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CHEMICAL DEFENSE AGAINST DIFFERENT MARINE HERBIVORES: ARE AMPHIPODS INSECT EQUIVALENTS?[1]

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Abstract. The structurally similar diterpenoid alcohols pachydictyol-A and dictyol-E are produced by the brown seaweed *Dictyota dichotoma.* This seaweed and several related species that also produce these compounds are known to be relatively low preference foods for tropical fishes and urchins. We evaluated the effect of various concentrations of these compounds on feeding by the three common types of herbivores that co-occur with *Dictyota* in coastal North Carolina. Fish (*Diplodus holbrooki*), sea urchins (*Arbacia punctulata*), and a mixed species group of gammarid amphipods were offered pieces of the palatable seaweed *Gracilaria tikvahiae* coated with either (1) dictyol-E or pachydictyol-A dissolved in diethyl ether or (2) diethyl ether alone.

Dictyol-E significantly reduced consumption by fish and urchins at concentrations of 0.5 and 1.0% of algal dry mass, but had no effect on amphipod grazing. Pachydictyol-A significantly reduced fish grazing at the relatively high concentrations of 1.0 and 1.3% of plant dry mass; at 0.5% it tended to decrease grazing, but the effect was not significant (P = .07). Pachydictyol-A had no effect on urchin grazing and significantly increased amphipod grazing. When Pachydictyol-A was fed to fish as 1.0% of food dry mass, their growth rate was reduced by a significant 48%.

In feeding preference experiments with several seaweeds, *Dictyota* ranks low for fish and urchins but high for amphipods. This is consistent with the hypothesis that the secondary metabolites produced by *Dictyota* play a major role in determining its susceptibility to herbivores. The ability of amphipods to circumvent the chemical defenses of *Dictyota,* and the fact that the two species of algae most readily consumed by amphipods (*Codium* and *Dictyota*) were the two species least readily consumed by fish, suggest that predation and herbivory by fishes may be major factors selecting for amphipods that can live on, and eat, seaweeds that are unpalatable to fishes. Amphipods that fed on *Dictyota* did not appear to sequester the *Dictyota* metabolites; when exposed to fish predation, *Dictyota*-fed amphipods were eaten as readily as amphipods that had fed on an alga with no defensive chemistry.

Tubicolous amphipods and other small marine herbivores that may spend significant portions of their lives on only a few plants may be under very different evolutionary constraints than the larger, more mobile herbivores that commonly move between many plants. Several characteristics of these smaller, less mobile, and much less studied, marine herbivores suggest that they may be ecologically similar to terrestrial insects and may play a large, but presently unappreciated, role in structuring marine plant communities.

Key words: *algae; amphipods;* Ampithoe longimana; Arbacia punctulata; *chemical defenses;* Dictyota; Diplodus holbrooki; *feeding effects; herbivory; plant–herbivore interactions; secondary metabolites; terpenes.*

INTRODUCTION

Secondary plant metabolites play a large and evolutionarily interesting role in determining the susceptibility of terrestrial plants to attack by both vertebrate and invertebrate herbivores (Rosenthal and Janzen 1979, Coley et al. 1985). Although the defensive nature of many of these compounds has been clearly demonstrated, it is not unusual to find that some herbivores have evolved a tolerance to these compounds and selectively consume plants that are toxic to many other grazers (Rosenthal and Janzen 1979, Crawley 1983). Most of these specialist feeders tend to be small invertebrates of limited mobility such as the larvae of butterflies, moths, and beetles (Ehrlich and Raven 1965, Freeland and Janzen 1974). Several of these insects sequester the plant toxins and use them as a defense against their own predators (Brower 1969, Rothschild 1973).

In contrast to the well-studied interactions between

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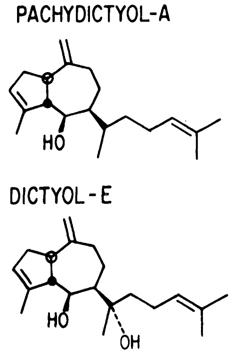

FIG. 1. The structure of the diterpene alcohols pachydictyol-A and dictyol-E.

terrestrial plant metabolites and herbivores, the effects of seaweed secondary metabolites on marine herbivores are largely uninvestigated. Most previous work on how secondary metabolites from seaweeds affect marine herbivores has been speculative or correlative (Norris and Fenical 1982, Hay 1984), and the few experiments on how specific compounds affect feeding by herbivores have been conducted primarily by chemists that used ecologically inappropriate test organisms or methodologies (see the examples of inappropriate tests cited in Hay 1984, Targett et al. 1986, and Hay et al. 1987). A very few ecologically relevant experiments have been conducted. However, these investigations have tested compounds against single species of herbivores, not against the diverse array of herbivores that normally encounter plants in the field. Investigations of this type include those of (1) Steinberg (1985) on how phenolics similar to those in kelps (Laminariales) deter the gastropod *Tegula funebralis,* (2) Geiselman and McConnell (1981) on how phenolics from rockweeds (Fucales) deter the gastropod *Littorina littorea,* (3) McConnell et al. (1982) on how several metabolites from tropical seaweeds affect feeding by the sea urchin *Lytechinus variegatus,* and (4) Targett et al. (1986) on how terpenes from tropical green algae affect feeding by the parrotfish, *Sparisoma radians.* Testing compounds against single herbivore species provides critical ecological and evolutionary data on how specific herbivores react to specific compounds but cannot provide adequate information on the relative protective value of these compounds under field conditions where the diversity of herbivores may be high. Since herbivores from unrelated taxa may have very different physiologies and foraging modes, the effectiveness of any single defensive characteristic may decrease as the diversity of herbivore types within the community increases (Lubchenco and Gaines 1981, Hay 1984, Gaines 1985). Additionally, no investigations have assessed how seaweed metabolites affect feeding by small, relatively immobile herbivores such as amphipods, isopods, and polychaetes, which could be ecologically similar to terrestrial insects in that they may be under strong selective pressure to evolve a tolerance to compounds that effectively deter larger and more mobile herbivores. In previous publications (Brawley and Adey 1981*a, b,* and others), these small herbivores have been called micrograzers. This term is potentially misleading since these herbivores are not microscopic. In this paper, we will refer to these small herbivores as mesograzers since this is more descriptive of their size and avoids confusing them with truly microscopic herbivores. Since mesograzers are subject to heavy predation (Nelson 1979*a, b,* 1981, Stoner 1980) and are consumed by fishes that also eat algae (Adams 1976, Stoner 1980), they might be predicted to be less susceptible to seaweed metabolites since an ability to live on and consume chemically defended seaweeds would provide them with a relatively safe habitat as well as a predictable food source. Thus, testing plant metabolites against a variety of potential consumers should significantly improve our understanding of how secondary metabolites affect the variable patterns of plant consumption that one often sees in the field.

In this investigation we study the herbivore deterrent properties of two structurally similar secondary metabolites (Fig. 1) that are produced by several species of fleshy brown algae in the order Dictyotales. We ask the following questions:

1) Do the diterpene alcohols pachydictyol-A and dictyol-E found in the Dictyotaceae function as herbivore deterrents?
2) If so, do herbivores behave differently toward these structurally similar compounds?
3) Are small, relatively immobile herbivores such as amphipods less susceptible to these chemical defenses than larger, more mobile herbivores such as fish and sea urchins?
4) Does chronic consumption of pachydictyol-A affect herbivore mortality or growth rate?
5) Can amphipods decrease their susceptibility to fish predation by consuming *Dictyota* and sequestering its defensive chemistry?

METHODS

Study site and organisms

All seaweeds and herbivores were collected from shallow (0.5–3 m deep) portions of a rock jetty located on Radio Island, near Beaufort, North Carolina, USA. From spring to fall, shallow portions of the jetty are dominated by a variety of seaweeds with *Sargassum filipendula, Dictyota dichotoma, Padina gymnospora* (=*P. vickersiae* in Taylor 1960), and *Codium fragile* being the most abundant species. *Hypnea musciformis, Chondria dasyphylla, Calonitophyllum medium, Rhodymenia pseudopalmata, Gracilaria tikvahiae,* and *Ulva* spp. are present but less common, and many of these species appear to decrease rapidly in abundance as omnivorous fishes (*Diplodus holbrooki, Lagodon rhom-*

boides, Monocanthus hispidus, and *Archosargus probatocephalus*) colonize the jetty in the summer.

Epifaunal amphipods are common inhabitants of most seaweeds on the jetty, but the density of amphipods decreases drastically in the spring and early summer as fish become abundant (Nelson 1979*b*). Although several species of amphipods occur on the jetty, the tubicolous amphipod *Ampithoe longimana* is the most common species (Holmlund 1984) and appears to be the species responsible for most of the macrophyte consumption documented in our study. The sea urchin *Arbacia punctulata* is patchily distributed on the jetty; some large areas are devoid of urchins while others have as many as 5–10 urchins/m^2. The spottail pinfish, *Diplodus holbrooki,* is by far the most common omnivorous fish on the jetty. In early summer mean densities are as high as 16 fish/m^2; by late summer densities are usually 6–8 fish/m^2 (M. E. Hay, *personal observation* based on counts of 50–100 0.25m^2-quadrats during the summers of 1984 and 1985). Other omnivorous fishes such as the pinfish, *Lagodon rhomboides*; the filefish, *Monocanthus hispidus*; and the sheepshead, *Archosargus probatocephalus,* are present in densities of <1 fish/m^2. Although our study area was a human-made jetty, these species commonly cooccur in grassbeds and in natural hard substrate habitats along most of the length of the American Atlantic coast. *Diplodus holbrooki* occurs in coastal habitats between New Jersey and southern Texas (Darcy 1985). *Ampithoe longimana* has a similar distribution, but extends northward as far as Maine (Bousfield 1973). *Arbacia punctulata* occurs from Maine to Florida (Miner 1950), and *Dictyota dichotoma,* the seaweed we worked with most intensively, is abundant throughout tropical and subtropical portions of the Atlantic and Caribbean (Taylor 1960).

The secondary metabolites of *Dictyota* and related genera (*Pachydictyon, Dilophus,* and *Glossophora*) that produce pachydictyol-A and dictyol-E (see Fig. 1) are relatively well studied (Hirschfeld et al. 1973, McEnroe et al. 1977, Norris and Fenical 1982, Hay et al. 1987). Pachydictyol-A was first isolated from *Pachydictyon coriaceum,* where it occurred as at least 0.7% of the algal dry mass and showed very mild antibiotic activity (Hirschfeld et al. 1973). In laboratory assays, the compound shows no strong activity against fungi, bacteria, diatoms, or fertilized sea urchin eggs; it also is not toxic to fish when mixed into their water (Gerwick 1981). Despite its inactivity in these standard pharmacological assays, pachydictyol-A deters feeding by Caribbean reef fishes and the tropical sea urchin *Diadema antillarum* (Hay et al. 1987). Pachydictyol-A is a common constituent of *Dictyota bartayresii, D. dichotoma, D. dentata, D. binghamiae,* and several other members of the Dictyotaceae (Faulkner et al. 1977, McEnroe et al. 1977, Pathirana and Andersen 1984); it can occur as >1% of the dry mass of some of these plants (W. Fenical, *personal observation*).

Dictyol-E differs from pachydictyol-A by only one hydroxyl group (Fig. 1); this compound was first isolated from *Dilophus lingulatus* at a concentration of at least 0.5% of the dry mass (Danise et al. 1977). It has subsequently been found in *Dictyota dichotoma, D. binghamiae,* and *D. indica* (Fattorusso et al. 1976, Amico et al. 1979, Niang and Hung 1984, Pathirana and Andersen 1984). Like pachydictyol-A, it is inactive against marine fungi and bacteria; but unlike pachydictyol-A, it is toxic to fish when added to their water (Gerwick 1981). Other aspects of the biological activity of dictyol-E remain uninvestigated. In feeding assays with tropical fishes and sea urchins, seaweeds containing pachydictyol-A and dictyol-E (*Dictyota* and *Dilophus*) have been shown to be relatively low preference food items despite their soft, fleshy morphology (Hay 1981, 1984, Littler et al. 1983, Paul and Hay 1986).

All of the metabolite concentrations cited above are very conservative since they are based on the yield of the purified compound and not on analytical techniques designed to measure actual concentration. Yield (dry mass of the pure compound per dry mass of plant) underestimates the true concentration for the following reasons: (1) extraction of the dried plant material is rarely complete, (2) some of the compound is lost at each step in the purification process, and (3) compounds may degrade to some extent during the extraction and purification process. Point number three is probably not a problem for pachydictyol-A and dictyol-E since both compounds are very stable. We have stored each compound for 2 yr with no detectable breakdown. It is possible that yield measurements may be only two-thirds to one-half of actual concentrations. We therefore ran our experiments over a gradient of concentrations that ran from 0.1 to ≈2 times the maximum published yield.

We have conducted only preliminary chemical investigations on the population of *Dictyota dichotoma* that occurs at our study site. This population of *Dictyota* contains low amounts (apparently 0.1% or less) of pachydictyol-A and moderate amounts (apparently 0.5% or less) of dictyol-E. It also contains unknown concentrations of an undescribed secondary metabolite that becomes unstable once it is purified by high performance liquid chromatography (HPLC). We have not yet developed methods for working with this compound. Our investigations are thus relevant to a wide variety of seaweeds that contain pachydictyol-A or dictyol-E but cannot completely assess the chemical defenses of our local population of *Dictyota dichotoma* since one of its three metabolites remains uninvestigated.

Chemical procedures

Dictyota dichotoma was collected from Radio Island jetty, quickly frozen at −30°C then freeze-dried to a constant mass and mailed to Scripps Institution of Oceanography where all extraction, purification, and identification procedures were performed. The *Dictyota* was extracted with a 2:1 mixture of dichloromethane and methanol. Compounds from the crude extract were purified by HPLC and structurally elucidated by proton nuclear magnetic resonance (NMR) spectrometry. Pure pachydictyol-A and dictyol-E were then returned to North Carolina for use in feeding assays.

Feeding preference assays

To evaluate the feeding preferences of *Diplodus, Arbacia,* and gammarid amphipods, several common algae were offered to each herbivore in the laboratory or in large (5000 L) outdoor tanks. Preferences of *Arbacia punctulata* were determined by simultaneously providing five species of seaweeds in excess amounts to 22 different urchins, each of which was held in a 3.8-L, aerated container. After spinning algae in a salad spinner to remove excess water, 5 g each of *Gracilaria tikvahiae, Dictyota dichotoma, Sargassum filipendula,* and *Padina gymnospora* and 10 g of *Codium fragile* were placed in each container. A greater mass of *Codium* was used because its surface area to mass ratio was so much less than the other species. Since urchins are not visual predators we assumed that their rate of encounter with *Codium* would be substantially lower than their rate of encounter with other species if all species were provided in equal masses. Even when we doubled the *Codium* mass, its surface area was still much less than any of the other species. Urchins were excluded from two containers; these served as controls for changes in algal mass unrelated to urchin grazing. After 24 h, the mass of each alga was again determined after it had been spun in a salad spinner to remove excess water. Mass changes of algae in containers without urchins were used to correct the initial wet mass determinations of all other algae to control for changes that were not caused by herbivores.

Amphipod feeding preferences for several species of macroalgae were performed in the same manner except that $N = 20$, the duration was 46 h, initial spun wet mass of each alga was 100 ± 10 mg, and the assay was conducted in 1.9-L containers, each of which contained 20 amphipods. Ten containers without amphipods served as controls. Amphipods for these tests were a mixed species assemblage collected by shaking them from algae gathered from the field or from large outdoor tanks behind the University of North Carolina Institute of Marine Sciences. Only three species of amphipods were common. *Ampithoe longimana* constituted 41% of the individuals, *Elasmopus levis* 33%, and *Dulichiella appendiculata* 26%. Amphipods were offered a choice of the following eight macroalgal species: *Dictyota dichotoma, Padina gymnospora, Sargassum filipendula, Codium fragile, Hypnea musciformis, Gracilaria tikvahiae, Rhodymenia pseudopalamata,* and *Chondria dasyphylla.* In this, and all other tests, we took care to use only plant portions that were free of epiphytes.

Since several studies have reported that amphipods often graze primarily on small epiphytic algae and rarely consume macroalgae, we conducted a second feeding assay to compare rates of feeding on *Dictyota* (the most rapidly eaten macrophyte in the first assay) with feeding rates on three common epiphytic species (*Cladophora ruchingeri, Polysiphonia harveyi,* and *Enteromorpha linziformis*). Methods for this assay were the same as for the first assay except that we did not use a mixed species group of amphipods; we used only *Ampithoe longimana* since this was the amphipod species responsible for most of the grazing during our first assay.

Feeding preferences of the spottail pinfish, *Diplodus holbrooki,* were conducted in eight large (5000 L) outdoor tanks supplied with continuously flowing seawater (see Hay 1986 for a description of these tanks). Each tank was split into two equal-sized sections using plastic mesh. Eight *Diplodus* were placed on one side and none on the other. Portions (≈700 mg) of *Dictyota dichotoma, Padina gymnospora, Sargassum filipendula, Codium fragile, Ulva* sp., *Hypnea musciformis, Chondria dasyphylla, Calonitophyllum medium,* and *Rhodymenia pseudopalmata* were held between the strands of a three-stranded rope and ropes were anchored in each side of the eight mesocosms. Algae in the sides without fish were used to correct for changes in algal mass that were not a result of grazing by *Diplodus.* This assay ran for 19 h.

We used methods similar to those of McConnell et al. (1982) and Hay et al. (1987) to evaluate how pachydictyol-A and dictyol-E affected feeding by *Diplodus, Arbacia,* and amphipods. Weighed portions of the palatable alga *Gracilaria tikvahiae* were coated with a solution of the test metabolite in diethyl ether so that the final metabolite concentration on the blade was 0.1, 0.2, 0.5, 1.0, or 1.3% of the dry mass of the *Gracilaria.* These concentrations span the range of concentrations that probably occur in dictyotalean algae that produce these compounds (see our earlier comment on known yield of compounds vs. their probable concentration). Dry mass of the wet alga was calculated using a previously determined wet mass/dry mass ratio. Control portions of *Gracilaria* were coated only with diethyl ether. Since dictyol-E and pachydictyol-A are lipid soluble, they adhere to the surface of *Gracilaria* after the ether evaporates. The treatment and control portions of *Gracilaria* can thus be placed in seawater for the feeding experiments. Previous workers using this methodology found that 0–12% of lipid-soluble compounds were lost from *Gracilaria* blades when these were reimmersed in seawater (McConnell et al. 1982). Following each of our assays we extracted the treatment plants in diethyl ether and used thin-layer chromatography (TLC) to test for presence of the compound and to see if the compound had degraded. Compounds were always present and never showed signs of breakdown.

For the spottail pinfish, *Diplodus holbrooki,* the bases of 200 ± 20 mg treatment or control portions of *Gracilaria* were placed through slits in numbered rubber discs and paired on the bottom of 12 40-L flow-through tanks that held individual *Diplodus.* Four similar tanks without fish served as controls. Fish were allowed to graze for 14–24 h, the algae were reweighed, corrected for mean change that occurred in the controls, and loss of treatment vs. control blades compared. Previous work had shown that our wet mass determinations were repeatable to within 2–3%, however we conservatively excluded any replicate with <5% change in wet mass since this indicated a lack of feeding by that fish. This decreased sample sizes for assays at some concentrations. If the initial assay at a given concentration of metabolite gave results indicating a significant ($P < .05$) effect on feeding or clearly indicated that the compound did not affect feeding ($P > .40$), then the assay was not repeated. If results from the initial assay suggested a trend toward increased or decreased feeding, then the entire assay was repeated with different fish to increase our sample size and ability to detect significant effects on feeding. These methods resulted in sample sizes of 8–20 for the various compounds and concentrations. Once a fish had fed during any of our assays, it was not reused. All replicates were therefore independent.

For the sea urchin *Arbacia punctulata* assays were performed in a similar manner, but urchins were held in 3.8-L jars supplied with 1.25 L of aerated seawater. Assays ran for 14–24 h and replicates were excluded from the analyses if urchins consumed <5% of either plant or all of both plants. This resulted in sample sizes of 13–23. Five jars without urchins served as controls during each assay. As with the fish, each feeding observation came from a separate urchin.

For amphipods, assays were performed by placing 100-mg pieces of treatment and control *Gracilaria* into 10.5 cm diameter dishes that held 20 amphipods. For each assay, 10 dishes with amphipods and 3 without amphipods (controls) were used. All assays ran for 40 h. Water was changed once during each assay.

The physiological effect of pachydictyol-A

In an effort to determine some of the longer term, physiological effects of consuming pachydictyol-A, we set up 15 38-L aquaria that were partitioned by plastic mesh (6 mm diameter holes) into two equal-sized subsections with one *Diplodus holbrooki* in each subsection. Fish within each aquarium were paired by standard length. Fish were placed in the aquaria on 6 October 1985, all aquaria and fish were treated for the protozoan parasite *Ichthyophthirius* ("ich"), and fish were allowed to acclimate for 10 d before the experiment began. One fish in each tank was then randomly assigned to receive food treated with pachydictyol-A and ether or ether alone. Pellets containing both plant and animal products (Koi pellets, Blue Ridge Fish Hatchery, Kernersville, North Carolina, USA) were used as food. Pachydictyol-A was added to some pellets at 1.0% of their dry mass by coating them with pachydictyol-A in ether. Control pellets were coated with an equivalent amount of ether. All ether was allowed to evaporate before the pellets were fed to the fish. To insure that each fish ate the same quantity of food, the following protocol was used for daily feedings. Before offering pellets to the fish, a very small piece (2–4 mg dry mass) of tuna-flavored cat food was offered to each fish; if either failed to eat this, then neither fish in that tank was fed that day. If both fish ate the cat food, then each was offered half a pellet (=28 mg dry mass) of the Koi food. This process was continued until one fish refused to eat. By watching the feeding behavior of the fish we were usually able to predict when a fish was about to stop eating and avoid offering a pellet to the more voracious fish until after the less voracious one had eaten. This allowed us to give each fish an equivalent quantity of food. On the 1st d of feeding, both the control and pachydictyol-A treatment fish ate equally well (control fish ate a mean ± SD of 7.5 ± 5.1 pellets each; treatment fish ate 7.7 ± 5.0 pellets). On the 2nd d, in 11 of the 15 tanks, the treatment fish stopped eating while the control fish still appeared to be willing to eat. Fish were not fed on the 3rd d. On the 4th d, and for all days thereafter, each pellet was dipped in an aqueous slurry of tuna-flavored cat food before being presented to either fish. The scent of the cat food increased feeding by the fish and enabled us to get the treatment fish to consume pellets containing pachydictyol-A. Whenever a fish died, the date was recorded and the standard lengths of both it and the fish with which it was paired were measured. On 4 November 1985 (i.e., 20 d after feeding started) only two pairs of fish remained so the experiment was terminated. Water in each aquarium circulated freely between the fish being fed treated pellets and those being fed control pellets. Thus, differences in growth or mortality rates must be attributed to ingestion and not to presence of pachydictyol-A in the water. We conducted this experiment with only pachydictyol-A because relatively large amounts of this compound (hundreds of milligrams) were available to us; it had been purified from several species of algae that one of us (W. H. Fenical) had studied previously. Dictyol-E was not easily available in these quantities.

To see if amphipods could alter their susceptibility to fish predators by sequestering *Dictyota* metabolites, we fed one group of *Ampithoe longimana* for 2 wk on *Dictyota dichotoma* and another group on *Hypnea musciformis*; amphipods from each group were then offered to juvenile pinfish (*Lagodon rhomboides*), which are voracious amphipod predators (Adams 1976). Pinfish, like spottail pinfish, rapidly consume *Hypnea,* avoid *Dictyota,* and are deterred from feeding by both dictyol-E and pachydictyol-A (M. Hay and P. Renaud, *personal observation*). Pinfish were paired by size (standard length), and each fish was placed in a separate

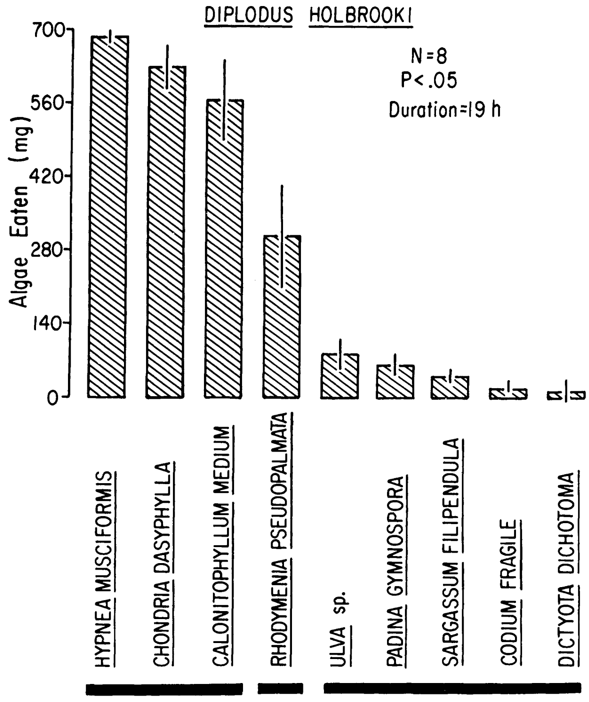

FIG. 2. Algal consumption by the spottail pinfish, *Diplodus holbrooki*, when offered nine species of common seaweeds for the indicated period. Vertical bars through each histogram represent ±1 standard error. Wet mass of each species was ≈700 mg. Dark bars below the species' names join seaweeds that do not differ significantly ($P \leq .05$, Kruskal-Wallis test and a nonparametric parallel of the Student-Newman-Keuls test).

3.8-L glass jar. After acclimating for 24 h, one fish of a pair was offered *Hypnea*-fed amphipods; the other member of the pair was offered *Dictyota*-fed amphipods. Fish were offered amphipods until they had either consumed 12 or rejected 3 (by 12 amphipods, these fish had visibly bloated bellies and appeared to approach satiation). We also used thin-layer chromatography (TLC) to qualitatively compare the chemistry of *Dictyota*-fed vs. *Hypnea*-fed amphipods.

All analyses of compound effects on herbivore feeding used the paired-sample *t* test if differences were normally distributed and the Wilcoxon paired-sample test if differences were not normally distributed.

RESULTS

For the spottail pinfish, *Diplodus holbrooki* (Fig. 2), and the sea urchin *Arbacia punctulata* (Fig. 3), *Dictyota dichotoma* was one of the least readily eaten of the several seaweeds tested. In marked contrast to this, *Dictyota* was one of the two macroalgal species that was most readily consumed by amphipods (Fig. 4). Since amphipods are often assumed to eat primarily small epiphytic species instead of larger macroalgae, we also assessed how readily the herbivorous amphipod *Ampithoe longimana* would eat *Dictyota* when excess amounts of several common epiphytic algae were available. *Ampithoe* ate significantly more *Cladophora* than *Dictyota, Enteromorpha,* or *Polysiphonia*; these last three algae were all eaten at similar rates (Fig. 5). *Sargassum filipendula* was not preferred by any of the three herbivores used in these tests. *Padina gymnospora* was eaten at an intermediate rate by amphipods but was low preference for both *Diplodus* and *Arbacia*; *Gracilaria tikvahiae* was consumed rapidly by *Arbacia* but at an intermediate to low rate by amphipods. *Codium fragile* was a preferred food of amphipods and *Arbacia* but was largely avoided by *Diplodus*. *Rhodymenia pseudopalmata* was of intermediate preference for both *Diplodus* and amphipods. *Chondria dasyphylla* was rapidly eaten by *Diplodus* but avoided by amphipods. It is interesting that the two species that were eaten least by the omnivorous fish *Diplodus* (Fig. 2) were the two species eaten most readily by amphipods (Fig. 4).

In assays designed to see if coating *Gracilaria* with only ether affected feeding by our various herbivores (Table 1), we found that ether-coated plants and uncoated plants were treated equally by fish and amphipods ($P = .95$ and $P = .60$, respectively; paired-sample *t* test). Urchins tended to graze more heavily on ether-coated plants ($P = .056$, Table 1).

When pachydictyol-A or dictyol-E was dissolved in diethyl ether and coated onto portions of *Gracilaria tikvahiae* at concentrations of 0.1–1.3% of plant dry mass, it had the following effects when compared with control plant portions that had been coated with diethyl ether alone: For the fish *Diplodus holbrooki* (Fig.

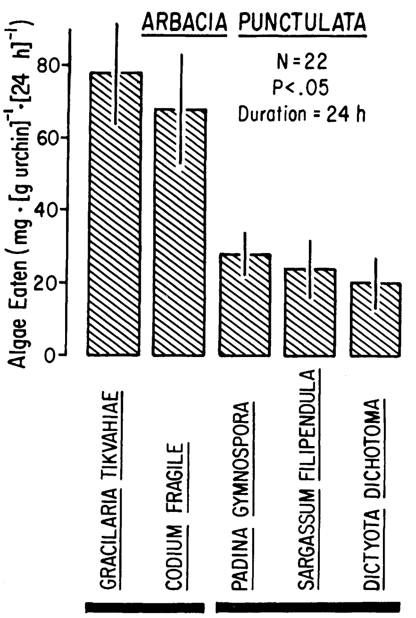

FIG. 3. Algal consumption by the sea urchin *Arbacia punctulata* when offered five species of common seaweeds. All seaweeds were available in excess (5–10 g wet mass) and no more than 50% of any species was ever consumed. Symbols are as in Fig. 2.

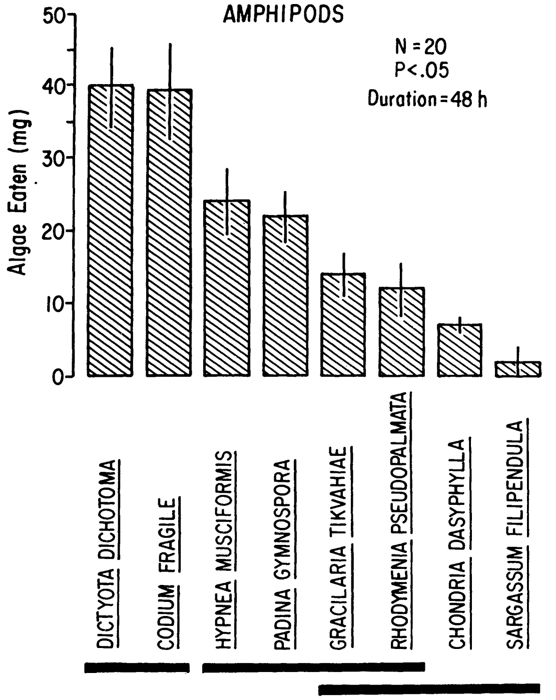

FIG. 4. Algal consumption by a mixed-species group of amphipods when offered eight common seaweeds. *Ampithoe longimana* (46%), *Elasmopus levis* (33%), and *Dulichiella appendiculata* (26%) were the major amphipod species. *Ampithoe* appeared to be responsible for most of the grazing. Mean wet mass of each species offered was ≈100 mg. Significant differences ($P \leq .05$) were assessed by ANOVA and the Student-Newman-Keuls test. Other symbols are as in Fig. 2.

6), dictyol-E significantly depressed feeding at concentrations of 0.5 and 1.0% (P = .04 and P = .02, respectively; paired-sample t test); this compound had no effect at 0.1% (P = .42). Pachydictyol-A significantly reduced feeding at a concentration of 1.0 and 1.3% (P = .04 and P = .01, respectively; Wilcoxon paired-sample test) and caused a large (45%) but nonsignificant (P = .07, paired-sample t test) reduction at 0.5%. For the sea urchin *Arbacia* (Fig. 7), dictyol-E caused a large (62–72%) and significant reduction in grazing at concentrations of 0.5 and 1.0% (P = .04 and P = .01, respectively; Wilcoxon paired-sample test). At 0.2% dictyol-E reduced grazing by a nonsignificant 23% (P = .36, paired-sample t test). Even at the highest concentrations, pachydictyol-A had no significant effect on feeding by *Arbacia*. Thus, dictyol-E was a rather strong feeding deterrent for both the fish and sea urchin; pachydictyol-A was less effective against the fish and ineffective against the sea urchin.

TABLE 1. Grazing by fish, sea urchins, and amphipods on ether-coated vs. uncoated *Gracilaria* plants.

		Algae eaten (mg, $\bar{X}$ ± 1 SE)		P values by the paired-sample t test
Species	(N)	Ether-coated plants	Uncoated plants	
Diplodus	12	45 ± 10	46 ± 11	.947
Arbacia	14	234 ± 43	86 ± 32	.056
Ampithoe	15	50 ± 7	55 ± 5	.604

In contrast to the patterns seen for the other herbivores, dictyol-E had no significant effect on feeding by amphipods (Fig. 8). Pachydictyol-A did not affect feeding at a low concentration of 0.1%. At a concentration of 1.0%, pachydictyol-A increased amphipod feeding by a significant 64% (P = .05, Wilcoxon paired-sample test).

To see if amphipods eating *Dictyota* might sequester the *Dictyota* metabolites and thereby decrease their susceptibility to fish predation, we fed amphipods on either *Dictyota* or *Hypnea* for 13 d and then offered amphipods from each alga to small pinfish. The pinfish readily ate amphipods from either algal diet and showed no tendency to decrease their consumption of amphipods that had fed on *Dictyota*. Fish offered *Dictyota*-fed amphipods ate an average of 10 (SD = 3) amphipods each; fish offered *Hypnea*-fed amphipods ate an average of 9 (SD = 4) amphipods each (P = .47, paired-sample t test, N = 5). Thin-layer chromatography (TLC) analysis comparing the chemical characteristics of amphipods from each diet showed no qualitative differences.

When the fish *Diplodus holbrooki* was maintained in the laboratory on a diet of artificial food pellets coated with either pachydictyol-A and ether (=treatment; concentration was 1% of pellet dry mass) or ether alone (=control), growth of fish on the pachydictyol-A–containing diet was significantly slower than growth of fish that were fed the same amount of the control diet (Fig. 9, P = .01, Wilcoxon paired-sample test).

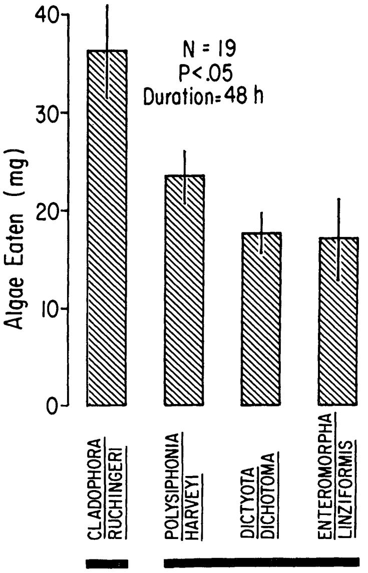

FIG. 5. Algal consumption by the amphipod *Ampithoe longimana* when offered *Dictyota* and three common epiphytic algae. Symbols and analysis are as in Fig. 4.

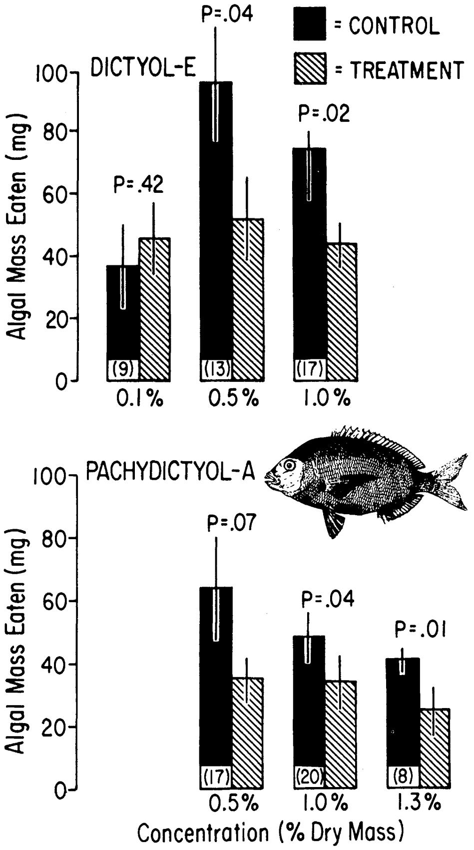

FIG. 6. The effect of dictyol-E or pachydictyol-A concentration on feeding by the spottail pinfish, *Diplodus holbrooki*. Vertical bars through each histogram represent ±1 standard error. Sample size is given in parentheses at the base of each histogram. The *P* value for each assay (Wilcoxon paired-sample test) is given above the histogram.

Of the 15 pairs of fish used in the experiment, only two pairs were still alive when the experiment was terminated on 4 November 1985 (after 20 d of feeding). In three pairs, both the fish receiving the control diet and the fish receiving the experimental diet died on the same day. In 7 of the 10 remaining pairs, the fish on the pachydictyol-A–containing diet died before the control fish. Time of death comparisons were complicated by the tendency for the two paired fish within a tank to die synchronously (the three instances mentioned above), or nearly synchronously (in five cases paired fish died within 1 d of each other). The cause of death was not clear in most cases, and some of the near synchronous deaths could have resulted in part from handling the living member of the pair. When one fish died, both were immediately removed from the tank and measured; the living fish was then returned to the tank. These fish often died the next day. However, on three occasions, when one fish died in the afternoon, we did not immediately handle and measure the remaining fish but waited until the next morning. In all three cases the remaining fish did not live through the night. In other feeding experiments where chemicals were not involved, we noted similar patterns of nearly simultaneous death of paired fish (M. Hay, *personal observation*). It is possible that rapid bacterial growth on the dead fish or some chemical leaching from the dead fish was responsible for this pattern. These problems, along with the relatively small sample size ($N = 15$), severely limit the value of the mortality data, but the trend suggests that consumption of pachydictyol-A may have caused increased mortality as well as the better documented inhibition of growth.

DISCUSSION

Chemical defense against herbivory

For the compounds investigated here, it is clear that herbivory by fish or urchins could select for production of dictyol-E and that herbivory by fish, but not urchins, could select for production of pachydictyol-A (Figs. 6 and 7). If amphipods were the dominant herbivores, production of dictyol-E would have no selective value and production of pachydictyol-A would be selected against (Fig. 8). In an example somewhat similar to this, recent studies in terrestrial habitats have shown that increased concentrations of toxic secondary metabolites may increase, instead of decrease, the insect damage that a plant experiences if the insects are specialized to use the plant toxin as a defense against their own predators (Smiley et al. 1985). Although terrestrial arthropods commonly sequester plant metabolites (Brattsten 1979), we did not detect sequestering by *Ampithoe longimana,* and individuals that had fed only on *Dictyota* were no less palatable to a common fish

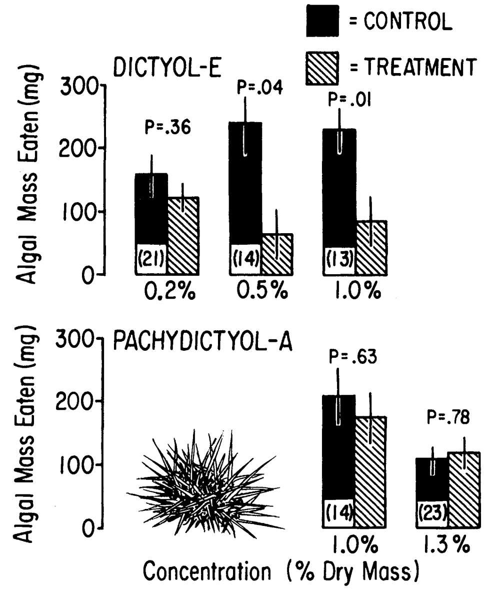

FIG. 7. The effect of dictyol-E or pachydictyol-A concentration on feeding by the sea urchin *Arbacia punctulata*. Symbols are as in Fig. 6.

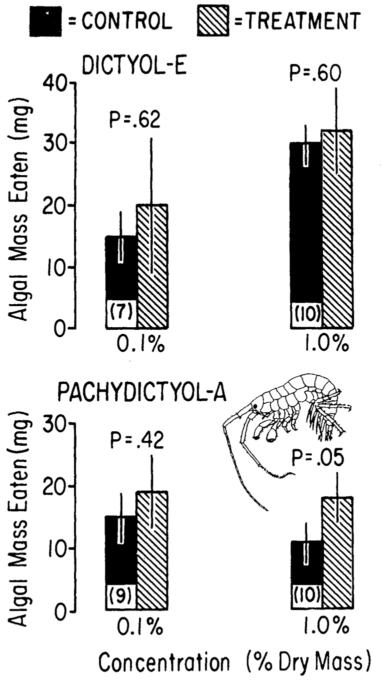

FIG. 8. The effect of dictyol-E or pachydictyol-A concentration on feeding by a mixed-species group of amphipods. Symbols are as in Fig. 6.

predator, *Lagodon rhomboides,* than individuals that had fed on *Hypnea.*

The single previous study that tested algal metabolites against multiple herbivores (Hay et al. 1987) focused on coral-reef fishes and the tropical sea urchin *Diadema antillarum.* For these large, mobile herbivores, five of the six compounds tested had similar effects on both types of herbivores; however, one compound decreased fish feeding but increased consumption by urchins.

It is clear that structurally similar compounds (Fig. 1) can differ markedly in their effects on herbivore food choice, and that a compound that deters one herbivore may have very different effects on another (Figs. 6–8). Marine ecologists often would like to classify the activity of compounds in a very general way, such as, terpenes are toxins or terpenes are herbivore deterrents. This is clearly inappropriate given the data presented here and in other recent investigations (Hay et al. 1987). As examples, pachydictyol-A deters feeding by a mixed-species group of coral reef fishes and by the tropical sea urchin *Diadema* (Hay et al. 1987). It also deters the spottail pinfish, *Diplodus* (Fig. 6), but has no effect against *Arbacia* (Fig. 7), and significantly stimulates feeding by amphipods (Fig. 8). Dictyol-E is structurally almost identical to pachydictyol-A; however, it is a stronger deterrent of fish and urchin grazing and has no effect on amphipods (Figs. 6–8). A similar pattern has been shown for a metabolite produced by species of the red algal genus *Laurencia.* Isolaurinterol is a sesquiterpene phenol that deters grazing by reef fishes and the sea urchin *Diadema* (Hay et al. 1987). Under very mild acid conditions, isolaurinterol converts to aplysin, a structurally similar sesquiterpene ether. Aplysin has no effect on feeding by reef fishes or *Diadema* (Hay et al. 1987).

Although a number of terpenoid compounds from seaweeds have been screened for biological activity in a variety of pharmacological assays (see Norris and Fenical 1982, Hay 1984, and Hay et al. 1987 for references), the value of these assays for predicting the effect of chronic consumption of these compounds is questionable. For example, the brown alga *Stypopodium zonale* produces a C_{27} compound called stypotriol that is derived from a mixed biosynthesis of diterpenoid and acetate precursors (Gerwick and Fenical 1981). In lab assays, stypotriol and its oxidation products are toxic to fish when added to their water in very small amounts (0.2 μg/mL), prevent cell divison by inhibiting tubulin polymerization, immobilize sperm, and inhibit both amino acid and nucleoside uptake (Gerwick and Fenical 1981, White and Jacobs 1983, O'Brien et al. 1984). In contrast to the strong activity of stypotriol, pachydictyol-A shows none of these properties. However, stypotriol and pachydictyol-A are equally effective feeding deterrents against *Diadema* and reef fishes (Hay et al. 1987). Thus, the pharmacological assays do not appear to be good predictors of how effective these compounds will be against herbivores. Absolutely no investigations have been conducted on the mechanism of action of seaweed metabolites when consumed by herbivores, and the data presented in Fig. 9 are the first assessing even the crude physiological effect of one of these compounds. Chronic consumption of pachydictyol-A at 1.0% of food dry mass significantly reduced growth in the spottail pin-

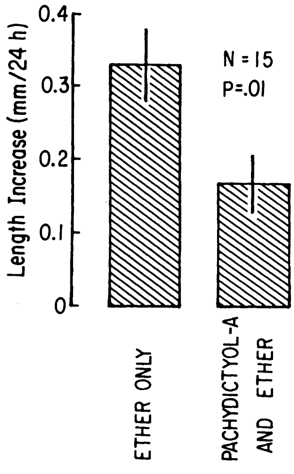

FIG. 9. Increases in standard length of *Diplodus holbrooki* fed food pellets treated with ether alone (=control) or ether and pachydictyol-A at 1% of pellet dry mass (= treatment). Vertical bars show ±1 standard error. The *P* value is from Wilcoxon paired-sample test.

fish, *Diplodus holbrooki.* There was no demonstrated effect on mortality. However, as discussed in the results section, the mortality data are problematic since paired fish often died synchronously, suggesting a lack of independence between fish fed the treatment or control diet.

The data on feeding preferences of the three types of herbivores (Fig. 2–5) and on their responses to secondary metabolites from *Dictyota dichotoma* are all consistent with the hypothesis that these metabolites are of major importance in determining herbivore feeding patterns. However, the *D. dichotoma* used in these studies possesses a third, and as yet unidentified, secondary metabolite, the effects of which are unknown. In addition, we know nothing about between-plant, between-site, or between-season variations in compound concentration or production.

Specialist vs. generalist herbivores and the potential importance of mesograzers

Specialist herbivores are relatively common in terrestrial communities (Crawley 1983) but appear to be rare in marine habitats (Lubchenco and Gaines 1981, Steneck 1982). Although the perceived specialization of terrestrial insect herbivores is, in part, dependent upon the spatial scale at which one samples the insects' feeding habits (Fox and Morrow 1981), it still seems that specialist plant feeders are relatively rare in marine as opposed to terrestrial communities. The specialist herbivores in terrestrial communities are often relatively immobile insects that tend to spend most of their lives on one, or a very few, individual plants (Dethier 1959, Crawley 1983). Although small and relatively immobile herbivores (amphipods, isopods, and polychaetes) are common in marine communities, almost all investigations of herbivory have focused on the larger, more mobile, and more obvious herbivores such as the fishes, urchins, and larger gastropods (see Lawrence 1975, Ogden 1976, Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983, Hay 1984). The mobility and well-developed sensory ability of fishes, the spines of urchins, and the shells of gastropods may allow these herbivores to move between plants with relatively little probability of being successfully attacked by their predators. For small and relatively soft-bodied amphipods, isopods, and polychaetes, between-plant dispersal could be a time of intense predation. Some of these small herbivores are surprisingly mobile, but most movement appears to occur at night when visual fish predators are less active or appears to be confined primarily to juveniles, which are smaller and therefore less susceptible to fish predation (Jansson and Källander 1968, Williams and Bynum 1972, Vince et al. 1976, Robertson and Howard 1978, Hammer 1981, Wallerstein and Brusca 1982, Edgar 1983). There are also limited data suggesting that the common nocturnal movements typical of infaunal amphipods do not occur, or occur much less frequently, for amphipods that live on seaweeds (Edgar 1983). Thus, tubicolous amphipods, polychaetes, and other mesograzers that spend extended periods of time on one plant may be under very different evolutionary constraints than the larger, more mobile herbivores that commonly move between many plants. These less mobile, and much less studied, marine herbivores may be similar to terrestrial insects (Kareiva 1982) in that dispersal to plants that provide adequate food and protection from predators may be one of the major difficulties these herbivores face during their lifetime. These small herbivores are among the major prey items for common benthic fishes (Randall 1967, Adams 1976) and numerous experimental studies show that they are subject to intense predation (Young et al. 1976, Young and Young 1978, Nelson 1979*a, b,* 1980*a, b,* 1981, Stoner 1980, Brawley and Adey 1981*a*). Although numerous studies show that even large, mobile herbivores such as fishes, urchins, and gastropods may constrain their foraging movements to avoid predators (Randall 1965, Ogden et al. 1973, Cowen 1983, Carpenter 1984, Power 1984, Hay 1985) or may risk increased predation when moving between large seaweeds (Watanabe 1984), this constraint appears to be a much more rigorous one for tubicolous amphipods and polychaetes.

The few specialized marine herbivores that are known tend to be relatively small and immobile (Steneck 1982) and to consume selectively, or live on, plants that appear to provide them with some protection from their predators. For example, some limpets feed almost exclusively on smooth coralline algae that provide an excellent attachment site and lower their risk to predation (Steneck 1982). Other limpets that specialize on kelps form grazing scars that decrease their risk of predation (Phillips and Castori 1982). Species of the opisthobranch genus *Aplysia,* such as *A. californica,* selectively settle on and consume species of *Laurencia* and *Plocamium* that produce toxic secondary metabolites that are sequestered by the opisthobranch and are apparently used in its own defense (Stallard and Faulkner 1974, Norris and Fenical 1982). Since *Aplysia* can grow and reproduce equally well on either *Plocamium* or *Enteromorpha* (Carefoot 1967), the preference for the chemically rich seaweeds appears to reflect the need for predator defense as opposed to some unique dietary requirement.

Although our feeding studies used a mixed-species group of gammarid amphipods, the large frass piles near the tubes of *Ampithoe longimana* and the absence of frass near other species indicated that *Ampithoe* was responsible for most of the grazing. This amphipod builds small tubular domiciles on plants and spends most of its time in these tubes (Holmes 1901, Nicotri 1977). Despite this cryptic behavior, *Ampithoe* in North Carolina suffer large losses to fishes such as the spottail pinfish, *Diplodus holbrooki,* and the pinfish, *Lagodon rhomboides* (Adams 1976, Nelson 1980*a, b*). Since these fishes eat both seaweeds and small invertebrates, cryptic invertebrates living on seaweeds preferred by fishes might still be rapidly consumed as fishes eat the algae. This indirect consumption should select for individuals that prefer plant species that are not consumed by fishes. In our feeding preference assays, the two seaweeds least attractive to fishes (Fig. 2) were the two species that were most attractive to amphipods (Fig. 4). In addition, several findings of a previous study conducted at our study site by Holmlund (1984) suggest that selection has favored amphipods that avoid seaweeds that are preferred by fishes. First, when equal masses of amphipod-free *Sargassum, Padina* (both avoided by fishes; Fig. 2), and *Hypnea* (preferred by fishes; Fig. 2) were placed in the field, amphipods recruited more rapidly to *Sargassum* and *Padina* than to *Hypnea.* This pattern occurred whether or not fish had access to the plants. Second, when fish were included with or excluded from *Sargassum, Padina,* and *Hypnea* plants, amphipod density of inclusion vs. exclusion treatments differed by only 8–10% for *Sargassum* and *Padina,* but amphipod density on *Hypnea* plants exposed to fish decreased by >60%. Third, as fishes became more abundant during the summer months, the density of amphipods per wet mass of alga declined by 83% for *Hypnea* but showed no change for *Sargassum* or *Padina.* Using plastic models, Holmlund (1984) demonstrated that some of the increased loss of amphipods from *Hypnea* vs. *Padina* or *Sargassum* plants was due to plant morphology. However, a significant portion of the difference could also have been a result of the differing palatabilities of the plants to fishes.

Although our data on amphipod feeding appeared to be generated primarily by the single species *Ampithoe longimana,* other studies suggest that our findings may apply to several common amphipods. Lewis and Kensley (1982) studied the amphipod *Pseudamphithoides incurvaria* on a coral reef in Belize, Central America and noted the following aspects of its biology. The amphipod makes, and lives in, an unusual bivalved domicile cut from the blades of *Dictyota bartayresii.* The major metabolite of this alga is pachydictyol-A (Norris and Fenical 1982), which has been shown to reduce feeding by reef fishes (Hay et al. 1987). The amphipod is common on *Dictyota* but is not found on the related genera *Stypopodium, Padina,* or *Lobophora.* In the lab, the amphipods would not eat *Padina, Thalassia,* or *Halimeda* (all common plants in the amphipod's habitat) but voraciously consumed *Dictyota.* When forced from their bivalved domiciles, *Pseudamphithoides* would not construct domiciles from *Padina* or *Lobophora* (both herbivore-susceptible species at this site: Lewis 1985) but immediately began construction when they contacted *Dictyota* (a relatively herbivore-resistant species: Hay 1981, 1984).

Other amphipods that live inside the alga they consume include *Ampithoe humeralis,* which makes chambers from the kelps *Macrocystis* (Barnard 1969, Jones 1971) and *Ecklonia* (Griffiths 1979), *Amphitholina cuniculus,* which burrows into the stipe of the kelp *Alaria esculenta* (Myers 1974), and *Ampithoe tea,* which may excavate chambers in the brown alga *Pelvetia* (Gunnill 1985). Although little information is available on herbivory by temperate fishes, feeding studies conducted by Horn et al. (1982) show brown seaweeds to be very low preference foods for the two herbivorous fishes that they studied.

Although amphipod–amphipod interactions (Caine 1977, Van Dolah 1978, Edgar 1983), food availability (Norton and Benson 1983), physical factors (Fenchel and Kolding 1979, Kneib 1982), and availability of sheltering sites (Nicotri 1980, Edgar 1983), have all been suggested to affect habitat choice by amphipods, it is likely that predator avoidance will also play an important role since predators play such a large part in regulating amphipod densities (Young et al. 1976, Young and Young 1978, Nelson 1979*a, b,* 1981, Stoner 1980, Brawley and Adey 1981*a, b,* Edgar 1983). For relatively immobile invertebrates that consume the macroalgae on which they live, habitat choice and food choice become synonymous. Since food availability rarely limits amphipod abundance (Zimmerman et al. 1979, Stoner 1980), predator avoidance may play the dominant role in determining habitat, and thus food, choices for the amphipods. Nicotri (1980) recognized this constraint on the foraging activities of small crustaceans and postulated it as a possible explanation for the complete lack of correlation between the seaweed species to which the isopod *Idotea* was attracted and those that it ate most rapidly. Interestingly, percent nitrogen was negatively correlated with algal attractiveness. This is surprising since marine herbivores appear to be nitrogen limited (Mann 1982). However, since herbivorous fishes tend to prefer seaweeds rich in nitrogen and proteins (Horn and Neighbors 1984), this is the pattern that would be expected if small crustaceans choose safe habitats over high-quality, but risky, foods.

The specialized marine herbivores such as the limpets and opisthobranch that were discussed earlier may play a very important role in the biology of their host plant (Black 1976, Steneck 1982), but will rarely have a large impact on marine communities in general because of their limited density and distribution. However, amphipods and other small crustaceans are widespread and tremendously abundant in most marine habitats. At our study site, there are often several hundred amphipods per *Sargassum* plant (M. Hay, *personal observation*). Nelson (1980*b*) reported densities of 6500 amphipods/m^2 in nearby grassbeds, Fenchel (1970) reported the unusually high density of 90 000/m^2 for a grassbed in Florida, and Gunnill (1982) reported mesograzer densities of 5000–10 000 individuals per kilogram (wet mass) of the brown alga *Pelvetia.* The fact that large numbers of mesograzers are often found on healthy seaweeds has been used to argue that interactions between arthropods and seaweeds are very different than interactions between arthropods and terrestrial plants. Schiel and Choat (1980) noted that terrestrial plants were often damaged by insects and that there appeared to be no equivalent form of herbivory on large marine algae. Brawley and Adey (1981*a, b*) pointed out that increased densities of arthropods on seaweeds could even be beneficial since these mesograzers often consumed small epiphytes and prevented them from overgrowing the host alga. Although many amphipods do feed primarily on small epiphytic algae that foul the seaweed on which they live (Greze 1968, Zimmerman et al. 1979, Caine 1980, Brawley and Adey 1981*a, b,* Norton and Benson 1983, D'Antonio 1985, Gunnill 1985), it is becoming increasingly clear that some amphipod species commonly consume significant quantities of large macrophytes and can significantly damage large seaweeds when other foods are scarce (Glynn 1965, Martin 1966, Greze 1968, Nicotri 1977, 1980, Zimmerman et al. 1979, Lewis and Kensley 1982, Norton and Benson 1983, D'Antonio 1985, Gunnill 1985). At our study site, amphipods and polychaetes appear to be the only herbivores that cause obvious damage to plants such as *Sargassum, Padina,* and *Dictyota* that are not readily consumed by fish (Fig. 2) or urchins (Fig. 3) (M. Hay, *personal observation*). We have noted similar patterns among some *Sargassum* and *Dictyota* populations in the Bahamas and Florida Keys (M. Hay and P. Renaud, *personal observation*). Both the pattern of damage (holes cut through the blades), and the extent of damage (from 1–20% of blade area, or very rarely almost total defoliation) are similar to patterns and extent of insect attack on terrestrial vegetation (Crawley 1983). Thus, it appears that some species of small, relatively immobile marine invertebrates may be ecologically similar to terrestrial insects and may play a significant, but largely unstudied, role in the dynamics of marine plant populations.

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