement of amphipods between tanks, but no new recruitment of the stocked species. Seven *Elasmopus levis* and one *Ampithoe longimana* were found in the tanks at the end of the experiment; these presumably colonized through the water system. The number

**Table 2.** Changes in amphipod densities during the course of the outdoor tank experiments. All values expressed as mean ± 1 SE, except for initial numbers which were identical in each replicate of a treatment. $N = 6$ for all treatments except the *A. marcuzii* treatment in experiment 3 ($N = 5$). Effective number = average of the initial and final numbers for each replicate. Effective density = effective number/initial *Sargassum* mass for each replicate. Contaminating amphipods = amphipods that immigrated from other tanks + amphipods recruited from the seawater system

| Experiment, Treatments | Initial # | Final # | Effective # | Effective density (#/g algae) | Contaminating amphipods (#) |
|---|---|---|---|---|---|
| 1) *Sargassum* initially epiphyte-free<br>Amphipods at natural densities | | | | | |
| No amphipods | 0 | – | – | – | 0.8 ± 0.4 |
| *E. brasiliensis* | 16 | 4.3 ± 1.4 | 10.2 ± 0.7 | 2.5 ± 0.2 | 0.8 ± 0.5 |
| *A. marcuzii* | 8 | 7.0 ± 0.4 | 7.5 ± 0.2 | 1.8 ± 0.5 | 1.8 ± 0.7 |
| *J. falcata* | 80 | 60.5 ± 4.8 | 70.2 ± 2.5 | 17.2 ± 0.9 | 0.8 ± 0.5 |
| *C. penantis* | 80 | 28.8 ± 4.5 | 54.4 ± 2.2 | 13.6 ± 0.8 | 0.6 ± 0.2 |
| 2) *Sargassum* initially fouled<br>Amphipods at natural densities | | | | | |
| No amphipods | 0 | – | – | – | 0.8 ± 0.5 |
| *E. brasiliensis* | 16 | 8.2 ± 1.0 | 12.1 ± 0.5 | 3.0 ± 0.2 | 0.7 ± 0.3 |
| *A. marcuzii* | 8 | 6.5 ± 0.6 | 7.2 ± 0.3 | 1.8 ± 0.1 | 0.7 ± 0.3 |
| *J. falcata* | 80 | 57.7 ± 3.4 | 68.8 ± 1.7 | 15.2 ± 2.2 | 2.8 ± 1.3 |
| *C. penantis* | 80 | 65.3 ± 3.2 | 72.7 ± 1.6 | 15.7 ± 2.4 | 0 |
| 3) *Sargassum* initially fouled<br>Amphipods at initially equal densities | | | | | |
| No amphipods | 0 | – | – | – | 5.3 ± 1.1 |
| *A. marcuzii* | 26 | 11.8 ± 2.3 | 18.9 ± 0.5 | 6.3 ± 0.3 | 2.2 ± 0.6 |
| *C. penantis* | 26 | 2.5 ± 1.2 | 14.2 ± 0.6 | 4.4 ± 0.2 | 2.8 ± 1.1 |

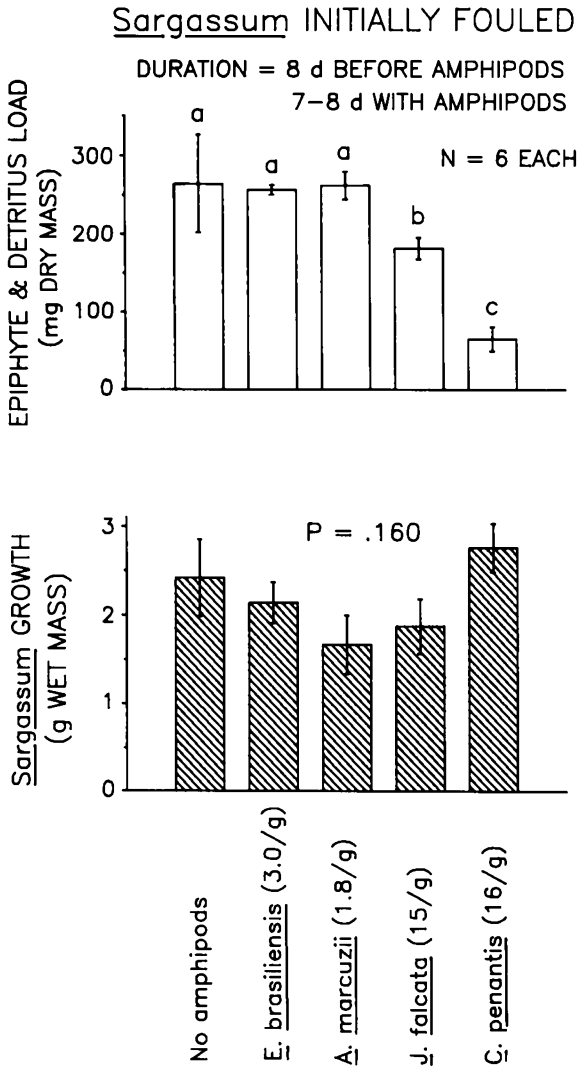


**Fig. 5.** Change in mass (mean ± 1 SE) of *Sargassum* plants and net accumulation of epiphytes after 8 d in outdoor tanks without amphipods (to accumulate an initial fouling load), followed by 7–8 d either exposed to one of four species of amphipods at natural densities or in the absence of amphipods ($N = 6$ each). Initial masses of cleaned *Sargassum* plants ranged from 3.50–4.45 g wet mass. Symbols as in Fig. 4

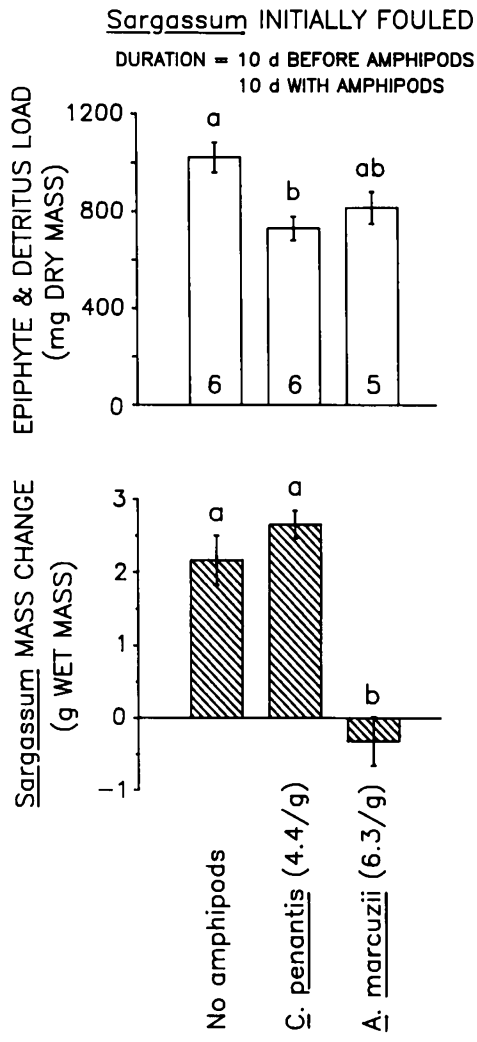


**Fig. 6.** Change in mass (mean ± 1 SE) of *Sargassum* plants and net accumulation of epiphytes after 10 d in outdoor tanks without amphipods (to accumulate an initial fouling load), followed by 10 d either exposed to one of two amphipods or in the absence of amphipods. Both amphipods were stocked at the same initial density (see Table 2). Initial masses of clean *Sargassum* plants ranged from 2.76–3.48 g wet mass. Numbers at the base of each bar in the upper graph are sample sizes. Symbols as in Fig. 4

of contaminating amphipods was less than 10% of the number of stocked amphipods in all treatments (Table 2).

There was no significant difference among treatments in the change in *Sargassum* mass during the experiment ($P = 0.160$, ANOVA, Fig. 5).

*Distinguishing species effects from density effects.* When stocked at initially equal densities (26 animals/plant), *Caprella penantis* and *Ampithoe marcuzii* had very different effects on growth of *Sargassum* and its epiphytes (Fig. 6). *C. penantis* significantly depressed epiphytes ($P < 0.05$, ANOVA with SNK test, Fig. 6) despite an effective density (4.4/g wet algae) only 1/17 that of the maximum recorded in the field (75.9/g in June 1987, Fig. 1). However, this depression was much more modest than in the previous experiments; mean epiphyte mass on *C. penantis*-stocked plants was 76% of control values. *C. penantis* had no significant effect on *Sargassum* growth ($P > 0.05$, SNK test, Fig. 6). In contrast, *A. marcuzii* did not significantly affect epiphyte load (though poor replication probably lowered the power to detect an apparent trend) but had a severe and highly significant impact on *Sargassum* ($P < 0.001$, ANOVA with SNK test, Fig. 6). While control and *C. penantis*-stocked plants gained an average 81% and 95% in wet mass respectively, *Sargassum* in the *A. marcuzii* treatment lost an average of 11%.

Amphipod survival was very low in this experiment, particularly for *C. penantis* (Table 2). Twenty-four juvenile *A. marcuzii* were recovered from the tanks but, as they were much smaller than the stocked individuals,

they were not included in the final number of *A. marcuzii*. Foreign amphipods retrieved from the tanks at the end of the experiment included 32 *Gammarus mucronatus*, 12 *Ampithoe longimana*, 9 *Corophium* spp., and 1 *Elasmopus levis*. Contaminating amphipods represented less than 20% of the effective number of stocked amphipods in all treatments (Table 2).

## Discussion

Mesograzers may increase macroalgal fitness by eating epiphytes that compete with their host (Brawley and Adey 1981a), or by facilitating host spore dispersal (Buschmann and Santelices 1987). They may also decrease macroalgal fitness by eating host tissue (Tegner and Dayton 1987). This study demonstrates that amphipod impact on the macroalga *Sargassum filipendula* depends on the species composition of the fauna. Three sympatric amphipods in this study had significant but divergent effects on *Sargassum* and its epiphytes. *Caprella penantis* and *Jassa falcata* reduced epiphyte growth in all experiments (Figs. 4–6) but did not graze *Sargassum* (Figs. 2, 4–6). Conversely, *Ampithoe marcuzii* moderately reduced epiphyte growth in one experiment (Fig. 4) but also significantly damaged *Sargassum* in another, despite the presence of abundant diatoms and filamentous epiphytes (Fig. 6). Though not significantly different, growth of *Sargassum* exposed to *A. marcuzii* was low relative to amphipod-free controls in the first two experiments as well, consistent with *A. marcuzii*'s damage to *Sargassum* in the third experiment.

Grazing rates in the tank experiments could have been affected by two potential artifacts. First, the effective density of *A. marcuzii* in the third experiment (Fig. 6) was 2–3 times higher than that measured in the field (Fig. 1). Second, grazing by *C. penantis* and *J. falcata*, which obtain part of their food by filter-feeding (Table 1), may have been increased by low concentration of suspended food. Though these factors might have changed absolute feeding rates, it is unlikely that they would have changed the relative feeding rates on *Sargassum* versus epiphytes.

The relationship between epiphyte grazing and host plant fitness has received much attention (Brawley and Adey 1981a; Orth and van Montfrans 1984). Because epiphytes can have important negative effects on their hosts (Sand-Jensen 1977; Sousa 1979; Orth and van Montfrans 1984; D'Antonio 1985), epiphyte grazing is widely considered to benefit host plants, as suggested by a wealth of observations on seagrasses (van Montfrans et al. 1984). In only a few cases, however, have authors presented convincing evidence that epiphyte grazing by natural densities of small invertebrates increases seagrass growth (Robertson and Mann 1982; Hootsmans and Vermaat 1985; Howard and Short 1986).

Amphipods and other mesograzers are commonly suggested to benefit macroalgae as well (Brawley and Adey 1981b; Shacklock and Doyle 1983; D'Antonio 1985; Brawley and Fei 1987). However, evidence for beneficial effects of mesograzers on seaweeds is scarce. Three previous studies are relevant. The clearest example comes from a coral reef mesocosm, where grazing amphipods enhanced macroalgal recruitment by clearing space of filamentous competitors; when amphipods were kept at low density by fish predators, filamentous algae inhibited the establishment of macroalgae (Brawley and Adey 1981a). Zeller (1988) found a strikingly similar pattern in the field when damselfish gardens, initially consisting of filamentous algae, were caged. Amphipod abundance increased inside cages, and macroalgae appeared to dominate at the expense of filaments; however, the role of amphipods in this process was not explicitly tested. Lastly, the only study to directly test amphipod impact on macroalgae in the field found that amphipods reduced epiphytes, but had no significant effect on host (*Gracilaria*) growth (Brawley and Fei 1987). Unfortunately, amphipod density in their removal treatments appears to have remained too high to allow epiphytes to reach densities that would inhibit host growth (see Brawley and Fei 1987, Table 8).

In agreement with Brawley and Fei's (1987) results, none of the amphipods in this study significantly increased *Sargassum* growth, despite consistently significant reductions in epiphyte mass by *C. penantis* and *J. falcata*. Possibly, as suggested by Brawley and Fei for the plants they studied, shallow-water seaweeds may be light-saturated in the field, such that a modest cover of epiphytes does not decrease productivity. A couple of caveats are in order, however. First, the small sample sizes and short duration of my experiments, and the low density of *C. penantis* in the third experiment (Fig. 6) may have obscured potentially beneficial effects. Second, these experiments considered only the effects of individual amphipod species; simultaneous presence of all amphipod species at natural densities might have resulted in enhanced macroalgal growth. However, this seems unlikely since grazing of *Sargassum* by *A. marcuzii* would likely offset any beneficial effects of the other amphipod species. Finally, the most detrimental effect of epiphytes on their hosts may be increased drag, and consequent higher risk of being torn or dislodged by waves (D'Antonio 1985). The potential role of epiphyte grazers in ameliorating this risk could be important, but has not been studied. In summary, stimulation of macroalgal growth or survival by mesograzers under field conditions remains to be shown.

The ability to eat filaments, diatoms, and other epiphytes is clearly widespread among amphipods. It is important to recognize, however, that amphipods are a trophically diverse group (Table 1). For example, within the family Ampithoidae, epiphyte feeders (Brawley and Adey 1981a), grazers on kelp (Griffiths 1979; Tegner and Dayton 1987) and other macroalgae (this study; Nicotri 1977; Zimmerman et al. 1979; Norton and Benson 1983; Brawley and Fei 1987), and stem borers (Myers 1974) are found. Unlike grazing gastropods (Steneck and Watling 1982), herbivorous amphipods show no obvious differences in mouthpart morphology that could be used to predict their diets. Even within the single genus, *Ampithoe*, species differ in feeding pref-

erences among macroalgae, responses to seaweed secondary metabolites, and in use of different seaweeds as habitats (Duffy 1989). In contrast to studies focused on seagrasses, studies of amphipods on macroalgae routinely report grazing on the host (Moore 1977; Zimmerman et al. 1979; Norton and Benson 1983; D'Antonio 1985; Buschmann and Santelices 1987). Moreover, some amphipods feed at higher rates on macroalgae than on epiphytes and detritus, even when both are superabundant (*Ampithoe marcuzii*, this study; *Cymadusa compta*, Zimmerman et al. 1979). Indeed, grazing scars resembling those of *A. marcuzii* and/or *A. longimana* are ubiquitous on *Sargassum* plants in the field (personal observation). In this study, *Sargassum* plants exposed to *A. marcuzii* grazing were 54% smaller than amphipod-free controls, while epiphyte load was not significantly different in the two treatments (Fig. 6). The diversity in feeding patterns of seaweed-associated amphipods suggests that they could have equally diverse impacts on seaweed populations and communities, depending on their density and the species composition of the fauna.

Despite the destructive potential of some species, amphipod populations appear generally to be kept well below carrying capacity by predation (Van Dolah 1978; Young and Young 1978; Nelson 1979; Stoner 1980), and are probably rarely significant grazers on macroalgae in subtidal habitats. Though logistical difficulties have hampered field experiments on mesograzers, circumstantial evidence suggests that predators may mediate the potential impact of herbivorous amphipods on benthic communities as they do for better-studied sedentary herbivores (Dayton 1971; Ogden et al. 1973). When released from predation, amphipods can have significant to catastrophic effects on seaweed communities. For example, excluding fishes from damselfish territories resulted in increased amphipod abundance, decreased algal biomass, and a shift in algal species composition (Zeller 1988). On another coral reef, amphipods had no significant impact on algae when predators were excluded (Carpenter 1986), although amphipod abundances did not increase to nearly the levels common in temperate algal beds. In a kelp forest, exclusion of fishes with cages enhanced amphipod abundance and decreased abundance of ephemeral algae (Kennelly 1983). Most dramatically, amphipods destroyed entire kelp beds in California after El Nino reduced predatory fish populations (Jones 1965; Tegner and Dayton 1987). It is clear that the faunas of small invertebrates inhabiting seaweeds are a trophically diverse group, and generalizations about their ecological role should take this diversity into account.

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