Chemical defense in the seaweed *Dictyopteris delicatula:* differential effects against reef fishes and amphipods

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ABSTRACT: Many seaweeds produce chemicals that deter feeding by fishes and sea urchins. A growing body of evidence suggests that small, relatively immobile herbivores (mesograzers) such as amphipods, polychaetes, and ascoglossan gastropods are often unaffected by these compounds and may preferentially consume seaweeds that are chemically defended from fishes. We tested this hypothesis by examining the responses of reef fishes and amphipods to a mixture of 2 C_{11} hydrocarbons, dictyopterenes A and B, produced by the Caribbean brown alga *Dictyopteris delicatula.* This alga was intermediate in preference for reef fishes, and the dictyopterenes reduced fish grazing by a significant 40 %. In contrast, *D. delicatula* was highly preferred by a mixed-species group of amphipods and the dictyopterenes had no effect on their feeding. Despite the tendency for mesograzers to selectively consume some seaweeds that are chemically deterrent to fishes, true specialization by these or other marine herbivores appears to be rare in comparison with terrestrial systems. Plant-dwelling amphipods at our study site in the Grenadine Islands were found on, and consumed a variety of, macrophytes; they were not restrictively specialized to *D. delicatula.* Many terrestrial insects are very specialized feeders, sequester toxins from their food plants, and use these as direct defenses against predation. In contrast, sequestering of seaweed toxins by marine mesograzers appears to be relatively rare. However, the indirect advantage of living on seaweeds that are not eaten by fishes may be considerable. We hypothesize that mesograzers living on plants chemically defended from fishes will experience less predation than those living on plants preferred by fishes.

INTRODUCTION

In terrestrial communities, plant secondary metabolites play a large and evolutionarily important role in determining plant susceptibility to herbivore attack (Rosenthal & Janzen 1979, Denno & McClure 1983, Coley et al. 1985). In several instances, compounds that deter many herbivores attract and stimulate feeding by others (Rosenthal & Janzen 1979, Crawley 1983, Smiley et al. 1985). This is especially true for some specialist insects such as certain butterflies, moths, and beetles (Ehrlich & Raven 1965, Freeland & Janzen 1974) that prefer to feed on chemically-rich plants from which they sequester toxins that they use in their own defense (Brower 1969, Rothschild 1973).

The chemical ecology of marine plants has been studied less extensively than that of terrestrial plants; still, specialized herbivores that selectively feed on chemically defended plants appear to be relatively rare in marine systems (Lubchenco & Gaines 1981, Hay et al. 1987a, Hay & Fenical 1988). The apparent scarcity of more specialized marine herbivores may be an artifact of the emphasis in most previous marine studies on larger herbivores such as fishes and sea urchins, and the relative lack of attention to interactions between seaweeds and smaller, less mobile herbivores such as amphipods and polychaetes (hereafter called mesograzers). The mobility, size, and movement patterns of mesograzers are in many ways ecologically more similar to the insects discussed above (Hay et al. 1987a, 1988b).

Alternatively, it has been hypothesized (Hay & Fenical 1988) that fundamental differences between the life histories and recruitment patterns of marine versus terrestrial herbivores may account for the paucity of specialized marine herbivores. Many specialized terrestrial herbivores have mobile adult stages (e.g. butterflies) that search widely for appropriate host

plants, often cuing on compounds deterrent to more generalized herbivores, and very carefully place their less mobile young (e.g. eggs that hatch into feeding caterpillars) upon these plants (Gilbert 1975). In contrast, most marine herbivores have planktonic larvae that receive little, if any, aid from adults, spend considerable time drifting in the open sea before recruiting back into coastal habitats, and should then have a limited probability of finding a specific host plant upon their recruitment to the benthos. Since larvae may suffer very high rates of predation as they move from pelagic toward benthic environments (Gaines & Roughgarden 1987, Olson & McPherson 1987), they may be unable to extend their larval period to search carefully for appropriate host plants without risking much higher rates of predation. These factors may select for generalized feeders that can use a wide variety of plants and thus settle quickly once they re-enter appropriate coastal habitats.

Unlike the vast majority of other marine herbivores, amphipod (and other peracarid) crustaceans and some ascoglossan gastropods undergo direct development; their young do not pass through a planktonic larval stage (Barnes 1980). These young avoid many of the problems of locating a host plant and of being eaten while in the plankton. Herbivores that develop in this manner might be able to evolve a greater degree of feeding specialization than species that must go through a planktonic dispersal stage. A search for specialized marine herbivores might thus begin most profitably with the amphipods and ascoglossans. Indeed, it is well known that many ascoglossans feed on only one or a few genera of seaweeds (Jensen 1980), and at least 2 amphipods are reported to feed and live on only one or a few closely related host plants (Myers 1974, Lewis & Kensley 1982).

Two previous studies conducted in temperate latitudes addressed how seaweed defenses affect feeding by taxonomically diverse herbivores. These studies demonstrated that diterpene alcohols from the brown alga *Dictyota dichotoma* deterred feeding by fishes and a sea urchin, but either stimulated or did not affect feeding by an amphipod and a polychaete (Hay et al. 1987a, 1988b). As would be expected from the responses to chemistry, the amphipod and polychaete preferred to eat *D. dichotoma*, which was avoided by the fishes and sea urchin. Both the amphipod and polychaete involved in these studies build and live in mucilaginous tubes attached to their algal hosts. Such tube-dwelling mesograzers may spend considerable time on their host plant and are known to be heavily preyed on by fishes (Nelson 1979a, b, 1981, Stoner 1980, Brawley & Adey 1981, Edgar 1983). In contrast, larger herbivores feed from many different plants each day and are less clearly controlled by predation.

Differences in size, mobility, and susceptibility to predation led us to hypothesize (Hay et al. 1987a, 1988b) that small sedentary herbivores should select seaweeds primarily on the basis of their value as safe living sites, and secondarily on the basis of their value as foods, while most larger and more mobile herbivores should select seaweeds primarily on the basis of their value as foods. We reasoned that, since small herbivores suffer intense predation from both omnivorous and predatory fishes (Randall 1967, Nelson 1979a, b, 1981, Stoner 1980), mesograzers should experience strong selection to circumvent seaweed chemical defenses and to live on and eat seaweeds that are defended from, and thus not often grazed by, fishes.

The data presently available support this hypothesis but are limited in scope to those few herbivores that have been studied in coastal North Carolina, USA, and to the effects of 2 *Dictyota dichotoma* metabolites on their feeding. In hopes of assessing the generality of the contention that mesograzers often should be resistant to seaweed chemicals that deter fishes, we tested the hypothesis in a Caribbean coral reef habitat using fishes, amphipods, seaweeds, and seaweed metabolites that were taxonomically distant from those investigated in the previous temperate studies.

We asked the following questions: (1) Do amphipods selectively consume seaweeds that are low-preference foods for reef fishes? (2) What role do seaweed secondary metabolites play in determining the feeding pattern of fishes versus amphipods? (3) Is there evidence of host plant specialization among the amphipods in this system?

METHODS

Study site and organisms. *Dictyopteris delicatula* occurs throughout the Caribbean in a wide variety of habitats. It commonly grows epiphytically on other algae in shallow water but also occurs to at least 30 m deep (Taylor 1960). The plants used in our study grew in a dense band in the low intertidal at Mayreau Island in the Grenadines, West Indies. Within this turf of *D. delicatula* and associated algae (primarily *Sargassum hystrix* and a mixed species assemblage of *Dictyota* spp. and *Laurencia* sp.), amphipods were abundant. A haphazard collection of small crustaceans (955 individuals) from this turf during late July 1986 had the following composition: *Hyale macrodactyla* (84 %), *Elasmopus pectenicrus* (6 %), Isopoda (3 %), *Tethygenia longleyi* (2 %), *Ampithoe marcuzzi* (2 %), *Audulla chelifera* (1 %), and *Ampithoe* sp., *Stenothoe minuta*, *Lembos* sp., and *Lysianassa alba* (all less than 1 %). This natural mixed-species amphipod assemblage was used in our feeding assays in order to simu-

late the natural amphipod community occuring on plants in the field during the time of our tests. However it is likely that *H. macrodactyla*, the most abundant amphipod in our samples and a genus known to be herbivorous (McBane & Croker 1983, Paul et al. 1987, Buschmann & Santelices 1987), was responsible for most of the grazing in our experiments.

Field tests of algal susceptibility and chemical deterrance to fish grazing were conducted at Cannouan Island in the Grenadines. Herbivorous fishes observed in the area during our field experiments were primarily parrotfishes (Scaridae): *Scarus vetula*, *S. croicensis*, *S. taeniopterus*, *Sparisoma aurofrenatum*, *S. viride*, *S. chrysopterum*, and surgeonfishes (Acanthuridae): *Acanthurus coeruleus*, *A. bahianus*, *A. chirurgus*.

Chemical extraction and structural determination. Freshly collected *Dictyopteris delicatula* were mascerated in a blender with a 3:1 mixture of dichloromethane/methanol. The solvent was evaporated under reduced pressure and the residue fractionated by flash chromatography on silica gel, using increasingly polar mixtures of hexane and ethyl acetate. The material eluted with 5 % ethyl acetate in hexane contained a UV-absorbing product that was further purified by silica HPLC using 5 % ethyl acetate in hexane. Evaporation of the solvent provided a yellow oil that was used in the feeding experiments. Later, at Scripps Institution of Oceanography, samples of this oil were further purified by flash chromatography on silver nitrate impregnated silica gel (20 % silver nitrate), and eluted with 1 % diethyl ether in pentane to provide the odoriferous C_{11} hydrocarbons dictyopterene-A and dictyopterene-B (Fig. 1) in a 1:2 ratio. Their structures were established by comparison of their spectral data with previously published values (Moore et al. 1968, Pettus & Moore 1970).

We could not adequately determine the concentration of these compounds with the equipment available on the ship due to (1) incomplete extraction (after extraction the algae still had the characteristic smell of the dictyopterenes), (2) losses during evaporation of the extraction solvents (the dictyopterenes are volatile at room temperature and thus continually lost under vacuum), (3) losses during chromatography. Since many tropical seaweeds produce defensive compounds in concentrations of 0.5 to 2.0 % of algal dry mass (Hay & Fenical 1988) we tested the effects of the compounds (see below) at concentrations of 0.6 and 0.8 %.

Algal susceptibility assays: fishes. Susceptibility of 7 species of seaweeds – *Padina jamaicensis*, *Dictyopteris justii*, *Dictyopteris delicatula*, *Stypopodium zonale*, *Sargassum hystrix* (Phaeophyta); *Ulva lactuca* (Chlorophyta); *Halymenia duchassaignii* (Rhodophyta) – to grazing by herbivorous fishes was tested in the field by weaving a small (3 to 4 cm long) piece of each

alga, at 5 cm intervals, into a 0.5 m length of 3-strand polypropylene rope and fastening the rope to the bottom. Twenty-three replicate ropes were placed at a depth of ca 5 m on the reef slope at Cannouan Island. The 7 algal species were haphazardly arranged on the ropes and should have been equally apparent to fishes encountering the ropes. Grazing on these algae was allowed to continue for 3.5 h until we saw a clear distinction between the most and least susceptible plants. At the end of the experiment each species on every rope was recorded as either absent or still present. Similar methods have been used in previous studies (Hay 1984, Paul & Hay 1986). Data were analysed in a 2 × 7 contingency table by the simultaneous test procedure (Sokal & Rohlf 1981).

Algal susceptibility assays: amphipods. Susceptibility of the 7 algae to amphipod grazing was examined in the shipboard lab. A 1 cm diameter disc of each algal species was cut from the thallus with a cork borer and placed in a 100 ml plastic container with 25 to 40 amphipods (depending on size) from the mixed-species assemblage described above. Twenty-five of these containers were set up and the amphipods were allowed to graze for 57 h until a clear distinction could be seen between most and least susceptible algal species. The remaining surface area of each disc was then measured under a Wild M-5 stereomicroscope, equipped with an ocular grid, using a point-count method (each disc initially covered 39 points). After the cruise, preserved sample discs of each algal species were dried and weighed to determine the dry mass/area ratio. Since some of the algal species tested differed greatly in thickness, eating a large area of thin plants like *Ulva* sp. or *Dictyopteris delicatula* could have been equivalent on a mass basis to eating a small area of thicker plants like species of *Halymenia* or *Sargassum*. Therefore, the dry mass/area ratio was used to determine how much of each species had been eaten on a dry mass basis.

Within each replicate container, all 7 algal species were available simultaneously. This means that our
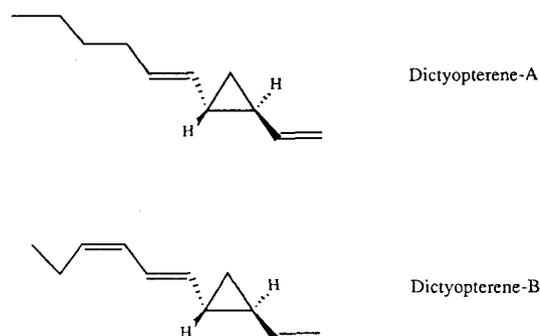

Fig. 1. Structures of the hydrocarbons dictyopterene-A and dictyopterene-B from *Dictyopteris delicatula*

treatments (= algal species) are not independent and therefore cannot be analysed using Analysis of Variance procedures (Hay et al. 1988b). Since contingency table analyses do not assume independence of treatments, we analysed the data with a 2 × 7 contingency table and simultaneous test procedure (Sokal & Rohlf 1981). To accomplish this, the 2 most heavily consumed species in each replicate were classified as high preference species and all other species in that replicate as less preferred species. Analyses were then run to determine which species differed from others in their frequency of occurrence as high preference species.

Chemical feeding deterrent assays: fishes. To test whether dictyopterenes deterred feeding by fishes in the field, the 1:2 mixture of dictyopterenes A and B was dissolved in diethyl ether and coated onto 6 cm strips of the seagrass *Thalassia testudinum*. Using a previously determined length/dry mass ratio for *T. testudinum*, we achieved a compound concentration of approximately 0.6 % of *T. testudinum* dry mass. *T. testudinum* strips coated only with ether served as controls. For the field experiment, 4 strips of dictyopterenes-coated *T. testudinum* were woven into a 0.5 m length of 3-strand polypropylene rope; the same number of control strips was woven into another rope and these 2 ropes were placed on the reef as a matched pair (0.25 to 0.5 m apart). Twenty-two replicate pairs were placed, at intervals of 2 to 4 m, on the reef at Dove Cay, near Cannouan Island. After 5.5 h, they were collected and the amount of each blade consumed was estimated by measuring its remaining length to the nearest 0.5 cm (see Hay et al. 1987b for elaboration of this method). This method primarily assays for grazing by parrotfishes (Lewis 1985, Hay et al. 1987b, 1988a).

Chemical feeding deterrence assays: amphipods. Effects of dictyopterenes on amphipod grazing were tested by coating the dictyopterene mixture onto 1 cm diameter discs of *Ulva* sp. at a concentration of 0.8 % of *Ulva* sp. dry mass. One dictyopterene-coated disc and one control disc (coated only with ether) were placed in a 100 ml plastic container with 15 amphipods taken haphazardly from the mixed-species group described above. Because the discs looked identical, treatment and control discs were marked by attaching them to small wires of slightly different lengths. As in the algal susceptibility assay, surface area removed from each disc was measured using a point-count method. This experiment was conducted twice, once with amphipods collected from a variety of algae in the intertidal turf at Mayreau Island, and once with amphipods taken only from *Dictyopteris delicatula*.

Field sampling of phytal amphipods. Four of the most common species of low intertidal algae (*Dictyopteris delicatula, Sargassum hystrix, Dictyota* sp., *Laurencia* sp.) at Mayreau Island were sampled in late July 1986 to determine amphipod abundance. Samples (2 to 10 g wet mass) were picked from the exposed rock, quickly sealed in individual plastic bags, and fixed in formalin. These were later washed through a 163 μm mesh sieve and plant surfaces were examined under a stereomicroscope for adhering animals which were added to the sieve contents. All animals were then sorted to species or to the lowest possible taxonomic category. Blotted wet mass of plant material in each sample was measured and amphipod densities were normalized to plant wet mass.

RESULTS

Feeding preferences of amphipods often differed from those of reef fishes (Fig. 2). Fishes consumed 100 % of the *Padina jamaicensis* and 87 % of the *Dictyopteris justii* individuals. *D. delicatula, Ulva lactuca, Stypopodium zonale,* and *Sargassum hystrix* were intermediate in preference (26 to 61 % of individuals consumed), and no *Halymenia duchassaignii* were consumed (see lines beneath the top histogram in Fig. 2 for significant differences). Amphipods preferentially consumed *D. delicatula* (intermediate for fishes) and to a lesser extent *H. duchassaignii* (none eaten by fishes). *P. jamaicensis* and *D. justii*, which were favored by fishes, were relatively low preference foods for amphipods. Species of *Ulva, Stypopodium,* and *Sargassum* tended to be low to intermediate preference foods for both fishes and amphipods. Statistical groupings for the amphipod feeding assays are denoted by the letter designation above the histograms in the center of Fig. 2. As discussed in the methods section, the data on the mass of each alga eaten could not be directly analysed. These data are, however, presented for comparative purposes in the lower histograms of Fig. 2; the pattern of consumption by amphipods was similar regardless of which way the data were presented.

Thin layer chromatography (TLC) of *Halymenia duchassaignii* showed no obvious secondary metabolites that were lipophilic and thus amenable to investigation with the equipment available on the ship. Our chemical investigations, therefore, focused exclusively on *Dictyopteris delicatula*.

At a concentration of 0.6 % ot *Thalassia testudinum* dry mass, the *Dictyopteris delicatula* dictyopterenes reduced fish grazing by a significant 40 % ($p = 0.016$, paired-sample t-test, Fig. 3). In contrast, these compounds had no effect on amphipod grazing (Fig. 4) even though the compounds were applied at a concentration 33 % greater than in the assay with fishes (i.e. 0.8 % of dry mass). Assays against amphipods gave similar results whether we used amphipods collected

from a mixed group of algal species, or only amphipods collected from *D. delicatula* (Fig. 4).

In late July 1986, amphipod assemblages on the 4 common seaweeds in the low intertidal at Mayreau Island were dominated by *Hyale macrodactyla*, with *Elasmopus pectenicrus* and members of the Ampithoidae (unidentifiable juveniles and females) being common but much less abundant (Fig. 5). Total densities of amphipods per g algal wet mass were similar for the species of *Dictyopteris*, *Dictyota*, and *Laurencia*; densities of all amphipod species were sig-
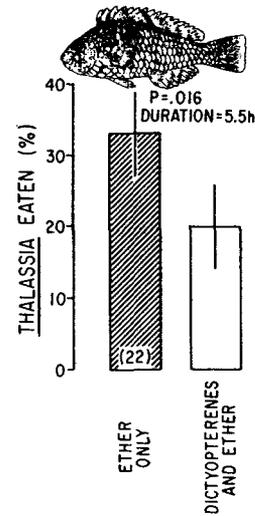
Fig. 3. Effect of dictyopterenes A & B, in a 1:2 ratio, on feeding by reef fishes in the field. Grazing was measured as the area removed from each *Thalassia testudinum* blade. Vertical bars: ± 1 standard error; *p*-value computed by paired-sample *t*-test. Sample size in parenthesis at base of histogram

Fig. 2. Consumption of seaweeds by reef fishes and amphipods when approximately equal amounts of 7 different species were synchronously available. Assays with fishes were conducted in the field and measured the number of individual pieces of each species that were totally consumed. Amphipod assays were conducted in the lab and measured grazing as the change in projected surface area of each alga; this was later converted to change in algal dry mass to avoid the bias caused by seaweeds with different area/mass ratios. Bottom histograms show the mean (± 1 standard error) mass eaten by amphipods; these types of data cannot be analysed directly (see methods section). Center histograms show these data arranged in a contingency table type of format that can be analysed. Letters above these histograms and the lines beneath the top histograms indicate species that do not differ significantly (*p* ≤ 0.05, 2 × 7 contingency table by the simultaneous test procedure
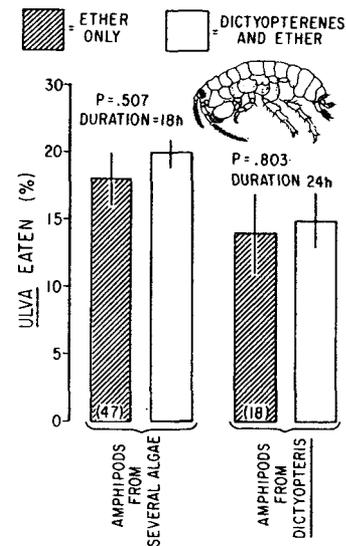
Fig. 4. Effects of dictyopterene mixture on feeding by a mixed-species assemblage of amphipods. Consumption was measured as the area removed from each disc of *Ulva* sp. *Left*: amphipods collected from several algal species. *Right*: amphipods collected exclusively from *Dictyopteris delicatula*. Symbols and statistical analyses are the same as in Fig. 3

nificantly lower on *Sargassum* sp. than on the other seaweeds (*p* < 0.05, Kruskal-Wallis test and non-parametric analog of the Student-Newman-Keuls test, Zar 1974). For the 3 most common amphipods, between-plant differences in density were as follows: (1) *Hyale macrodactyla*: Dictyota > Laurencia = Dictyopteris > Sargassum; (2) *Elasmopus pectenicrus*: Dictyopteris > Dictyota = Laurencia > Sargassum; and (3)

Ampithoidae: Dictyopteris = Dictyota > Laurencia > Sargassum (p ≤0.05, Kruskal-Wallis test and non-parametric analog of Student-Newman-Keuls test). Sargassum sp. was populated almost exclusively (354 out of 366 individuals) by Hyale macrodactyla, most of which were large adults. H. macrodactyla comprised 87, 62 and 82 % of the total amphipods on Dictyota sp., Dictyopteris delicatula and Laurencia sp. respectively. Given this, amphipods used in the 2 assays shown in Fig. 4 may have differed in recent history of feeding but probably did not differ much in species composition. While sorting our field samples we noted that the uneven scars of amphipod grazing were common on Sargassum sp. and D. delicatula, and relatively rare on Dictyota dichotoma and Laurencia sp. Samples of D. dichotoma appeared to contain more epiphytic filaments than the other algae.
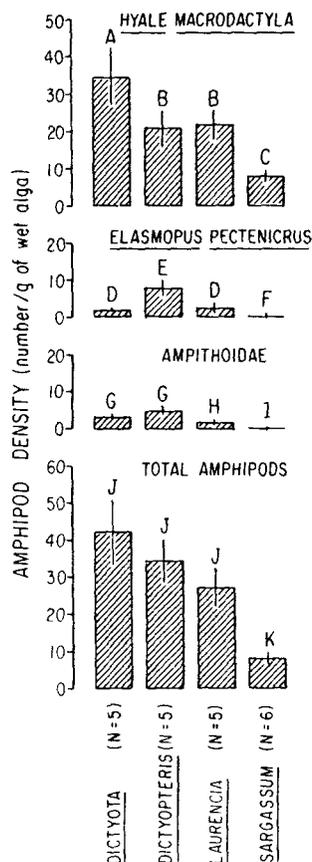

Fig. 5. Densities (normalized to plant wet mass) of the 3 most abundant phytal amphipods and of total amphipods on 4 common intertidal algae at Mayreau Island, Grenadines during late July 1986. Vertical bars: ± 1 standard error. Letters above each histogram designate amphipod densities that differ significantly among algal species (p ≤ 0.05, Kruskal-Wallis test and nonparametric analog of the Student-Newman-Keuls test). All tests were 1-way tests of how amphipod density differed as a function of algal species; tests do not assess differences among amphipod types on a single algal species

DISCUSSION

Some seaweeds that were rapidly consumed by fishes (Padina jamaicensis and Dictyopteris justii) were low preference for amphipods while some seaweeds that were relatively resistant to fish grazing (Halymenia duchassaignii and Dictyopteris deliculata) were preferentially consumed by amphipods (Fig. 2). The C_{11} compounds produced by D. delicatula significantly deterred fish grazing but had no effect on grazing by amphipods (Figs. 3 and 4). These findings are consistent with the hypothesis that many mesograzers may be resistant to seaweed chemical defenses that deter fishes and that these mesograzers may selectively live on and consume seaweeds that are avoided by fishes. Hay et al. (1987a, 1988b) documented similar patterns in the temperate Atlantic. The tropical amphipods, fishes, seaweeds, and chemicals used in this study all belong to groups that are only distantly related to those from the previous studies (Hay et al. 1987a, 1988b) yet the results are very similar. In still another case, Paul et al. (1987) demonstrated that the halogenated monoterpene, ochtodene, from the red seaweed Ochtodes secundiramea deterred feeding by fishes but was ineffective against the same group of amphipods examined here. These studies, involving distant geographic areas and taxonomically diverse plants, herbivores, and chemicals, provide a growing body of evidence for the generality of this pattern.

Most previous studies on the factors affecting herbivore feeding preferences have focused on how herbivores selectively choose plants that are most nutritious, or carefully avoid those that are most toxic (Vadas 1977, Carefoot 1980, Lobel & Ogden 1981, Lubchenco & Gaines 1981, Hay & Fenical 1988). In contrast to these, Price et al. (1980) speculated that herbivorous terrestrial insects might selectively consume plants upon which insect predators rarely foraged (i.e. plants that constitute relatively safe foraging sites for herbivorous insects). The feeding patterns demonstrated here and in other recent studies (Hay et al. 1987a, 1988b, Paul et al. 1987, Paul & van Alstyne in press) suggest that small marine herbivores may select foods and foraging sites primarily on the basis of predator avoidance.

Although the amphipods in this study selectively consumed Dictyopteris delicatula and were resistant to the dictyopterenes, we found no evidence for restrictive specialization to this particular host plant. Hyale macrodactyla was the most abundant amphipod on all 4 seaweeds that we studied (Fig. 5). Since species of this genus consume macrophytes (McBane & Croker 1983, Paul et al. 1987, Buschmann & Santelices in press) and since the other common species, Elasmopus pectenicrus, belongs to a genus described as a predator and detritivore (Nelson 1980), H. macrodactyla prob-

ably accounted for most of the feeding in our assays. *H. macrodactyla* density was highest on *Dictyota dichotoma*, intermediate on *Dictyopteris delicatula* and *Laurencia* sp., and lowest on *Sargassum* sp. *E. pectenicrus* was most abundant on *D. delicatula* but does not appear to be an important macrophyte grazer. Density of total amphipods and of each taxonomic category was lower on *Sargassum* sp. than on any of the other species. Thus, density of each amphipod type and of total amphipods showed significant differences across the seaweeds studied but there was no apparent specialization on *D. delicatula*.

These sorts of patterns are common among phytal amphipods, which often show relatively minor differences in community structure between host plant species (Stoner & Lewis 1985, Lewis 1987, Virnstein & Howard 1987) compared with the common specificity of terrestrial insects (Fox & Morrow 1981). Unlike the tube-dwelling amphipod and the polychaete examined in previous studies (Hay et al. 1987a, 1988b), *Hyale macrodactyla* is free-living and it does not build tubes. This lifestyle, together with the compact continuous turf of algae at Mayreau, probably allows easy movement among the various species of algae in the turf. Such rapid movement among plants by small crustaceans is known to occur in seagrass beds (Howard 1985, Virnstein & Curran 1986). Thus, while these amphipods thrive in a habitat dominated by chemically-rich genera such as *Dictyopteris*, *Dictyota*, and *Laurencia* (Hay & Fenical 1988), they are not restricted to any one of the species involved. In this sense, such mobile mesograzers may be ecologically different from their more sedentary herbivorous relatives that build tubes on or bore into seaweeds.

Although specialized marine herbivores appear to be relatively rare (Lubchenco & Gaines 1981, Steneck 1982, Hay & Fenical 1988), known ones are small, relatively immobile, and live on and selectively consume plants that provide them with some protection from their predators. Examples include the tube-dwelling amphipod and polychaete cases cited above, as well as (1) limpets that feed almost exclusively on seaweeds that provide stable attachment sites and thus lower the risk of predation (Phillips & Castori 1982, Steneck 1982), (2) ascoglossan gastropods that feed primarily on chemically rich green seaweeds (Jensen 1980), sequester deterrent compounds from these seaweeds, and use them in their own defense (Jensen 1984, Paul & van Alstyne in press), (3) amphipods that make, and live in, unusual bivalved domiciles cut from the terpene-rich brown alga *Dictyota dichotoma*; this alga is also their preferred food (Lewis & Kensley 1982), and (4) the amphipod *Amphitholina cuniculus*, which uses its specialized mandibles to bore into the tough stipe of the kelp *Alaria* sp., where it remains in burrows, presumably immune to fish predation (Myers 1974). Although ascoglossans and other opisthobranchs in the genus *Aplysia* commonly sequester and concentrate algal defenses (Faulkner 1984, Paul & van Alstyne in press), this does not appear to occur among the amphipods and polychaetes that have been studied to date (Hay et al. 1987a). These mesograzers appear to be less specialized in their feeding habits; they may indirectly reduce their susceptibility to predation by associating with plants that are rarely visited by their fish predators but they do not directly reduce predation by sequestering algal metabolites.

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