

## Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses

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**Summary.** Small, relatively sedentary herbivores like amphipods and polychaetes (mesograzers) often live on the plants they consume and should therefore view plants as both foods and living sites. Large, relatively mobile herbivores like fishes commonly move among, and feed from, many plants; they should view plants primarily as foods and rarely as potential living sites. In marine communities, fishes that consume plants are also important predators on mesograzers. Since seaweeds avoided by fishes should represent safer living sites for small herbivores, mesograzers living on and consuming seaweeds that are not eaten by fishes should have higher fitness than mesograzers living on plants preferred by fishes. In previous work, we demonstrated that seaweed secondary metabolites that deterred feeding by a fish and sea urchin had no effect on feeding by a common amphipod (Hay et al. 1987a). We then hypothesized that mesograzers would, in general, be less affected by seaweed chemical defenses than larger, more mobile herbivores like fishes. In this investigation, we evaluate the generality of this hypothesis by comparing the feeding of an omnivorous fish (*Lagodon rhomboides*) with that of an omnivorous, tube-building polychaete (*Platynereis dumerilii*) to see if the mesograzers prefer seaweeds avoided by the fish, and if it is less affected by seaweed chemical defense. *Platynereis dumerilii* fed almost exclusively on *Dictyota dichotoma*, the seaweed eaten least by *Lagodon rhomboides*. The diterpene alcohols (dictyol-E and pachydictyol-A) produced by *Dictyota* significantly deterred feeding by *Lagodon* but did not affect, or at one concentration stimulated, feeding by *Platynereis*. Our data support the hypothesis that small, relatively sedentary herbivores that live on plants are more resistant to chemical defenses than are large, relatively mobile herbivores that move among many plants.

**Key words:** Chemical defense – Herbivore mobility and size – Plant-herbivore interactions – Seaweeds – Terpenes

Herbivory by small, relatively sedentary herbivores such as amphipods, polychaetes, and isopods (mesograzers, *sensu* Hay et al. 1987a) has rarely been investigated (for exceptions see Nicotri 1977, 1980; Zimmerman et al. 1979; Brawley and Adey 1981a, b; Robertson and Lucas 1983; Hay et al. 1987a; Paul et al. 1988). Reasons for this include the lack of mesograzers' apparency in many habitats, the often

labor-intensive collection process, taxonomic difficulties, and a prevailing misconception that mesograzers consume only diatoms and small filamentous algae. Although many mesograzers do feed selectively on small epiphytic algae, it is becoming increasingly clear that several species commonly consume macrophytes and can significantly damage large seaweeds under natural conditions (see Hay et al. 1987a for references). Another reason that mesograzers-seaweed interactions have been neglected is that mesograzers apparently have a limited impact in most marine systems because intense predation usually limits mesograzers' densities (Nelson 1979a, b, 1981; Stoner 1980).

Many mesograzers that consume seaweeds live in mucilaginous tubes attached to the seaweeds. These mesograzers feed most near the mouth of their tubes but can make short forays from the tube or even abandon it altogether if conditions become unsuitable (Nicotri 1977, 1980; Fauchald and Jumars 1979; Brawley and Adey 1981a, b; Brostoff 1985; Hay et al. 1987a). Thus, mobility of mesograzers, relative to the size of their food plant, is limited when compared to larger and more intensively-studied herbivores like fishes and sea urchins. Therefore, tube-building mesograzers should select seaweeds on the basis of both their value as foods and as living sites (Nicotri 1980; Hay et al. 1987a) while most fishes and sea urchins should select seaweeds primarily on the basis of their value as foods (Vadas 1977; Lobel and Ogden 1981; Hay 1984).

Since mesograzers suffer intense predation from both omnivorous and predatory fishes (Nelson 1979a, b, 1981; Stoner 1980; Darcy 1985a, b), mesograzers that live on and eat seaweeds which are not eaten, and thus less often visited, by fishes should have higher fitness than those that select seaweeds favored by fishes. Mesograzers may, therefore, be under stronger selective pressure than fishes to circumvent seaweed chemical defenses, and might even use defensive chemicals as proximal cues for identifying appropriate habitats. Such cues are commonly used by terrestrial insects that feed on chemically-defended plants (Fox and Morrow 1981; Futuyama 1983). The hypothesis that mesograzers should be less affected by algal chemical defenses than larger, more mobile herbivores was first proposed by Hay et al. (1987a). They found that seaweed chemicals deterrent against a fish and sea urchin were ineffective against an herbivorous amphipod. Their findings support their hypothesis but leave open the possibility that this pattern resulted from feeding behaviors peculiar to the amphipods studied. We tested the generality of their hypothesis by in-

vestigating how seaweed chemical defenses affected feeding by the omnivorous pinfish, *Lagodon rhomboides*, versus feeding by the nereid polychaete, *Platynereis dumerilii*. *Platynereis* is taxonomically unrelated to the crustacean mesograzers studied and discussed by Hay et al. (1987a) but is ecologically similar in that it is small, relatively sedentary, and lives in a tube that is anchored on its algal host.

In this investigation we address the following specific questions:

(1) Does the mesograzer *Platynereis* selectively consume seaweeds that are avoided by the pinfish *Lagodon*?

(2) How do the diterpene alcohols produced by the brown seaweed *Dictyota dichotoma* affect feeding by *Lagodon* and *Platynereis*?

(3) Are variations in the effects of these compounds on different herbivores consistent with the hypothesis that small, relatively sedentary herbivores will be more resistant to chemical defenses than larger, more mobile herbivores?

## Methods

### Study sites and organisms

The seaweeds and herbivores used in our investigation occur in grassbed, mudflat, or shallow hard substrate (jetty and oyster reefs) communities throughout coastal North Carolina. With the exception of *Ulva rigida*, which was collected from outdoor microcosms at the Institute of Marine Sciences, Morehead City, NC, all seaweeds used in our feeding assays were collected at a depth of 0.5–3 m on the rock jetty at Radio Island near Beaufort NC (34°42'N, 75°41'W). From spring to fall, shallow portions of this jetty are dominated by a variety of seaweeds with *Sargassum filipendula*, *Dictyota dichotoma*, *Padina gymnospora*, and *Codium fragile* being most abundant. *Hypnea musciformis*, *Chondria dasyphylla*, *Calonitophyllum medium*, *Rhodomyenia pseudopalmata*, *Gracilaria tikvahiae*, and *Ulva* spp. are present but less common and many of these species decrease in abundance as omnivorous fishes (*Diplodus holbrooki*, *Lagodon rhomboides*, *Monocanthus hispidus*, and *Archargus probatocephalus*) colonize the jetty in the summer (Hay 1986). Several of these seaweeds (*Hypnea*, *Chondria*, *Gracilaria*, *Ulva*, *Dictyota*, and to a lesser extent *Codium* and *Sargassum*) are also common in grassbed and mudflat communities where they grow as epiphytes or attached to shell fragments or to tubes of large onuphid polychaetes such as *Diopatra*. Initial feeding assays were conducted with all of these seaweed species. We then focused on *Dictyota dichotoma* since it was preferred by the polychaete and not eaten by the fish. Additionally, the secondary compounds produced by *Dictyota* are well known and stable, making this a particularly good species to work with chemically.

*Dictyota dichotoma* is abundant throughout tropical and subtropical regions of the Atlantic and Caribbean (Taylor 1960). At our study sites, *D. dichotoma* produces two members of a class of diterpenoids possessing the perhydroazulene skeleton. These diterpene alcohols (called pachydictyol-A and dictyol-E) are identical except that dictyol-E possesses a single additional hydroxyl group on the side chain. The chemistry, pharmacological activities, patterns of occurrence, and concentrations of these secondary metabolites are discussed at length in Hay et al. (1987a).

We have conducted only preliminary chemical investigations on the populations of *Dictyota dichotoma* that occur

in coastal North Carolina. Yields (mass of pure compound per dry mass of plant) of pachydictyol-A and dictyol-E appear to vary among collections made at different times or locations. In some collections pachydictyol-A is the major metabolite with dictyol-E present in lesser amounts; this is reversed in other collections. Yield of the major metabolite is usually 0.5% or less. It is probable that concentrations vary among seasons, among populations, among individuals, and even among different portions of the same individual. These types of variations in secondary compound concentrations recently have been documented for seaweeds in the tropical Pacific (Paul and Van Alstyne in press), the temperate Pacific (J. Lubchenco and D. Carlson personal communication; K. Van Alstyne, personal communication), and the tropical Caribbean (Hay et al. 1988). Since we have not assessed these types of variation for *D. dichotoma* in North Carolina we conducted our experiments over a gradient of concentrations that ran from 0.1 to approximately 2 times the maximum published yield. We suspect that both the high and low ends of our concentration gradient are ecologically realistic for some plants, or plant parts, in some locations at some times of the year. Additionally, since the herbivores used in our assays are widely distributed species, our investigations are relevant for a variety of widely distributed seaweeds (*Dictyota*, *Pachydictyon*, *Dilophus*, and *Glossophora*) that contain pachydictyol-A and dictyol-E in concentrations covered by our assays.

The two most abundant herbivorous fishes along the east coast of North America are the pinfish *Lagodon rhomboides* and the spottail pinfish *Diplodus holbrooki*, both in the family Sparidae. Our experiments focused exclusively on *L. rhomboides* since it is the most common herbivorous fish in grassbed and mudflat areas in our region (Adams 1976; Darcy 1985b) and since the effects of *Dictyota* metabolites on feeding by *D. holbrooki* had been studied previously (Hay et al. 1987a). Pinfish occur in coastal waters from Cape Cod, Massachusetts to Florida, throughout the Gulf of Mexico to the Yucatan Peninsula, Mexico, and in Bermuda (Darcy 1985b). Near our study areas, pinfish are most abundant during the summer with peak densities of 2–5/m<sup>2</sup> in grassbeds (Adams 1976). All pinfish used in our assays were collected by seining shallow grassbeds and mudflats in Bogue Sound behind the Institute of Marine Sciences.

Common mesograzers in local habitats include numerous crustaceans (crabs, amphipods, shrimps, and isopods), gastropods, and a few polychaetes. We chose to concentrate our studies on the nereid polychaete, *Platynereis dumerilii*, since it was taxonomically distant from the amphipods studied by Hay et al. (1987a) but ecologically similar in that it is small (maximum length of our animals was approximately 4 cm), has limited mobility, and lives in a mucus tube it builds on algae. *P. dumerilii* is distributed worldwide in temperate and tropical seas (Day 1973). The nereid worms are generally omnivorous, feed preferentially around the mouth of their mucus tube, and are capable of leaving their tubes and building others when local conditions become unacceptable (Fauchald and Jumars 1979). In these respects, they are similar to the tube-building amphipods we studied previously (Hay et al. 1987a).

*Platynereis* were relatively rare in all habitats that we sampled but our unquantified collections suggested that they were unusually rare in hard-substrate communities where fishes were most abundant and predation on worms

potentially intense. Because *Platynereis* were not abundant at any of our sites, we were unable to rigorously quantify their density on different algal species and we had difficulty collecting enough individuals to perform all of our assays. In the field, we have seen *Platynereis* build tubes on, and feed from, several species of algae including *Dictyota dichotoma*, *Sargassum filipendula*, *Padina gymnospora*, *Codium fragile*, and *Gracilaria tikvahiae*; however our attempts to collect animals from most of these plants during September 1986 were unsuccessful. We could find animals only by bringing large quantities of *Dictyota* into the laboratory, packing the alga into shallow trays of seawater, and collecting the worms that came to the water's surface as oxygen levels in the trays dropped. We had to process many kilograms (wet mass) of *Dictyota* from mudflat habitats in order to collect the approximately 130 worms used in the experiments outlined below. Similar procedures using *Gracilaria tikvahiae* from mudflat or jetty habitat, or *Sargassum filipendula* and *Dictyota dichotoma* from jetty habitats, produced very few worms. Thus, although our collection attempts were not rigorously quantified, we could collect reasonable quantities of *Platynereis* only from *Dictyota* plants.

#### Feeding preference assays

To evaluate the feeding preferences of *Lagodon* and *Platynereis*, individual herbivores were simultaneously offered ten common seaweed species in the laboratory. The wet mass of each alga was determined at the beginning and end of each assay after spinning it for 10 revolutions in a salad spinner to remove excess water. This method is usually repeatable to within 1–2% of algal wet mass but occasionally produces readings that differ by as much as 5%.

Feeding preferences of pinfish were determined by simultaneously providing 12 fish (each in a separate aquarium) with 200 mg ( $\pm 20$  mg) of each seaweed species, allowing each fish to graze for 14 h, and then reweighing each seaweed. Twelve separate 38 l aquaria held both fish and seaweeds. Four aquaria contained only seaweeds and were used to correct for changes in algal wet mass that were unrelated to grazing by fish. Within each aquarium, seaweeds were anchored on the bottom by weaving their bases between the strands of a weighted length of 3-strand rope. The position of each alga on each rope was randomized using a random numbers table.

Feeding preferences of the polychaete, *Platynereis*, were determined by simultaneously placing 100 mg ( $\pm 10$  mg) of each seaweed species in a 15 cm diameter bowl with approximately 400 ml of seawater. All algae sank to the bottom and were thus readily available to the worms. Ten dishes contained seaweeds and one large worm; 5 contained only seaweeds and controlled for changes in mass unrelated to grazing. Worms were allowed to graze for 44 h before the algae were reweighed.

#### Chemical procedures and chemical feeding assays

*Dictyota dichotoma* was collected from Radio Island jetty and nearby mudflats, quickly frozen at  $-30^{\circ}$  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 high performance liquid chromatography (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.

We used methods similar to those of McConnell et al. (1982) and Hay et al. (1987a, b) to evaluate how pachydictyol-A and dictyol-E affected feeding by *Lagodon* and *Platynereis*. For *Lagodon* assays, 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, 0.5, or 1.0% 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 Hay et al. 1987a for a discussion of known yield of compounds versus 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 hydrophobic, 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 hydrophobic compounds were lost from *Gracilaria* blades when these were reimmersed in seawater for several hours (McConnell et al. 1982).

*Lagodon* assays were conducted by pairing one treatment and one control plant (each 300 mg  $\pm$  30 mg) in a 3-strand rope and placing this on the bottom of a 38 l aquarium. Twelve of these aquaria contained the paired seaweeds and one fish. Four aquaria contained seaweeds but no fish; these controlled for changes in algal mass unrelated to fish grazing. The *Gracilaria* pieces used in each pair were obtained by splitting a single plant; this eliminated variance in grazing that would have been caused by initial between-plant differences in palatability. Fish were allowed to graze for 20–24h, then all plants were reweighed. Since the error of our spun-wet-mass determinations may have been as much as 5%, we excluded any replicates in which neither the treatment nor control plant changed by that amount. This resulted in sample sizes as low as 8 for some assays. If the initial assay at a given metabolite concentration gave results indicating a significant ( $p < 0.05$ ) effect on feeding or clearly indicating that the compound did not affect feeding ( $p > 0.40$ ), then the assay was not repeated. If results from the initial assay suggested a trend toward increased or decreased feeding, then the entire assay for that concentration 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 to 18 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.

Effects of *Dictyota* metabolites on feeding by *Platynereis* were conducted similarly, but with the following procedural modifications: (1) We applied compounds to paired portions of *Padina* (100 mg each) instead of *Gracilaria* since our initial feeding assay suggested that *Padina* was more readily consumed by *Platynereis*. (2) Assays were conducted in 15 cm diameter bowls (10–20 with worms and *Padina*, 6 with *Padina* alone to control for changes in wet mass unrelated to grazing) instead of in aquaria. (3) Because we could find only a limited number of worms, we were unable to repeat our assays, and thus increase our sample sizes,

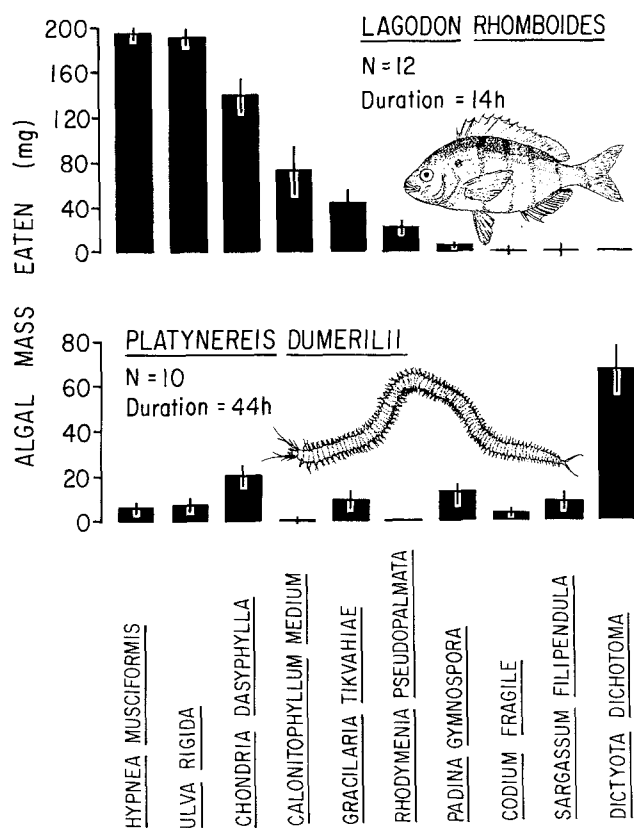


Fig. 1. The mean wet mass of algae consumed by the pinfish, *Lagodon rhomboides*, or the polychaete, *Platynereis dumerilii*, when simultaneously offered equal amounts (fish-200 mg; polychaetes-100 mg) of 10 different species

for those trials where feeding differences indicated an interesting but nonsignificant trend ( $0.1 < p < 0.2$ ). (4) Because several of the worms we collected changed from the normal atokous form to the reproductive and non-feeding epitokous form during, or just prior to, our assays, we did not have enough feeding individuals to use separate worms in all of our assays. Five of the 10 worms used in the assay of pachydictyol-A at 1.0% concentration had previously been used in the assay of dictyol-E at 0.5% concentration. They were held in the lab for 7 days between these tests. In all other assays, a worm was used once and then discarded or preserved as a voucher specimen.

## Results

The pinfish, *Lagodon rhomboides*, and the polychaete, *Platynereis dumerilii*, differed markedly in their pattern of feeding preference when offered a choice of 10 common seaweeds (Fig. 1). Pinfish consumed large amounts of *Hypnea* and *Ulva*; intermediate to low amounts of *Chondria*, *Calonitophyllum*, *Gracilaria*, and *Rhodymenia*; and negligible amounts of *Padina*, *Codium*, *Sargassum*, and *Dictyota*. The polychaete consumed large amounts of *Dictyota*; low amounts of *Chondria*, *Padina*, *Gracilaria*, *Sargassum*, *Ulva*, *Hypnea*, and *Codium*; and did not eat *Calonitophyllum* or *Rhodymenia*. It is obvious that *Platynereis* consumed much more *Dictyota* than any of the other seaweeds offered; the relative rankings of the remaining species are unclear due to the small amounts of each that were eaten.

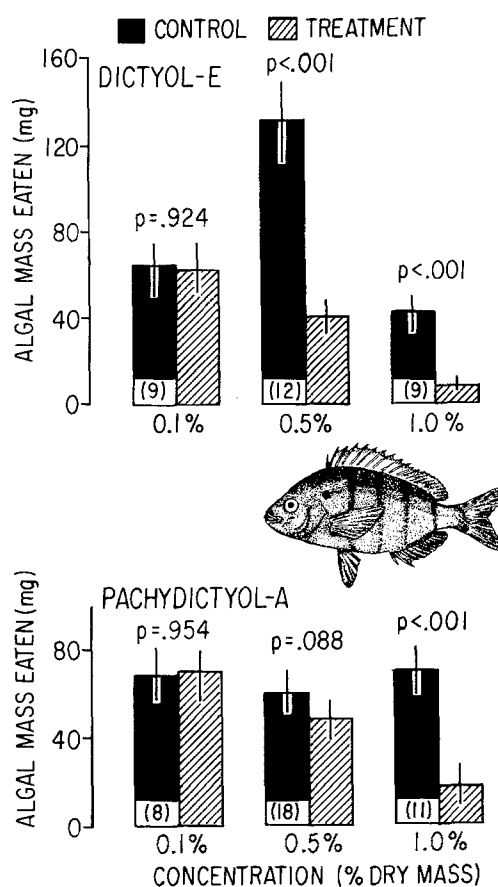
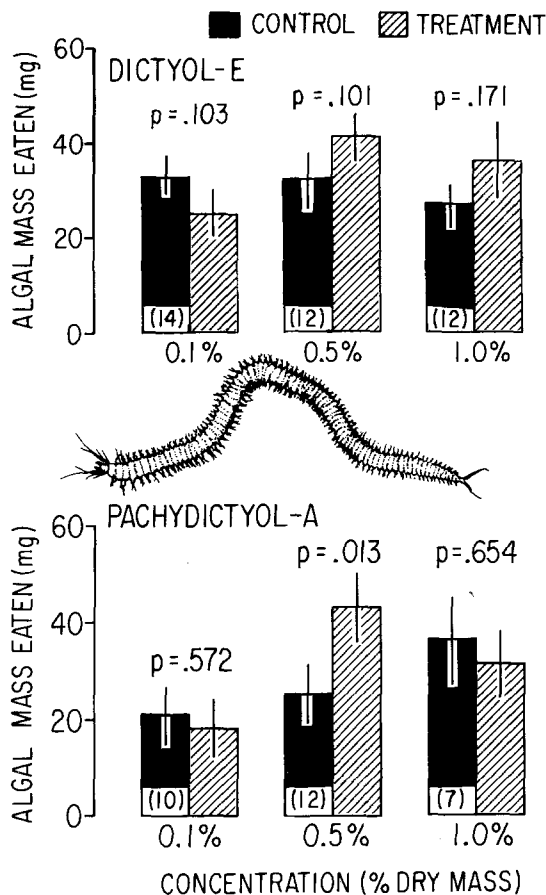


Fig. 2. The effect of dictyol-E or pachydictyol-A concentration on feeding by the pinfish, *Lagodon rhomboides*. Vertical bars through each histogram represent  $\pm 1$  standard error. P-values above each pair of histograms were computed by the paired-sample t-test. Sample size is in parentheses at the base of each histogram pair. Initial plant mass was 300 mg

Assays such as this, where more than two choices are offered simultaneously, are common in the ecological literature and are usually analyzed using an Analysis of Variance (ANOVA) or some variation on this procedure. Such analyses are inappropriate since treatments (in this case, different algal foods) are not independent (i.e. for *Platynereis*, the observed low rate of feeding on *Ulva* may have been a result of the high rate of feeding on *Dictyota*). In most cases, there are no statistical analyses appropriate for data such as these. Feeding animals on monospecific diets and comparing consumption rates on each provide data that can be analyzed using conventional methods but address a different question (how much of a species will be eaten when no choice is available; not what are the relative rankings of several species?). Assays with no choice can yield confusing results if animals consume large quantities of low preference foods in order to compensate for low nutritional quality. Given these constraints on appropriate statistical analyses, we chose to present our data without statistical analysis since the point we want to make is simply that *Dictyota dichotoma* is not eaten by *Lagodon* but preferentially consumed by *Platynereis* (Fig. 1).

When coated onto otherwise-palatable plants, the diterpene alcohols produced by *Dictyota dichotoma* reduced feeding by *Lagodon rhomboides* (Fig. 2). Dictyol-E was a stronger deterrent than pachydictyol-A. At a concentration



**Fig. 3.** The effect of dictyol-E and pachydictyol-A concentration on feeding by the polychaete, *Platynereis dumerilii*. Initial plant mass was 100 mg. Symbols and statistical analyses are the same as for Fig. 2

of 0.1% of algal dry mass, dictyol-E had no effect on *Lagodon* feeding ( $P=0.924$ ,  $N=9$ , paired-sample t-test). At concentrations of 0.5% and 1.0%, dictyol-E significantly reduced grazing by 69% ( $P<0.001$ ,  $N=12$ ) and 83% ( $P<0.001$ ,  $N=9$ ), respectively. Pachydictyol-A had no effect at 0.1% ( $P=0.954$ ,  $N=8$ ), decreased consumption by a non-significant 20% when applied at 0.5% ( $P=0.088$ ,  $N=18$ ), and caused a significant 74% decrease when applied as 1.0% of algal dry mass ( $P<0.001$ ,  $N=11$ ). Thus, at a concentration of 0.5%, dictyol-E was approximately 3.5 times more deterrent than pachydictyol-A. At a concentration of 1.0%, both dictyol-E and pachydictyol-A were strongly deterrent.

Treating palatable seaweeds with dictyol-E or pachydictyol-A either stimulated or had no effect on feeding by the polychaete, *Platynereis dumerilii* (Fig. 3). Dictyol-E had no significant effect on *Platynereis* grazing at either 0.1, 0.5, or 1.0% of plant dry mass; p-values ranged from 0.101 to 0.171 (paired-sample t-test). At a concentration of 0.1%, dictyol-E treated plants were eaten slightly less than controls (24% decrease); at concentrations of 0.5% and 1.0%, treatments were eaten slightly more than controls (increases of 27% and 35% respectively). At a concentration of 0.5%, pachydictyol-A stimulated *Platynereis* grazing by a significant 72% ( $P=0.013$ ,  $N=12$ , paired-sample t-test). At concentrations of 0.1% and 1.0%, pachydictyol-A had no effect on *Platynereis* grazing ( $P=0.572$  and  $P=0.654$ , respectively).

## Discussion

### Seaweed chemical defense

Most early investigations of seaweed chemical defenses tested compounds against a single species of herbivore (Geiselman and McConnell 1981; McConnell et al. 1982; Steinberg 1985; Targett et al. 1986). This study (Figs. 2 and 3) and other recent investigations (Hay et al. 1987a, b; Paul et al. 1988) show that responses to algal secondary metabolites vary between herbivore species, and that important ecological interactions can be missed if studies focus on defense against a single species of herbivore. In the system studied here, grazing by *Lagodon* would select for synthesis of dictyol-E and, to a lesser extent, pachydictyol-A (Fig. 2); grazing by *Platynereis* would not select for, and could select against, synthesis of these secondary metabolites (Fig. 3). The extreme variance in how different herbivore species respond to seaweed secondary metabolites raises several questions about the ecology and evolution of plant-herbivore interactions in general.

Most seaweeds are consumed by a diverse array of herbivores including: fishes, sea urchins, gastropods, polychaetes, and crustaceans. Within any one of these groups, herbivore physiology, feeding behavior, and mouthpart morphology and strength may vary considerably (Lubchenco and Gaines 1981; Steneck and Watling 1982; Gaines and Lubchenco 1982; Hawkins and Hartnoll 1983). Variance among the different groups is tremendous and has been used to argue that herbivore pressure on seaweeds has escalated through evolutionary time as herbivores evolved new and increasingly more-powerful feeding modes (Steneck 1983, 1986). The evolution of seaweed defensive characteristics should be responsive to how these characteristics affect the overall rate of herbivory on the plant, not necessarily how they affect grazing by individual herbivore species. Compared to other algal secondary metabolites, pachydictyol-A and dictyol-E have been studied extensively and appear to be relatively effective, although variable, deterrents against a broad range of marine herbivores. Pachydictyol-A deters feeding by tropical parrotfishes, the tropical sea urchin *Diadema antillarum* (Hay et al. 1987b), and the temperate omnivorous fishes *Lagodon rhomboides* (Fig. 2) and *Diplodus holbrooki* (Hay et al. 1987a). It does not deter the temperate sea urchin *Arbacia punctulata*, the temperate amphipod *Ampithoe longimana* (Hay et al. 1987a), or the cosmopolitan polychaete *Platynereis dumerilii* (Fig. 3). Dictyol-E deters feeding by the temperate fishes *Lagodon* (Fig. 2) and *Diplodus* and by the temperate sea urchin *Arbacia*; however it is not effective against the temperate amphipod *Ampithoe longimana* (Hay et al. 1987a) or the polychaete *Platynereis* (Fig. 3). The relatively strong deterrent effects of pachydictyol-A or dictyol-E on fishes and urchins from different habitats and geographic areas suggest that these compounds are generally effective against large mobile herbivores. In contrast, the compounds are ineffective against the polychaete and amphipod we studied. In North Carolina, these mesograzers preferentially consume the only seaweed in their respective habitats that produces these compounds (Fig. 1; Hay et al. 1987a).

The general effectiveness of seaweed secondary metabolites against fishes and sea urchins (McConnell et al. 1982; Targett et al. 1986; Hay et al. 1987a, b, 1988; Paul et al. 1988; Paul and Van Alstyne 1988) suggests that their feeding constitutes strong selection for the evolution of seaweed

chemical defenses. Experimental field studies have repeatedly shown that these herbivores have a profound effect on the organization of benthic seaweed communities (Lawrence 1975; Ogden 1976; Lubchenco and Gaines 1981; Hay 1985; Lewis 1986; Carpenter 1986). In contrast, it appears that feeding by mesograzers is less often affected by seaweed metabolites (Fig. 3; Hay et al. 1987a; Paul et al. 1988). This suggests that feeding by these herbivores less commonly selects for secondary metabolite production in seaweeds. Studies of these smaller herbivores show that they are rarely resource limited (Zimmerman et al. 1979; Stoner 1980) but are often strongly affected by their predators (Young et al. 1976; Young and Young 1978; Nelson 1979a, 1980, 1981; Brawley and Adey 1981a, b; Stoner 1980; Edgar 1983; Robertson and Lucas 1983). They appear to have only limited impact on seaweeds (Carpenter 1986) because predators usually keep mesograzers below carrying capacity.

#### *Herbivore size, mobility, and resistance to chemical defenses*

The feeding patterns documented here for the omnivorous fish *Lagodon rhomboides* and the polychaete *Platynereis dumerilii* (Figs. 1–3) are remarkably similar to those documented in a previous study focusing on the omnivorous fish *Diplodus holbrooki* and the herbivorous amphipod *Ampithoe longimana* (Hay et al. 1987a). In both cases, seaweeds avoided by the fishes were preferred by the mesograzers. Hay et al. (1987a) argued that relatively sedentary amphipods which are commonly consumed by omnivorous fishes should be under strong selective pressure to circumvent seaweed chemical defenses since this would provide a relatively safe living site coupled with a food source. Our data for a taxonomically unrelated, but ecologically similar, mesograzers support this hypothesis (Figs. 1 and 3). Additionally, other recent studies suggest that this pattern may be widespread. A halogenated monoterpene produced by the red alga *Ochtodes secundiramea* deters feeding by both Caribbean and Pacific reef fishes but does not affect feeding by a mixed species group of Caribbean amphipods (Paul et al. 1988), and the C<sub>11</sub> hydrocarbons produced by the brown alga *Dictyopteria delicatula* deter Caribbean fishes but not amphipods (M. Hay, E. Duffy, K. Gustafson, and W. Fenical, unpublished work). Hay et al. (1987a) discuss the evolutionary implications of this pattern, the relative degree of feeding specialization in small marine versus small terrestrial herbivores, and the ecological parallels between marine mesograzers and terrestrial insect herbivores.

Within this framework, it is interesting to note that both the polychaete *Platynereis* and the amphipod *Ampithoe* show a strong preference for *Dictyota* and are not deterred by its secondary metabolites (Fig. 3; Hay et al. 1987a); however, neither herbivore is restrictively specialized to this seaweed. *Platynereis* is found world-wide on a variety of seaweeds; in Hawaii, it inhabited 27 of the 29 seaweeds sampled by Brostoff (1985) and consumed 28 of the 29 species in laboratory feeding trials. *Ampithoe* is similar in that it occurs in a wide variety of habitats, is associated with many different types of seaweeds (Bousfield 1973; Stoner 1980; Nelson 1979b, 1980), and will consume numerous unrelated species (Hay et al. 1987a).

The pattern that appears to be emerging from this study and those cited above is that mesograzers are generalist

feeders with strong food preferences, and are better able to circumvent seaweed chemical defenses than are larger more mobile herbivores. Similar patterns have been documented for terrestrial insects that use the mixed-function oxidase (MFO) system to carry out the hydroxylation, demethylation, and epoxidation of diverse groups of lipophilic metabolites (Dauterman and Hodgson 1978; Brattsten 1979; Futuyama 1983). The ability of marine amphipods and polychaetes to tolerate seaweed compounds that deter fishes and urchins suggests that they may be ecologically similar to terrestrial insects and may rely on similar detoxifying mechanisms.

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