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CHEMICAL DEFENSE AGAINST DIVERSE CORAL-REEF HERBIVORES[1]

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Abstract. Five secondary metabolites from tropical marine algae and one related compound from an herbivorous sea-hare (Aplysidae) were coated, at approximately natural concentrations, onto the palatable seagrass *Thalassia testudinum* and placed on coral reefs where they could be eaten by the diverse group of herbivorous fishes that occur there. Laboratory feeding assays with the herbivorous sea urchin *Diadema antillarum* were also conducted. When compared to appropriate controls, the following terpenoid compounds significantly reduced the amount of *Thalassia* eaten by both *Diadema* and reef fishes: stypotriol, from the brown seaweed *Stypopodium zonale*; pachydictyol-A, which is produced by several genera of tropical (*Dictyota* and *Dilophus*) and warm-temperate (*Pachydictyon* and *Glossophora*) brown seaweeds; elatol, from the tropical red alga *Laurencia obtusa*; and isolaurinterol, which is produced by several tropical and warm-temperate species of *Laurencia.* Under very mild acid conditions, isolaurinterol is converted to a structurally similar compound, aplysin, found in high concentrations in sea-hares that feed on isolaurinterol-containing *Laurencia* species. Aplysin did not deter feeding by either type of herbivore. Cymopol, a terpenoid bromohydroquinone from the green alga *Cymopolia barbata,* significantly reduced feeding by reef fishes but significantly stimulated feeding by *Diadema.*

Pharmacological and crude bioactivity tests suggest that several of these compounds function as generalized toxins. However, these generalized laboratory assays are not necessarily good predictors of how compounds will affect feeding by herbivores. For example, pachydictyol-A and stypotriol were equally effective at deterring fishes and *Diadema,* even though pachydictyol-A shows almost no bioactivity in laboratory assays while stypotriol and its oxidation product, stypoldione, are very bioactive.

Herbivory on coral reefs is more intense than in any other habitat studied and the diversity of herbivore types is high. It appears that this intense grazing has provided strong selection for seaweeds that synthesize unique secondary metabolites that significantly reduce the consumption of plants exposed to attack by a diverse group of reef herbivores.

Key words: *algae*; *Caribbean*; *chemical defense*; *coral reef*; Diadema antillarum; *feeding effects*; *fish*; *herbivory*; *parrotfish*; *plant–herbivore interactions*; *terpenes.*

INTRODUCTION

The importance of plant compounds in reducing herbivory in terrestrial communities is well studied and generally accepted as one of the most effective of a number of important defensive mechanisms (Rosenthal and Janzen 1979, Coley et al. 1985) even though some specialist herbivores invariably evolve a tolerance to, or even need for, the compounds (Brower 1969, Rothschild 1973, Smiley et al. 1985). In marine communities, the potential importance of secondary compounds from seaweeds is not well studied and is more controversial. Most authors have tended to emphasize either morphological defenses (Littler and Littler 1980, Hay 1981*a*, Steneck and Watling 1982, Littler et al. 1983) or chemical defenses (Norris and Fenical 1982, Paul and Fenical 1983, Hay 1984*a*, Steinberg 1984, 1985, Targett et al. 1986). However, with the exception of recent studies on the chemical ecology of temperate brown seaweeds (Geiselman and McConnell 1981, Steinberg 1985), these contentions have rarely been evaluated using ecologically relevant, controlled experiments. In addition, studies that have used large numbers of species to correlate resistance to herbivory with various chemical or morphological characteristics may be seriously confounded, since the most common calcified species (an obvious morphological deterrent) also contain unusual, and apparently toxic, secondary metabolites (Paul and Fenical 1983, Hay 1984*a*, Targett et al. 1986, Paul and Hay 1986). In this study

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we focused primarily on compounds from fleshy species with no obvious morphological deterrents. We felt that compounds from these species offered the greatest opportunity to test unambiguously the potential deterrent effects of secondary metabolites from seaweeds. In addition to the fleshy species, we also investigated a compound from one calcified species (*Cymopolia*) to see if the compound, in the absence of calcification, could decrease herbivory.

Previous studies on the ability of algal metabolites to deter grazing have tested compounds against single herbivore species (Geiselman and McConnell 1981, McConnell et al. 1982, Paul and Fenical 1983, Steinberg 1985, Targett et al. 1986). This method provides ecologically and evolutionarily interesting results about specific herbivores, but cannot provide adequate information on the relative protective value that these compounds provide under field conditions where the diversity of herbivores may be high. This is especially true for tropical coral reefs where the richness of herbivorous species is very high and where different herbivore types can show striking differences in feeding preferences (Littler et al. 1983, Lewis 1985).

Herbivory on coral reefs is more intense than in any other habitat studied; grazers often remove 50–100% of total plant production (Hatcher and Larkum 1983, Carpenter 1986). For the seaweeds, this means that reducing herbivory by one species or type of herbivore may have little, if any, selective value, since abundant herbivore species that are unaffected may still be able to remove all plant production. As an example, either fishes alone or urchins alone can remove 100% of plant production on the shallow forereef in St. Croix, United States Virgin Islands (Carpenter 1986). In addition, effective defenses against one herbivore may cause increased feeding by another. Recent field studies in terrestrial habitats have shown that increased concentrations of toxic secondary metabolites may increase the herbivore damage that a plant receives if some grazers are specialized to use the plant toxin as a defense against their own predators (Smiley et al. 1985).

To address how secondary metabolites from tropical seaweeds affected the mean feeding rate of the diverse group of herbivores that occur on coral reefs, we applied natural concentrations of chemically pure metabolites to blades of the palatable seagrass *Thalassia testudinum* and placed these treated blades, along with appropriate controls, on coral reefs where they would be accessible to grazing fishes. Gut content studies of Caribbean reef fishes show that at least 23 different species consume *Thalassia* (Randall 1967); however, our observations, and those of Lewis (1985), suggest that almost all grazing in our tests was done by parrotfishes and not by the other herbivorous fishes that Randall shows occasionally consume *Thalassia.* Since parrotfishes have fused teeth and a strong jaw musculature that allows them to feed on tough or even heavily calcified algae (Steneck 1983, Hay 1984*a*, Lewis 1985), chemical defenses against this group of fishes may be especially important, since the evolution of effective morhpological defenses seems unlikely (Hay 1984*a*, Lewis 1985, Targett et al. 1986). Therefore, our field assay method does not assess how specific herbivore species respond to these compounds; it assesses the potential deterrent properties of these compounds against the mixed species group of herbivorous fishes that consume large seaweeds like *Thalassia.* We also performed laboratory tests to evaluate the effect of these compounds on feeding by the sea urchin *Diadema antillarum.*

Methods

Study sites, compounds, and herbivores

All compounds were tested against the herbivorous sea urchin *Diadema antillarum* and the group of herbivorous reef fishes that consume the seagrass *Thalassia testudinum.* Until very recently, *Diadema* was the most numerous and ecologically important sea urchin on Caribbean coral reefs (Ogden et al. 1973, Lawrence and Sammarco 1982). In 1983 and 1984, a pathogen destroyed 95–99% of all Caribbean *D. antillarum* (Lessios et al. 1984). Before this large-scale death of *Diadema,* grazing by these urchins appeared to be intense on shallow portions of heavily fished reefs but relatively light on remote and unfished reefs (Hay 1984*b*). All assays involving *Diadema* were conducted at the Galeta Marine Laboratory of the Smithsonian Tropical Research Institute located at Galeta Point, Panama (9°24′ N, 79°52′ W). The reef at Galeta is typical of fringing reefs on the Caribbean coast of Panama and has been described in several previous publications (Glynn 1972, MacIntyre and Glynn 1976, Hay 1981*b*).

Diadema available in the area included a few large individuals that had survived the 1983 die-off and rare juveniles that had settled since the die-off. Initial attempts to use large individuals in our assays were unsatisfactory, since they would not feed when placed in the small 3.8-L jars that were available as feeding arenas, and since getting them into and out of the jars necessitated clipping their spines. For these reasons, we used only small individuals (2.5–4 cm test diameter) in our tests. These urchins came from two separate sources. Eight had settled on Galeta Reef ≈2 yr before our tests (J. Cubit, *personal communication*); they had been collected shortly after settlement and held in a flowing seawater table until used in our tests. Twelve additional juveniles were collected from the lee side of reefs near Galeta before our feeding assays began; midway through the trials, four more were found in the same location. Since juveniles from the seawater table had no experience with foraging in nature and had probably been on unnaturally low rations, we were concerned that they might feed less discriminately than urchins collected from the reef. During our first assay (Table 1, pachydictyol-A), only four of the urchins from

TABLE 1. The order in which compounds were tested against *Diadema* and the number of replicates that were excluded from the paired analyses because urchins either ate all of both plants or ate none of either.

Order of test	Compound	Date	Number of urchins available	Number of urchins that did not feed	Number of urchins that ate all of both treatments	Final sample size	% of urchins used in analyses
1st	Pachydictyol-A	25 Oct	20	12	0	8	40
2nd	Elatol	26 Oct	20	9	0	11	55
3rd	Cymopol	26 Oct	24	5	3	16	67
4th	Stypotriol	27 Oct	24	9	1	14	58
5th	Aplysin	27 Oct	24	5	3	12	50
6th	Isolaurinterol	28 Oct	24	3	2	19	79

each source fed; however, the feeding urchins from the two sources showed similar preferences. Urchins from the seawater table ate 48% more of the control than treatment blades; urchins from the field ate 40% more ($P \gg .50$ t test). Because these feeding patterns were so similar, we assumed the urchins from the seawater table were as representative as those collected from the field and did not keep separate data on these groups in later assays.

Since juvenile *Diadema* were rare, we had to use the same 20–24 urchins in all six of our feeding assays. Table 1 shows the order in which the compounds were tested, the number of urchins used in each trial, and the numer of urchins that did not feed or that ate all of both plants during a trial. This design did not allow us to control for carry-over effects (i.e., it is possible that urchins become increasingly sensitive to these types of compounds with increasing exposure and that the probability of detecting a deterrent effect will increase in the later assays); however, the feeding patterns of urchins did not show any clear directional changes during the course of our assays (see Table 1 and the Results section), indicating that carry-over effects were probably minimal.

We did not assay compounds against specific species of herbivorous fishes but chose instead to ask, "Do these compounds significantly deter herbivory by the mixed species of herbivorous fishes that consume seaweeds on coral reefs?" We assessed this by placing treated and control pieces of the palatable seagrass *Thalassia testudinum* on the reef at Galeta or on the reef at Pte. Borgnesse in Martinique (14°26′ N, 61°56′ W). Fish assays using the compound cymopol were conducted at a depth of 3–6 m on the reef at Galeta. Fish assays with all other compounds were conducted at a depth of 8–15 m on the reef at Pte. Borgnesse, Martinique. From the surface, the Martinique reef dropped steeply to a depth of ≈30 m where it merged with a plain of unconsolidated sediments. Numerous species of herbivorous fishes (primarily Scaridae, Acanthuridae, and Pomacentridae) occurred on the reef, but our qualitative observations, like the well-quantified observations of Lewis (1985), suggested that most, if not all, of the grazing on *Thalassia* was due to several species of parrotfishes (primarily *Sparisoma rubripinne, S. vivide, S. aurofrenatum,* and *Scarus taeniopterus*). Given that hundreds to thousands (when schools passed through) of parrotfishes used the reef in the immediate vicinity of our transplants, and that these transplants were spread along a transect of >400 m in length during the course of the assays, we felt that replicate pairs were independent and that there were no carry-over effects from one test to the next.

In all assays, we used only pure compounds and not crude algal extracts. Compounds were purified in the laboratory using high performance liquid chromatography, then immediately weighed and frozen until used in the assays with herbivores. The normal concentrations of these compounds in reef algae are poorly documented, since most literature on algal secondary metabolites has been generated by chemists interested primarily in describing new compounds and not in meticuously documenting their natural concentrations. These chemists rarely list the yield of the compound (i.e., mass of compound per mass of plant). When yields are listed they are conservative, since extraction is rarely, if ever, complete and since most isolation and purification techniques entail the loss of significant quantities of the metabolite. Maximum yields of the compounds we tested ranged from 0.6% to 3% of algal dry mass (see Appendix); we tested all of our compounds at a concentration of 1% of *Thalassia* dry mass. Each of the compounds, the algae in which they occur, their yields, and their known biological effects are described in the Appendix. The structure of each compound is shown in Fig. 1.

Grazing assays

For our grazing assays, blades of the palatable seagrass *Thalassia testudinum* were coated with a solution of the metabolite in diethyl ether so that the final metabolite concentration on the blade was ≈1% of the dry mass of the *Thalassia.* Dry mass of wet blades was calculated using a previously determined wet mass/dry mass ratio. Control *Thalassia* blades were coated only with diethyl ether. Since all of these metabolites are lipid soluble, they adhere to the surface of the *Thalassia* after the ether evaporates and can then be placed in

seawater for the feeding experiments. Much of our experimental protocol is based on previous work by McConnell et al. (1982). These investigators studied similar metabolites (i.e., nonpolar, lipid-soluble ones) from the green alga *Caulerpa* and the red alga *Gracilaria*. When coated onto palatable seaweeds that were placed in seawater for 2–3 h, they recovered 100% of the *Gracilaria* extracts and 88% of the *Caulerpa* extracts from the surface of the treated seaweeds. They also tested the effect of ether coating alone (i.e., ether coated vs. uncoated control plants) on grazing by the sea urchhn *Lytechinus variegatus*; all ether appeared to evaporate from the blades and treated blades did not differ from controls in their susceptibility to urchin grazing. D. Morrison (*personal communication*) has conducted similar assays using parrotfishes and the sea urchin *Diadema*; he also reports no effects of ether alone.

Following each of our field assays, all remaining *Thalassia* blades that had been treated with a metabolite were extracted in ether and the extract analyzed by thin layer chromatography (TLC). This TLC was compared with a TLC of the pure compound to determine qualitatively if the compound was still present and if degradation to some other compound had occurred. In all cases, TLC indicated that easily detectable quantities of the compounds remained on the plants. TLC does not yield quantitative results, and the analytical HPLC equipment that could be used for such an analysis was not available at these remote field sites. We can thus say that some of the compounds we applied stayed on the plants; however, we cannot determine if this was 100% or only 50% of the original concentration. We do not view this inability to determine final concentrations as a major problem in this study since any losses of compounds would make our assays more conservative and most assays showed a significant effect of the compound. With one exception, all compounds were stable and showed no conversion to other products; a small proportion of stypotriol oxidized to stypoldione (we visually estimated this to be <10–20%) during our tests.

For field assays on how compounds affected feeding by reef fishes that eat *Thalassia,* five 6-cm lengths of *Thalassia* were woven between the strands of a 50-cm length of three-strand rope. In the field, treatment blades of *Thalassia* on one rope were paired with control blades on a separate rope by placing the ropes within ≈1 m of each other. Twenty-five to 43 pairs of ropes were used in tests with each compound. After 2–3 h, all ropes were recovered from the reef and grazing was measured by estimating the decrease in length (to the nearest 0.5 cm) of the *Thalassia* blades. In cases where blades were grazed along the sides instead of from the top down, we cut upper portions of the blades to fill in the grazing scars along the margins and then estimated the length missing. See Hay (1984*b*) for an elaboration on this methodology. All assay results were analyzed by the Wilcoxon Paired-Sample Test after excluding rope pairs from which all plants, or no plants, had been consumed (total consumption of all plants in a rope pair occurred on only one occasion). This is a standard procedure for paired-sample tests (Zar 1974); it resulted in sample sizes that ranged from 22 to 39 pairs.

Parametric statistical procedures could not be used in several of our tests because the differences among pairs were not normally distributed. This appeared to occur because of the spatial patchiness of grazing intensity that occurs on most reefs (Hay 1985). It appeared that pairs were either often encountered, heavily grazed, and showed large between-treatment differences, or pairs were seldom encountered, only lightly grazed, and showed small between-treatment differences. This produced a bimodal distribution of differences. Since the Wilcoxon Paired-Sample Test is usually conservative when compared to the paired-sample *t* test, we chose to use this procedure on all of our comparisons.

Assays involving the sea urchin *Diadema antillarum* were conducted in 3.8-L glass containers with one urchin in each container. One treatment and one control *Thalassia* blade (6 cm long) were held in the bottom of each container by placing the base of each blade through a slit in a heavy rubber disc. This allowed blades to protrude from the bottom of the container much as they do in nature. Twenty to 24 urchins were used in each assay, and assays lasted for 2–9 h depending upon how rapidly the urchins fed. Blades were checked at ≈2-h intervals and both blades were removed and measured (as described above) whenever 50% of either blade appeared to have been consumed. Despite these frequent checks, urchins occasionally consumed both blades in a 2-h period or failed to graze at all before the experiment was terminated (see Table 1). As in the fish assays, these pairs were excluded from the analyses, resulting in sample sizes of 8–19 pairs for the different assays. All urchin assays were analyzed by the Wilcoxon Paired-Sample Test.

Results

Aplysin did not affect ($P > .50$) grazing by reef fishes that consume *Thalassia*: all other compounds significantly reduced grazing by this herbivore group ($P < .05$, Wilcoxon Paired-Sample Test, Fig. 1). Most of the compounds tested were nearly equivalent in their ability to deter feeding by these fishes: cymopol (−32%), isolaurinterol (−28%), stypotriol (−33%), and pachydictyol-A (−29%). Elatol was approximately twice as effective as the other compounds and reduced loss of *Thalassia* by 60% (Fig. 1).

Although our design precluded a rigorous test of the importance of carry-over effects in the *Diadema* feeding assays, the general patterns, or lack thereof, shown in Table 1 do not support the contention that these urchins were becoming more or less sensitive to compounds as these assays continued. The first, second,

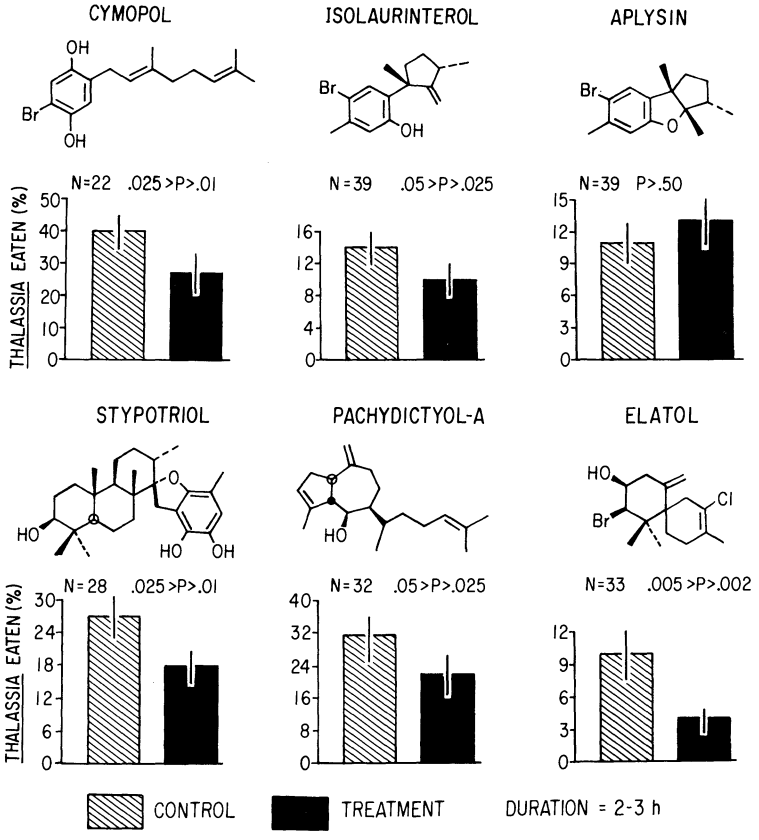

FIG. 1. The effect of six different metabolites on feeding by herbivorous reef fishes. Tests with cymopol were conducted on the reef at Galeta, Panama; all other tests were conducted on the reef at Pte. Borgnesse, Martinique. Vertical bars through each histogram show ± one standard error. Significance values are from the Wilcoxon Paired-Sample Test.

fourth, and sixth compounds tested all significantly decreased *Diadema* grazing; the third compound increased grazing and the fifth compound had no effect. Exclusion from the Wilcoxon Paired-Sample Test of those replicates where all of both *Thalassia* blades were eaten also had little effect on the patterns documented. Complete consumption of both blades occurred commonly only in the tests with cymopol, which enhanced feeding, and aplysin, which had no effect on feeding.

As with the fishes, aplysin had no effect ($P > .50$) on feeding by the sea urchin *Diadema antillarum* (Fig. 2). Isolaurinterol (−44%), stypotriol (−52%), and pachydictyol-A (−58%) were again roughly equivalent in their ability to decrease grazing losses. Elatol was the most effective deterrent. It reduced *Diadema* grazing by 86%. For fishes that consume *Thalassia,* cymopol caused a significant reduction in grazing (Fig. 1). In direct contrast, when cymopol-coated *Thalassia* blades were presented to *Diadema,* the compound increased grazing losses by a significant 94%. ($P < .01$, Fig. 2).

Most of the reduced *Diadema* grazing on treated blades resulted from lower rates of consumption once the urchins had bitten the blades, as opposed to detection and avoidance of the compound-treated blades before any consumption occurred (Table 2). Only elatol-treated blades were significantly less likely to be bitten than control blades ($P = .05$, Fisher's Exact Test). This analysis was not done for fishes, since almost all ropes showed some grazing and since direct observations of fish grazing had been made during previous studies (see Discussion).

DISCUSSION

Previous investigations on the function of secondary compounds from seaweeds have focused primarily on how phenolics from temperate kelps (Laminariales), or rock weeds (Fucales), affect feeding by the gastropods *Tegula funebralis* (Steinberg 1985) or *Littorina littorea* (Geiselman and McConnell 1981). The exception to this is McConnell et al. (1982), who investigated the feeding deterrent effects of several tropical algal metabolites against the herbivorous sea urchin *Lytechinus variegatus.* Their experimental design and low sample size prevented any of their results from being significant at the 95% confidence level, but their tests suggested ($P = .10$) that cymopol and caulerpenyne, an oxygenated sesquiterpene from the green alga *Caulerpa prolifera,* inhibited grazing by *Lytechinus.* The other compounds they tested included the pure compound caulerpin, crude extracts from several species of *Cau-*

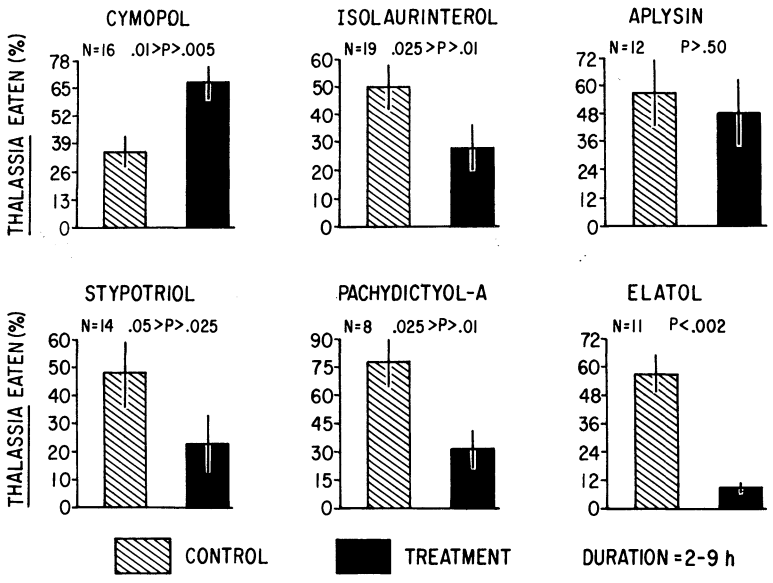

FIG. 2. The effect of six different metabolites on feeding by the herbivorous sea urchin *Diadema antillarum*. All tests were conducted in the laboratory at Galeta, Panama; symbols and statistical tests are as in Fig. 1.

lerpa, and the crude extract from *Gracilaria foliifera,* which has no secondary compounds. These compounds or extracts did not appear to affect *Lytechinus* feeding.

Numerous previous studies on the palatability of coral-reef seaweeds have shown that *Laurencia obtusa, Stypopodium zonale,* and various species of *Dictyota* are consumed at relatively low rates by Caribbean reef herbivores (Ogden 1976, Hay 1981*c*, 1984*a*, Hay and Goertemiller 1983, Littler et al. 1983, Paul and Hay 1986). All of these authors, and others (Fenical 1975, Gerwick and Fenical 1981, Norris and Fenical 1982), have commented on the potential importance of secondary metabolites as herbivore defenses in these species, but the hypothesis has not been subjected to an ecologically relevant test. The relative resistance to grazing that characterizes *Cymopolia barbata* and the Caribbean species of *Laurencia* that produce isolaurinterol is not well known.

In the field, all compounds but aplysin significantly reduced plant loss to the group of fishes that consume *Thalassia* (Fig. 1). The magnitude of these reductions, relative to losses in control plants, ranged from −28% for isolaurinterol to −60% for elatol. These reductions should be very conservative since fishes appear to recognize *Thalassia* visually as an appropriate food and have to bite treated blades before recognizing that they are less palatable than expected. Given the large numbers of herbivorous fishes (hundreds to thousands depending upon location) using the reefs in the vicinity of our ropes, most of the loss of treatment plants may have resulted from numerous individual fish testing and then rejecting the treatments. This sampling by multiple fish could cause large losses, even if each fish took only one bite and then swam away. Preliminary tests of the methodology using different numbers of *Thalassia* blades per rope suggested that plants had to be presented in sufficient quantity so that multiple fish could sample a patch enough to "learn" the location of the defended and control patches before all plants were depleted due to this sampling. Observations in other field tests with compounds from the green alga *Halimeda* (M. Hay and V. Paul, *personal observation*) showed that fishes did not avoid coated blades without biting them. When one treatment and one control blade were placed in each rope, parrotfishes bit both blades with equal frequency and consumed equal amounts of both blades. When we made patches larger by placing five blades in each rope and easier to distinguish by placing treatment and control blades in separate ropes

TABLE 2. The number of *Thalassia* blades (control vs. treatment) that showed scars from *Diadema* grazing following the feeding assays. *P* values are from one-tailed Fisher's Exact Tests.

Treatment	With grazing scars	No grazing scars	*P*
Cymopol	14	2	.11
Control	10	6	
Isolaurinterol	14	5	.20
Control	17	2	
Aplysin	8	4	.50
Control	9	3	
Stypotriol	7	7	.20
Control	11	3	
Pachydictyol-A	5	3	.50
Control	7	1	
Elatol	5	6	.05
Control	10	1	

that were located within 0.5–1 m of each other, we still noted no significant difference in the probability of a newly arriving fish taking its first bite from a treatment or control rope (i.e., fish did not detect treated blades without tasting them), but we did note a significant decrease in the amount of treatment blades consumed. After taking one or two bites from a patch of treated blades, fishes usually swam away and did not return; after biting control blades, fishes often continued to feed on plants in that rope or swam away but usually returned and ate more. Thus, it appears that herbivorous reef fishes can respond to food quality differences even among patches of plants that are morphologically identical. We suspect that feeding differences between treatment and control plants would have been much greater if treatment and control plants had been visually distinguishable, as is the case with different algal species. Given that *Thalassia* is (1) one of the most preferred macrophytes that grows near reefs (Lobel and Ogden 1981, Hay 1981*c*, Paul and Hay 1986), (2) visually recognized as a palatable species, (3) contacted by several to several hundred parrotfishes (when schooling) during the course of our assays, and (4) visually indistinguishable from control blades when coated with compounds, we find it remarkable that these compounds significantly reduced consumption during our 2–3 h field assays. This argues strongly for the deterrent properties of these compounds.

The 28–60% reductions in fish grazing shown in Fig. 1 clearly indicate that these compounds will enhance the fitness of macrophytes that grow on or near coral reefs where herbivores are abundant. The fact that more than 20% of the treatment plants were consumed in only 2–3 h in some of our tests does not contradict this contention. Our tests were conservatively designed to detect relative differences in palatability caused by these compounds; they were not designed to measure feeding rates on common reef plants under natural conditions. Our assays placed plants in reef areas where herbivory by fishes is maximal (Hay 1981*c*, 1984*b*, 1985) and used an assay plant that parrotfishes visually recognize as a favored food. If we had placed our assay ropes in deeper or shallower areas where grazing is lower (Hay 1984*a*, 1985), had made our treatment and control blades visually distinguishable, or had assayed compounds in the laboratory against individual animals that could more easily learn the location of treatment and control blades, then consumption of our treatment blades would probably have been considerably reduced. Reef fishes have had thousands of years to evolve an aversion for *Dictyota, Stypopodium, Laurencia obtusa,* and *Cymopolia*; in our tests they had only 2–3 h to "learn" which plants contained compounds and to recognize that these were spatially isolated from the control plants.

Most of the compounds that deterred reef fishes in the field also deterred the sea urchin *Diadema antillarum* in the laboratory (Fig. 2). As in the assay with fishes, aplysin had no significant effect on *Diadema* grazing ($P > .50$). Cymopol significantly reduces fish grazing (Fig. 1) and appears to inhibit grazing in the sea urchin *Lytechinus variegatus* (McConnell et al. 1982). However, in striking contrast to these patterns, cymopol nearly doubled (+94%) the grazing rate of the sea urchin *Diadema antillarum* ($P < .01$, Fig. 2). Although results like this are not unusual for specialized herbivorous insects that are coevolved with a specific species or group of toxic plants (Smiley et al. 1985), this result is surprising for a generalist marine herbivore. At present, we are reluctant to interpret this as a coevolved interaction for the following reasons. *Diadema* and the species of common parrotfishes that consumed our *Thalassia* transplants co-occur with *Cymopolia* throughout the northern Caribbean, but *Cymopolia* has never been reported from either Martinique or Panama (Taylor 1960), where our assays were conducted. Thus, the individual herbivores used in our assays could never have contacted *Cymopolia.* In addition, *Cymopolia* is rarely very abundant on coral reefs anywhere in the Caribbean. This makes it difficult to understand the selective advantage that would be involved in the evolution of some specialized feeding relationship with *Cymopolia.* We are thus unable to comment on the ecological or evolutionary significance of *Diadema*'s attraction to cymopol. It is, however, a clear example of the need to test secondary plant compounds against multiple types of herbivores, since not all compounds have similar effects even against generalist grazers.

As with the fishes, *Diadema* rarely avoided treatment blades before consuming some portion of them. With the exception of elatol, treated and control blades did not differ in their probability of showing the jagged-shaped scars of *Diadema* grazing ($P > .10$ for all compounds but elatol, Table 2). In contrast to the less deterrent compounds, elatol-coated blades were bitten less frequently than control blades; 91% of ether-coated blades showed scars while only 45% of the ether-and-elatol-coated blades exhibited scars ($P = .05$). Therefore, for strongly repellent compounds like elatol, *Diadema* may be able to sense, and avoid, these on contact. However, most compounds appear to minimize consumption once the plant is attacked but have little effect on the probability of its being attacked.

With the exception of cymopol, which inhibits fish grazing but enhances urchin grazing, these compounds appear to be effective at deterring herbivores in general. Nothing is known about the physiological effects of ingesting these compounds, but the results of very general laboratory assays and of more specific pharmacological assays (see Appendix) suggest that elatol, stypotriol, and its oxidation product stypoldione could be toxins.

Elatol is a cytotoxin and inhibits 50% of the cell divisions in fertilized sea urchin eggs at a concentration of 7 μg/mL (Norris and Fenical 1982). Extracts from

Stypopodium are toxic to damselfish at concentrations of only 0.2 μg/mL and also show antibiotic effects (Gerwick and Fenical 1981, Norris and Fenical 1982). In addition, the compound stypotriol rapidly oxidizes to the orthoquinone stypoldione when *Stypopodium* is mascerated; we assume this would occur in the mouth and gut of an herbivore. Stypoldione is lethal to fish at a concentration of 1 μg/mL and is a potent inhibitor of cell cleavage in fertilized sea urchin eggs and of motility in urchin sperm; it also inhibits both amino acid and nucleoside uptake (White and Jacobs 1983, O'Brien et al. 1984, Jacobs et al. 1985). It appears to inhibit cell division by a novel mechanism that involves inhibition of microtubule polymerization (O'Brien et al. 1984). Other inhibitors of cell division, such as the *Vinca* alkaloids, that are mitotic spindle poisons have similar kinetics but the mechanisms by which they produce this effect differ (Jacobs et al. 1985). In contrast, pachydictyol-A shows no strong cytotoxicity, fish toxicity, or antimicrobial activity (see Appendix), yet it significantly inhibits grazing by both fishes and *Diadema* (Figs. 1 and 2). Like pachydictyol-A, aplysin shows little biological activity in laboratory tests, but in contrast to pachydictyol-A, it shows no activity as a feeding deterrent. Thus, from the few compounds investigated here, it appears that strong biological activity in laboratory tests may indicate compounds that would be interesting to test as feeding deterrents. The converse is not true; pachydictyol-A appears to be an important feeding deterrent that shows little bioactivity in the standard pharmacological screening assays.

Several of these compounds appear to be potent toxins whose effects are not specific to certain organisms. If this is true, then they may be as toxic to the seaweeds that contain them as they are to herbivores. Little is known about how these compounds are stored in the plants, but several studies suggest that they are partitioned away from other cellular products and processes, and are contained in membrane-bound vesicles that are close to the plant surface. Young et al. (1980) have shown that halogenated sesquiterpenes in *Laurencia snyderae* are concentrated in cytoplasmic vesicles within cells of the outer cortex; these cells would be the first ones contacted by an herbivore. These vesicles are absent from cells of the inner cortex. They also show these vesicles to be present in all investigated *Laurencia* species that produce haloterpenoid compounds and absent from those that do not produce these compounds. These halogenated terpenes are not secreted into the environment (Howard 1978) but are held within these membrane-bound vesicles. This is consistent with the contention that they function as herbivore deterrents that are released when cortical cells are broken by grazers; it would appear to be an ineffective means of retarding the growth of epiphytes (a common alternate hypothesis for the function of these compounds).

The examples presented are clear evidence that secondary metabolites from seaweeds may significantly inhibit feeding by a variety of common herbivores. Although most compounds showed a similar activity against both *Diadema* and reef fishes, the effects of cymopol differed sharply for fishes vs. *Diadema*. Isolaurinterol deterred both fishes and *Diadema*; however, the structurally related terpene aplysin was inactive against both types of herbivores. While all the compounds are terpenoid in nature, they show significant differences in their carbon skeletons and in their chemical functionalities. Thus, with only these six compounds, it would be premature to assume that any particular structural features were directly responsible for the observed suppression of feeding. Neither the structure of the compounds nor their biological activity, or inactivity, in laboratory tests against standard microbes appear to be particularly good predictors of the function these compounds may have in nature.

The herbivore-deterrent properties of these compounds do not rule out the possibility that they may also serve as antifouling or allelopathic agents. However, many of the compounds do not appear to be released into the water where they could play such a role. Even in the case of *Stypopodium zonale,* which does release stypotriol and stypoldione into the environment (Gerwick and Fenical 1981), these compounds show no activity against several marine fungi, bacteria, and diatoms that could foul seaweeds (Gerwick 1981).

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APPENDIX

The biological effects listed below were derived almost entirely from the chemical and pharmaceutical literature. In many instances these investigators perform only preliminary, and sometimes unreplicated and uncontrolled assays to look for strong biological activity. Results from these assays are listed here only to indicate the possible effects of these compounds. These assays are almost never ecologically realistic and their results should be questioned until the compounds have been shown to produce similar effects in controlled and replicated experiments that are ecologically relevant. As one example, the fish toxicity assays do not involve ingestion but are conducted by adding the compound to the water in which the fish is held. Such tests may or may not be of value in predicting the effects of these compounds when they are ingested.

Cymopol

Cymopol is a monoterpenoid-bromohydroquinone isolated from the green, calcified alga *Cymopolia barbata* (Högberg et al. 1976). Five other related compounds occur in *Cymopolia*, but cymopol is the major constituent, comprising ≈0.7% of the plant dry mass; the remaining five compounds comprise ≈0.5% of the dry mass (McConnell et al. 1982). The crude organic extract of *Cymopolia* shows antibiotic effects (Martinez-Nadal et al. 1966) and inhibits grazing by the sea urchin *Lytechinus variegatus*; the compound cymopol appears to be partially responsible for the deterrent effect that the crude extract shows against *Lytechinus* (McConnell et al. 1982). Cymopol is 100% cytotoxic to fertilized sea urchin eggs at 16 μg/mL and shows strong biological activity in a range of other pharmacological tests (Jacobs 1978–1985). *Cymopolia barbata* occurs in shallow water in the northern Caribbean but is not known to occur in the southern Caribbean (Taylor 1960). It has never been reported from either Martinique or Panama, but the major herbivores in these areas also occur in the northern Caribbean where they would co-occur with *Cymopolia*. No data are available on *Cymopolia*'s susceptibility to grazers in field or laboratory tests.

Isolaurinterol

Isolaurinterol is a sesquiterpene phenol that occurs in many *Laurencia* species scattered throughout the world's oceans. In the Caribbean, it is a major metabolite in *Laurencia intricata* and a minor metabolite in *L. poitei* (W. Fenical, *personal observation*). It also occurs in *L. okamurai* from Japan and in *L. johnstonii, L. pacifica,* and *L. decidna* from Pacific Mexico (Erickson 1983). It has probably been detected, but not reported, in numerous other species of this diverse and taxonomically difficult genus. Isolaurinterol may be present in only trace amounts or may occur as >50% of the organic extract of *Laurencia*; at the higher concentrations, it comprises >1% of the dry mass of the plant (Howard 1978). In laboratory assays, isolaurinterol shows strong antimicrobial activity (Jacobs 1978–1985). The susceptibility of *L. intricata* and *L. poitei* to Caribbean herbivores has been assessed on several reefs in the Florida Keys (Paul and Hay 1986). In this area, *L. intricata* and *L. poitei* growing on unstructured algal flats leeward of the reefs do not produce secondary compounds and are moderately to highly susceptible to removal by fishes when transplanted onto the reefs. It appears that isolaurinterol production in these species is very variable.

Aplysin

Aplysin is a sesquiterpene ether that was first isolated from the sea hare *Aplysia kurodai* (Yamamura and Hirata 1963). Although it was subsequently isolated from several species of *Laurencia* (Erickson 1983), its validity as a true *Laurencia* metabolite must be questioned on the basis of its facile chemical production from laurinterol or isolaurinterol under mild acid conditions. Isolaurinterol kept in the laboratory for long periods of time slowly converts to aplysin (K. Gustafson, *personal observation*), and aplysin is produced in the gut of sea hares via acid-catalyzed rearrangement of laurinterol (Stallard and Faulkner 1974). Aplysin does not affect the fish *Eupomacentrus leucostictus* at concentrations of 10 μg/mL (W. Gerwick and W. Fenical, *personal communication*) and shows no activity against insects in a series of agrochemical tests (W. Fenical, *personal observation*). The concentration of aplysin in *Laurencia* species is unknown.

Elatol

Elatol is a chamigrene-class sesquiterpenoid that was first isolated from *Laurencia elata* in Australia (Sims et al. 1974). In the Caribbean it occurs in *L. obtusa* and may constitute 3% of the dry mass of the plant (Norris and Fenical 1982). *L. obtusa* is common on reefs throughout the Caribbean and is a very low preference food for both herbivorous fishes and sea urchins (Ogden 1976, Littler et al. 1983, Hay 1984*a*). Elatol is moderately antibiotic and inhibits 50% of the cell divisions in fertilized sea urchin eggs at a concentration of 7 μg/mL (Norris and Fenical 1982). In 1-h exposures, it is toxic to the pomacentrid fish *Eupomacentrus leucostictus* at a concentration of 5 μg/mL (W. Gerwick and W. Fenical, *personal communication*). Agrochemical assays show it to be very toxic to a wide range of insects (W. Fenical *personal observation*). The genus *Laurencia* is probably the most chemically rich plant genus ever studied; in addition to elatol and isolaurinterol, over 100 terpenoid and nonterpenoid secondary metabolites have been isolated from species of *Laurencia* scattered throughout the world's oceans (Fenical 1975, Erickson 1983).

Stypotriol

Stypotriol is a C_{27} compound derived from a mixed biosynthesis of diterpenoid and acetate precursors. It occurs in *Stypopodium zonale* as ≈0.6% of the algal dry mass (Gerwick 1981). *Stypopodium* also contains several related compounds in lesser quantities. Stypotriol is lethal to the pomacentrid fish *Eupomacentrus leucostictus* at a concentration of only 0.2 μg/mL (Gerwick and Fenical 1981). When liberated from the alga, stypotriol rapidly oxidizes to the related compound stypoldione; this compound is toxic to fish, prevents cell division by inhibiting tubulin polymerization, immobilizes sperm, and inhibits both amino acid and nucleoside uptake (Gerwick and Fenical 1981, White and Jacobs 1983, O'Brien et al. 1984). In laboratory assays, it shows no activity against marine fungi,

bacteria, or diatoms (Gerwick 1981). *Stypopodium zonale* is common on reefs throughout the entire Caribbean and is a relatively low preference food for both fishes and sea urchins (Hay and Goertemiller 1983, Littler et al. 1983, Hay 1984*a*, Paul and Hay 1986).

Pachydictyol-A

Pachydictyol-A is a bicyclic diterpenoid first isolated from *Pachydictyon coriaceum* where it occurred as 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 (Gerwick 1981). Pachydictyol-A is typical of a group of compounds isolated from ≈10 other species of *Dictyota, Dilophus,* and *Glossophora* (McEnroe et al. 1977). In the Caribbean pachydictyol-A is a common constituent of *Dictyota bartayresii, D. dichotoma, D. dentata,* and several related species. It may occur as >1% of the dry mass of the plant (W. Fenical *personal observation*). These species of *Dictyota* occur throughout the entire Caribbean, are relatively resistant to grazing (Hay 1981*c*, 1984*a*, Littler et al. 1983, Paul and Hay 1986), and are often among the most common fleshy species of seaweeds on coral reefs.