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Author(s): Mark E. Hay, J. Emmett Duffy, William Fenical
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HOST-PLANT SPECIALIZATION DECREASES PREDATION ON A MARINE AMPHIPOD: AN HERBIVORE IN PLANT'S CLOTHING[1]

MARK E. HAY AND J. EMMETT DUFFY
*University of North Carolina at Chapel Hill, Institute of Marine Sciences,
Morehead City, North Carolina 28557 USA*

WILLIAM FENICAL
*Institute of Marine Resources, Scripps Institution of Oceanography,
University of California at San Diego, La Jolla, California 92093 USA*

Abstract. We investigated the factors selecting for host-plant specialization and the roles that plant defensive chemistry may play in this process. We studied marine organisms because marine communities contain fewer specialized herbivores than terrestrial communities and, therefore, provide a simplified system for investigating certain aspects of host-plant specialization. Our study focused on the unusual domicile-building and feeding behavior of the amphipod *Pseudamphithoides incurvaria,* which is the only herbivorous marine amphipod known to specialize on a few closely related seaweeds. *P. incurvaria* lives in a portable, bivalved domicile that it constructs from the chemically defended brown alga *Dictyota bartayresii.* Chemical assays indicate that natural populations of *Pseudamphithoides* construct their domiciles from *D. bartayresii* even when this alga is rare compared to other *Dictyota* species and to other related genera in the family Dictyotaceae. In both choice and no-choice tests in the laboratory, *Pseudamphithoides* built domiciles from and selectively consumed species of *Dictyota* that produced dictyol-class diterpenes that deter feeding by reef fishes. Other brown seaweeds in the family Dictyotaceae, including a *Dictyota* species, that did not produce these fish-feeding deterrents were avoided by the amphipod. Amphipods removed from their domiciles were rapidly eaten when presented to predatory fish; amphipods in their normal domiciles were consistently rejected by fish. The defensive value of the domicile appeared to result from specific characteristics of the *Dictyota* from which it was built, since amphipods forced to build domiciles from the palatable green seaweed *Ulva* were rapidly eaten when these amphipods, in their domiciles, were exposed to predatory fish.

Algal defensive chemistry directly cued domicile building. When the green alga *Ulva* was treated with pachydictyol-A (the major secondary metabolite produced by *Dictyota bartayresii*), domicile building by *Pseudamphithoides* increased in proportion to the concentration of pachydictyol-A. All data collected during this study are consistent with the hypothesis that predator escape and deterrence are primary factors selecting for host specialization by *Pseudamphithoides incurvaria.* Similar conclusions can be drawn for the limited number of other marine herbivores that are relatively specialized.

Key words: amphipod; chemical defense; Dictyota; *diterpenes; feeding specialization; herbivory; pachydictyol-A; plant–herbivore–predator interactions; predator escape and deterrence;* Pseudamphithoides; *seaweeds.*

INTRODUCTION

It has recently been argued that much of the specialized feeding that is typical of herbivorous terrestrial insects may be driven by the need for "enemy-free space" (Price et al. 1980, 1986, Bernays and Graham 1988). However, the relative importance of predation vs. other factors in selecting for specialization has been questioned by numerous authors (Barbosa 1988, Courtney 1988, Ehrlich and Murphy 1988, Fox 1988,

Janzen 1988, Jermy 1988, Rausher 1988, Schultz 1988, Thompson 1988).

Evaluation of factors selecting for feeding specialization may be easier in marine than in terrestrial systems. In terrestrial communities, most herbivores are insects, with a large proportion being relatively specialized feeders (Futuyma and Gould 1979, Price 1983, Strong et al. 1984). As an example, Ehrlich and Murphy (1988) note that >80% of all North American butterflies each feed only within one plant family. In contrast, specialized feeding by marine herbivores appears to be relatively rare (Lubchenco and Gaines 1981, Hay et al. 1988*b, c,* Hay and Fenical 1988). Thus, it may be

easier to determine what factors select for specialized feeding among the few marine herbivores that specialize rather than to approach this within the bewilderingly diverse framework of specialized herbivores in terrestrial communities.

Marine phytal amphipods are similar to herbivorous terrestrial insects (Strong et al. 1984) in that they are subject to heavy predation (Vince et al. 1976, Van Dolah 1978, Nelson 1979a, b, Stoner 1979, 1980, Edgar 1983a, b), appear to rarely experience competition for food (Van Dolah 1978, Nelson 1979a, Zimmerman et al. 1979), are small relative to their host plants, and may often rely on their host plants to provide both food and appropriate habitat (Hay et al. 1987a, 1988b, c). These amphipods, and almost all other groups of marine herbivores, differ dramatically from herbivorous terrestrial insects in their degree of feeding specialization. Marine herbivores typically feed from several divisions of marine algae (Randall 1967, Lawrence 1975, Steneck and Watling 1982); specialization on only a few related species or genera of seaweeds is common only among the ascoglossan gastropods (Jensen 1980), and to a lesser extent among some limpets (Steneck and Watling 1982).

Several recent studies of seaweed chemical defenses against different types of marine herbivores have noted that small herbivores of limited mobility (mesograzers) often graze selectively on seaweeds that are not eaten by fishes, and that the seaweed metabolites which significantly deter fish feeding may stimulate or not affect feeding by the mesograzers (Hay et al. 1987a, 1988b, c, Paul et al. 1987, Paul and Van Alstyne 1988). Decreased predation associated with living on a chemically defended host plant has been hypothesized to be a major factor selecting for the feeding preferences of the mesograzers and for their resistance to seaweed chemical defenses that deter fishes (Hay et al. 1987a, 1988b, c). However, despite the apparent advantage of association with certain host plants, and the strong feeding preference of some amphipods for those host plants, phytal amphipods have rarely become specialized to particular host plants (Hay et al. 1988b, c).

In this study we investigated the amphipod *Pseudamphithoides incurvaria*, which appears to be very specialized on brown algae in the genus *Dictyota* (Lewis and Kensley 1982). Because *Dictyota* is a chemically rich genus (Faulkner 1984, 1986) that produces a variety of diterpenoid compounds that deter fish feeding (Hay and Fenical 1988), and because *P. incurvaria* appears to be one of the only amphipods to have become specialized to a small number of potential host plants, we reasoned that this system might provide insights into the factors selecting for host specialization and the role that defensive chemistry plays in this process.

We asked the following question: (1) Is *Pseudamphithoides incurvaria* really specialized, and if so does it choose host plants on a species-specific, genus-specific, or family-specific level? (2) Is specialization by *P. incurvaria* cued by seaweed metabolites that deter fishes? (3) Does host specialization reduce predation?

METHODS
Organisms and study site

Several species of herbivorous amphipods excavate galleries in, or build tubes on, the seaweeds they consume (Holmes 1901, Barnard 1969, Jones 1971, Myers 1974, Griffiths 1979, Anderson and Velimirov 1982, Gunnill 1985). However, *Pseudamphithoides incurvaria* appears to be unique in that it constructs portable bivalved domiciles by cutting each valve from its primary food plant and fastening these together (Lewis and Kensley 1982). The amphipod keeps pereopods 5–7 anchored within the domicile. Thus, much of its body remains within the domicile even while swimming or walking. Amphipods can withdraw entirely into the domicile and can turn to face either the front or rear opening. In most instances the first and second antennae protrude from the entrance, and appear to be used for swimming.

The amphipod was first described by Just (1977), who found it in shallow habitats around Barbados. In that location it was reported to be making its domiciles from a brown seaweed in the genus *Dictyopteris*. Lewis and Kensley (1982) investigated the distribution, feeding, and domicile construction behavior of *Pseudamphithoides incurvaria* on the reef at Carrie Bow Cay, Belize. They found it from depths of 1.5 to 27 m, but only on the brown alga *Dictyota bartayresii*; the amphipod did not occur on other brown seaweeds (*Stypopodium zonale*, *Padina sanctae-crucis* = *P. jamaicensis*, and *Lobophora variegata*) common in their study areas. Additionally, in limited laboratory feeding assays, the amphipods would eat only *D. bartayresii*, their own or other amphipod's domiciles, or small epiphytes on *Dictyota*. When amphipods were forced from their domiciles and given access to the brown seaweeds *D. bartayresii*, *Padina jamaicensis*, or *Lobophora variegata*, those confined with *Dictyota* built domiciles while those with the other seaweeds did not (Lewis and Kensley 1982).

Our study of *Pseudamphithoides incurvaria* was conducted between 22 January and 3 February 1988 on Carrie Bow Cay, Belize, and between 19 June and 6 July 1988 on numerous reefs in the Bahamas. We concentrated most of our efforts on shallow (2–5 m deep) rubble habitats between the sand bores located south-southwest of Carrie Bow Cay. *P. incurvaria* were common within these rubble areas as were the brown seaweeds *Dictyota cervicornis*, *Dictyota dichotoma*, *Dilophus alternans*, and *Sargassum platycarpum*. Very small amounts of *Dictyota bartayresii* were usually present within the thickly matted clumps of *D. cervicornis*. Other seaweeds that were present but less common included *Padina jamaicensis*, *Sargassum hystrix*, *Lobophora variegata*, *Anadyomene stellata*, and *Dictyopteris delicatula*.

Field collections

The abundance of *Pseudamphithoides incurvaria* on different species of seaweeds was determined by gently bagging individual plants underwater and carefully sorting each sample in the lab. The water was then drained from each seaweed sample and its wet mass determined. Although several species of brown seaweeds occurred at our study site, we assayed amphipod densities only for *Dictyota cervicornis, D. dichotoma, Dilophus alternans,* and *Sargassum platycarpum,* since these species could be collected as single plants or clones that were not extensively intertwined with other plants. However, when closely inspecting *Dictyota cervicornis* in the lab, we found that most clumps of this plant contained small amounts (estimated at 2–5% of the wet mass) of *Dictyota bartayresii.*

Domicile building

We conducted two separate assays to determine the willingness of *Pseudamphithoides incurvaria* to build domiciles from different seaweeds. In the first, we removed amphipods from their domiciles and placed each in a separate container with three 3.5 mm diameter discs cut from a single species of alga. We used all the flat-bladed seaweeds we could find near Carrie Bow Cay, Belize (*Dictyota bartayresii, D. cervicornis, D. dichotoma, Dilophus alternans, Lobophora variegata, Padina jamaicensis, Sargassum platycarpum, Sargassum hystrix, Ulva* sp., and *Anadyomene stellata*). Sample size was 10 for each seaweed, and a replicate was excluded from the analysis if the amphipod died during the 16-h duration of the experiment. In this experiment each amphipod was confined with a single species and had no choice of building materials.

In the second assay each amphipod could choose among five different seaweeds. This assay used intact upper portions from each seaweed with *Dictyota*-like morphology (*Dilophus alternans, Dictyopteris delicatula, Dictyota bartayresii, D. cervicornis,* and *D. dichotoma*) to see if domicile building behavior using intact plants differed from that documented using discs. Twenty-six amphipods were removed from their domiciles and each was placed in a separate container with approximately equal surface areas of all five seaweeds. After 56 h the domicile and the seaweeds in each container were examined microscopically to determine which seaweeds had been used for domicile construction. Nineteen domiciles were constructed from only one species; seven were constructed from multiple species, with one valve or even half of a valve being made of one species and the rest of the domicile from another. In these instances, the domiciles were recorded by the proportion (¼, ½, or ¾) of the domicile constructed from that species.

To see if algal secondary metabolites were important in affecting the decision of *Pseudamphithoides incurvaria* to build domiciles, we treated the green seaweed *Ulva* with the diterpene alcohol, pachydictyol-A, which is a common secondary metabolite produced by several species of *Dictyota*; it significantly deters fish feeding (Hay et al. 1987*a, b,* 1988*a, c*) and is a major metabolite of *Dictyota bartayresii* at Carrie Bow Cay, Belize (Norris and Fenical 1982). Since pachydictyol-A is lipid soluble, we dissolved it in diethyl ether and applied this volumetrically to 1 cm diameter discs of *Ulva* that had been blotted dry. After the ether evaporated, a disc and an amphipod without its domicile were placed into a 100-mL container with ≈80 mL of seawater. In similar assays (Hay and Fenical 1988), 93% of pachydictyol-A was shown to remain on treated algae after 24 h in seawater. Pachydictyol-A was applied at 0% (only ether applied to the *Ulva*), 0.2%, 0.5%, or 1.0% of *Ulva* dry mass (calculated using a previously determined dry mass : area ratio). Natural concentrations of pachydictyol-A range from trace amounts to >1% of plant dry mass in various species of *Dictyota* (Hay et al. 1987*b*). Each disc was placed in a separate container with a single amphipod; $N = 18$ for each concentration. After 48 h each container was examined to see if the amphipod had started (defined as at least one valve being cut completely free from the alga) or completed a domicile.

To see if domiciles reduced fish predation on *Pseudamphithoides incurvaria,* we conducted laboratory feeding assays with the abundant Caribbean wrasse *Thalassoma bifasciatum*. Wrasses were captured from the reef, stocked at three fish per 40-L container in four separate containers, and taught to feed on freeze-dried *Euphausia* squirted from a pipette. After several feedings, the wrasses would orient to the pipette opening when it was placed in the water. This allowed us to make sure that the fish would immediately see whatever foods were offered to them. Five amphipods with domiciles and five without domiciles were individually squirted into each fish container with a pipette. Amphipods with and without domiciles were offered in alternating sequence. The fate of each amphipod was recorded as either rejected or eaten. In the field, fish might usually fail to detect amphipods in domiciles. This assay does not address this potential escape; it determines if amphipods in domiciles are less susceptible to predation even though the domiciles are clearly seen and investigated by the fish.

To determine if the algal material used to build the domicile affected the susceptibility of *Pseudamphithoides incurvaria* to predation by the wrasse *Thalassoma bifasciatum,* we collected large numbers of *P. incurvaria* at Chub Cay, Bahamas, removed many from their domiciles, and confined these in containers with *Ulva* sp. as their only possible building material. After 48 h a limited number of these amphipods had constructed domiciles from *Ulva*. Using a pipette as described above, we then dropped one amphipod in a domicile built of *Ulva* and one amphipod in a domicile built of *Dictyota* into seven separate aquaria each of

which held one male and three female wrasses. In each tank, we recorded the immediate fate of the amphipod and the behavior of the fish.

Feeding assays

In the Bahamas, we compared feeding by *Pseudamphithoides incurvaria* and reef fishes when both were offered four common seaweeds in the family Dictyotaceae (*Dictyota bartayresii, D. dentata, Padina jamaicensis,* and *Lobophora variegata*). Since our primary goal was to determine if the amphipods preferred seaweed avoided by natural groups of reef fishes, we transplanted ≈6 cm tall portions of each seaweed onto a reef (5-m depth) at Eleuthera, Bahamas, and investigated each plant for the crescent shaped scars of fish grazing at the end of the 5-h transplant period. We chose this assay because we reasoned that amphipods hiding in plant material would be advantaged if they used plants that were less often bitten by reef fishes. For transplantation, an undamaged blade of each of the four seaweeds was placed in a 50-cm length of 3-strand rope, and 31 of these ropes were placed along the reef at intervals of ≈3 m (see Hay 1984 for methods).

Amphipod feeding was assayed on board ship by providing *Pseudamphithoides incurvaria* with five 3.5 mm diameter discs of each alga and allowing the amphipods to feed for 5 d. The remaining area of each disc was then measured under a dissecting microscope using an ocular grid and a point–intercept method; each intact disc was hit by 69 points. So that the different algal species would constitute independent treatments (see Hay et al. 1988c, Peterson and Renaud 1989), individual amphipods were not given a choice of algae. A single amphipod, in its domicile, was placed in a 100-mL container with only one of the algal species. $N = 14$ separate amphipods and containers for each algal species. Water was changed daily.

Chemical investigations

Our work in Belize was conducted from a remote field station where rigorous chemical investigations could not be conducted. Therefore, secondary compounds present in the various algal species and in the amphipod's domiciles were compared in the field using only thin layer chromatography (TLC). This method is not quantitative and cannot rigorously confirm the presence of specific compounds but it did allow us to compare the chemistry of the domicile material to that of all the *Dictyota*-like species it could have been made from.

In the Bahamas we had access to some chemical equipment, and thus conducted more in-depth studies on the chemistry of one of the brown algal species (*Dictyota dentata*) that was a preferred food of *Pseudamphithoides incurvaria* and that appeared to be chemically interesting but relatively unstudied. Fresh

collections of *D. dentata* were extracted in a 1:3 mixture of methanol : dichloromethane and separated into polarity fractions using vacuum elution chromatography (see Norris and Fenical 1985). TLC analysis of the various fractions indicated large amounts of an unusual secondary metabolite in the 20% ethyl acetate fraction. The effects of this fraction on feeding by reef fishes was assayed in the field (see Hay et al. 1987b for methods) by dissolving this fraction in diethyl ether, applying it at a concentration of 1% dry mass to the palatable seagrass *Thalassia testudinum,* transplanting treated and control (coated with only diethyl ether) *Thalassia* blades onto the reef at Great Harbor Cay, Bahamas, and measuring the amount of each consumed during a 6-hr period. The major metabolite and its concentration in this fraction were determined later in the lab using high pressure liquid chromatography (HPLC) and nuclear magnetic resonance (NMR).

RESULTS

In the rubble habitats near Carrie Bow Cay, Belize, *Pseudamphithoides incurvaria* were ≈10 times as abundant on *Dictyota cervicornis* as on *D. dichotoma*; no *P. incurvaria* were found on *Dilophus alternans* or *Sargassum platycarpum* (Fig. 1). Density on both *Dictyota cervicornis* and *D. dichotoma* differed significantly ($P < .05$) from all other species; densities on *Dilophus alternans* and *Sargassum platycarpum* did not differ (Kruskal-Wallis and a non-parametric parallel of the Student-Newman-Keuls Test, see Zar 1974). Although individual fronds of *Dictyota dichotoma* and *Dilophus alternans* are morphologically very similar to *Dictyota cervicornis,* these plants did not form the dense clumps that were typical of *D. cervicornis,* nor were they entwined with small amounts (estimated at 2–5% of wet mass) of *D. bartayresii* as were the *D. cervicornis* plants. Thin layer chromatography (TLC) of the amphipod's bivalved domiciles vs. all the *Dictyota*-like species found in the area indicated that the amphipods were building their domiciles from *Dictyota bartayresii.* The TLC of the domiciles matched exactly that of *D. bartayresii*; it differed from all other *Dictyota*-like seaweeds (*Dictyota dichotoma, D. cervicornis,* and *Dilophus alternans*) present in the area where the amphipods were collected.

Similar analyses of amphipod domiciles and five forms of *Dictyota* collected at Chub Cay, Bahamas, showed the same relationship. Although *D. bartayresii* was rare compared to several of the other species, the TLC composition of the domiciles was exactly like that of *D. bartayresii* and clearly differed from all other *Dictyota*s sampled. Their small size prevented TLC analysis of individual domiciles. At each site, we extracted groups of 20–50 domiciles. It is therefore possible that a small proportion of domiciles could have been made from a seaweed other than *D. bartayresii* and that the compounds from these species were below
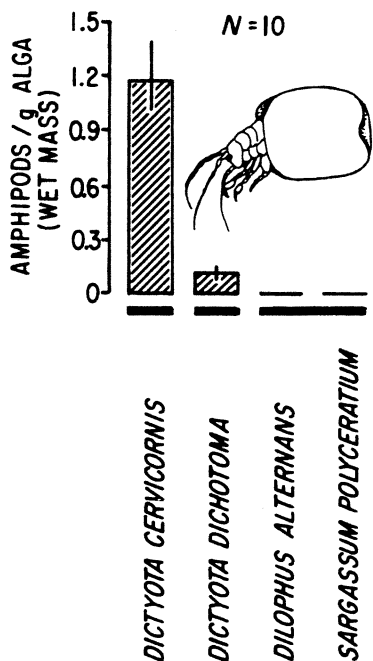
our level of detection. However, both in Belize and in the Bahamas, the TLC results were very clear-cut, indicating that the large majority of domiciles, if not all domiciles, were made exclusively of *D. bartayresii*.

When *Pseudamphithoides incurvaria* were removed from their domiciles and placed in containers with discs cut from various species of flat-bladed seaweeds, those confined with *Dictyota bartayresii* all built domiciles (Fig. 2). Only 0 to 20% of those confined with other species built domiciles. Contingency table analysis indicated that the significant ($P < .001$) effect of algal species on domicile building was due entirely to the increased frequency of building that occurred among amphipods with access to *D. bartayresii*.

Amphipods removed from their domiciles and confined with a choice of the upper portions of five different *Dictyota*-like seaweeds constructed the majority of their domiciles (54%) from *Dictyota bartayresii* (Fig. 3). However, several (39%) were also constructed from *Dictyota dichotoma* with minimal portions of some domiciles being built of *Dilophus alternans* (6%) or *Dictyopteris delicatula* (1%). No portion of any domicile was constructed from *Dictyota cervicornis*. Since the different treatments (i.e., algal species) in this experiment were all available to each amphipod, the treatments were not independent of one another and cannot be statistically analyzed. However, the magnitude of the differences in use clearly indicates that

D. bartayresii and *D. dichotoma* were much more heavily used for domicile construction than were *Dilophus alternans, Dictyota cervicornis,* or *Dictyopteris delicatula* (Fig. 3).

When discs of *Ulva* were coated with varying concentrations of a major secondary metabolite (pachydictyol-A) produced by *Dictyota bartayresii* and *Dictyota dichotoma,* the frequency of domicile building increased with increasing compound concentration (Fig. 4). A polynomial regression analysis (cubic model) showed that pachydictyol-A significantly stimulated domicile building ($r^2 = 0.98$, $P = .011$).

When *Pseudamphithoides incurvaria* with intact domiciles were offered equal areas of four flat-bladed seaweeds (all in the family Dictyotaceae) that were common in the Bahamas, they consumed primarily *Dictyota bartayresii* ($\bar{X} \pm 1$ SE = 4.4 ± 1.2 mm^2) and *Dictyota dentata* (2.4 ± 0.6 mm^2), limited amounts of *Padina jamaicensis* (0.8 ± 0.4 mm^2), and no *Lobophora variegata* (Fig. 5). When undamaged portions of these same seaweed species were exposed to grazing by reef fishes, the fishes were significantly more likely to take bites from *Padina* and *Lobophora* than from either of the *Dictyota* species ($P < .05$, 2 × 4 contingency table by the simultaneous test procedure) (Fig. 5). When the 20% ethyl acetate fraction of the crude extract of *D. dentata* was applied to *Thalassia* and
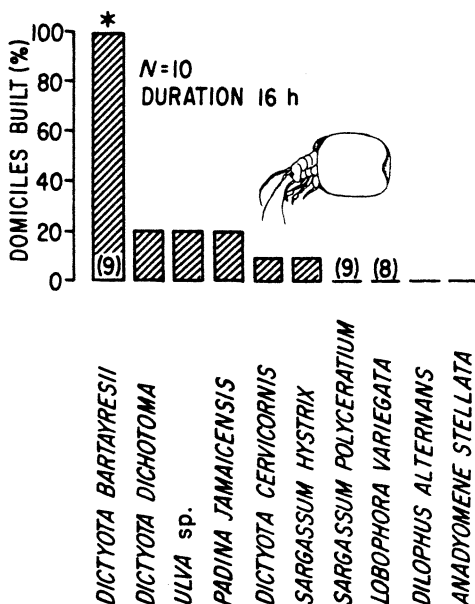

FIG. 2.   Percentage of *Pseudamphithoides incurvaria* individuals that built domiciles when confined with equal-sized discs of various algal species. Numbers in parentheses show sample sizes that differed from 10 due to death of amphipods during the 16-h experimental period. The * above *D. bartayresii* indicates that there was a highly significant ($P < .001$) effect of algal species on domicile building in a 2 × 10 contingency table analysis, but that this effect disappeared completely in a 2 × 9 contingency table analysis that excluded *D. bartayresii*.
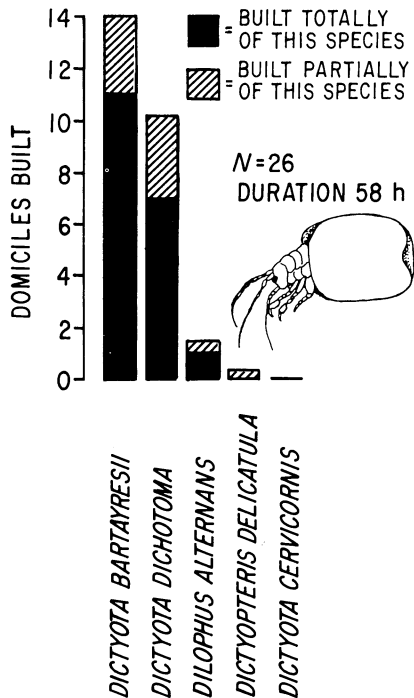
FIG. 3. The number of domiciles built entirely or partially from five morphologically similar seaweeds in the family Dictyotaceae when equal amounts of these species were simultaneously available to each amphipod. If a domicile was built from multiple species, each species was recorded as comprising ¼, ½, or ¾ of the entire domicile, and these amounts were added to the hatched portion of the appropriate histogram bar.

exposed for 6 h to grazing reef fishes, the extract reduced losses by a significant 58% ($P < .001$, Wilcoxon paired-sample test, $N = 18$). The fish ate 29.6 ± 2.7% of control blades (mean ± 1 SE), while only 12.4 ± 2.5% of treatment blades were eaten. HPLC and NMR analyses of this fraction showed that dictyol-B acetate (see Faulkner et al. 1977 for the structure) made up 80% of this fraction; the remainder of the fraction was composed of numerous additional metabolites, none of which comprised more than 2% of the total fraction mass. Dictyol-B acetate differs from pachydictyol-A (Fig. 4) only by the presence of an acetoxyl group in the 7-membered ring. Previous tests with pachydictyol-A, the major metabolite from *D. bartayresii* (Norris and Fenical 1982), had shown it to be a significant feeding deterrent for reef fishes and the sea urchin *Diadema antillarum* (Hay et al. 1987b, 1988a).

Domiciles provide the amphipods with significant ($P < .001$, paired t test, $N = 4$) protection from fish predators. When amphipods without domiciles were offered to fish, 100% were consumed. When exposed to fish while in their domiciles, only 10 ± 6% (mean ± 1 SE) were consumed. These differences are conservative since amphipods in domiciles are very cryptic when on their host plant but very obvious when we

separate them from the plant and drop them to fish that have been trained to feed from our pipettes. In many cases, amphipods in domiciles were taken into the fishes' mouths and then rejected without damage to the amphipod. In both cases where an amphipod in a domicile was consumed, the valves became uncoupled when the fish spat out the domiciles; the exposed amphipod was then eaten.

The type of alga used to construct the domicile was important in determining the domicile's defensive value. When an amphipod in a domicile of *Ulva* and one in a domicile of *Dictyota* were dropped in seven aquaria with wrasses, the fish immediately ate all of the amphipods in *Ulva* but only one of the amphipods in *Dictyota* ($P = .016$, two-sample sign test). In six of the seven cases where amphipods in *Ulva* were eaten, the fish ate both the amphipod and the alga (in one case, a fish retained the amphipod but spat out the *Ulva*). In the seven trials with amphipods in *Dictyota* domiciles, fish took all seven domiciles into their mouths but immediately spat each out. In six cases the amphipod, in its domicile, then swam away without being attacked again. In one replicate the domicile fell apart as the fish spat it out; the fish then ate the amphipod but avoided consuming any of the domicile.

DISCUSSION

All of our findings are consistent with the hypothesis that predator avoidance and deterrence are major advantages arising from the specialization of *Pseudamphithoides* on certain chemically defended seaweeds in the genus *Dictyota*. It seems unlikely that resource partitioning is important in maintaining the specialized behavior of this amphipod since both field experimentation and comparative-descriptive studies indicate that
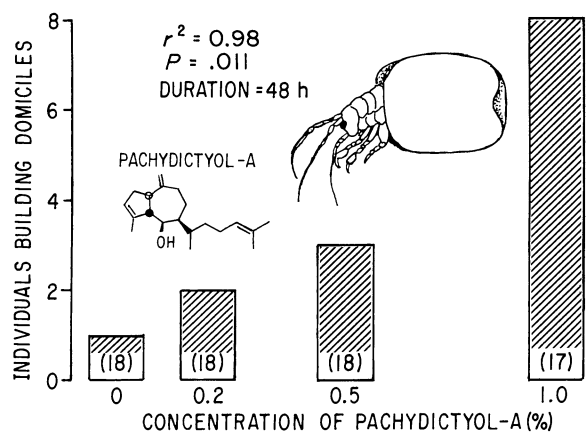
FIG. 4. The number of *Pseudamphithoides incurvaria* building domiciles from discs of the green seaweed *Ulva* that were treated with differing concentrations of the diterpene alcohol pachydictyol-A, which is the major secondary metabolite produced by *Dictyota bartayresii*. Numbers in parentheses indicate the number of individually isolated amphipods used in each treatment. r^2 and P values are from a polynomial regression using a cubic model.

amphipod populations are often limited by predation and seldom limited by food (Vince et al. 1976, Van Dolah 1978, Nelson 1979a, b, Stoner 1979, 1980, Zimmerman et al. 1979, Edgar 1983a, b). When unusual environmental circumstances free herbivorous amphipods from predation, some species may deplete their food resources (e.g., decimate entire kelp beds—Jones 1965, Tegner and Dayton 1987, Dayton and Tegner, in press); however, the extreme rarity of such events suggests that herbivorous amphipod populations are usually kept well below carrying capacity due to high rates of predation.

Rigorous review of the literature on plant–insect interactions in terrestrial systems indicates that insects also are seldom food limited and often appear to be predator limited (Strong et al. 1984). Therefore resource partitioning also may not be a dominant factor selecting for host-plant specialization among these herbivores. Realization of this has generated considerable controversy regarding the evolutionary forces selecting for feeding specialization in insects; much of this controversy has centered around the relative importance of "enemy-free-space" vs. other factors in selecting for host-plant specificity (Gilbert and Singer 1975, Lawton 1978, Price et al. 1980, 1986, Barbosa 1988, Bernays and Graham 1988, Courtney 1988, Ehrlich and Murphy 1988, Fox 1988, Janzen 1988, Jermy 1988, Rausher 1988, Schultz 1988, Thompson 1988). Evidence from this study suggests that the arguments advanced by Bernays and Graham (1988) and others (Gilbert and Singer 1975, Price et al. 1980) regarding terrestrial insects may have applications in marine communities as well. The concept of "enemy-free-space" may also help explain strong feeding preferences among small marine herbivores that are not specialized feeders (Hay et al. 1987a, 1988b, c).

Thin layer chromatography of Pseudamphithoides incurvaria domiciles in both Belize and the Bahamas indicated that domiciles were being built primarily, and perhaps exclusively, from Dictyota bartayresii even though other, closely related, seaweeds were more common. In both choice and no-choice assays in the lab, amphipods built domiciles primarily (Fig. 3) or almost exclusively (Fig. 2) from D. bartayresii. Of the 11 seaweeds tested, D. dichotoma was the only species other than D. bartayresii that was ever used extensively for domicile construction. Both of these Dictyotas are low preference foods for fishes (Hay 1984, Paul and Hay 1986, Hay et al. 1987a, 1988c), and both produce the diterpene alcohol pachydictyol-A, which significantly deters feeding by Caribbean (Hay et al. 1987b), Pacific (Hay et al. 1988a), and Atlantic (Hay et al 1987a, 1988c) reef fishes. In contrast to this, Dictyota cervicornis is susceptible to fish grazing (Littler et al. 1983, Lewis 1986), does not appear to produce the dictyol class of defensive diterpenes (Teixeira et al. 1986a, b, Kelcom and Teixeira 1988), and was almost never used for domicile construction (Figs. 2 and 3). The
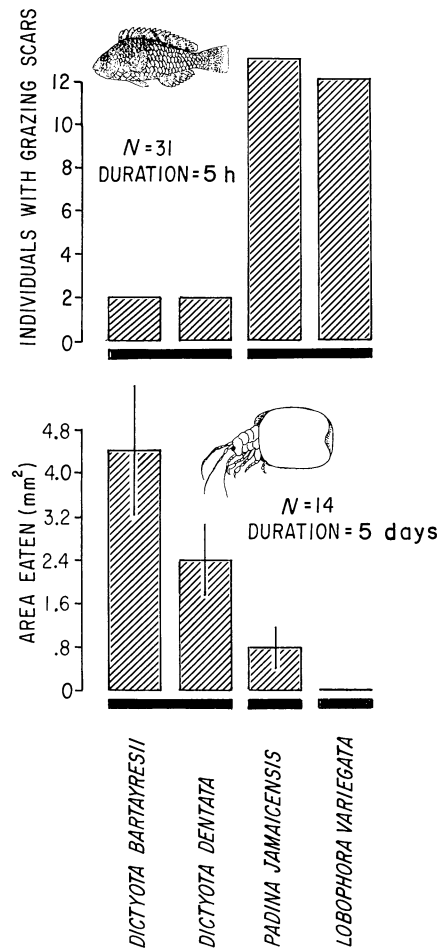

FIG. 5. Feeding by reef fishes (i.e., field assays) vs. Pseudamphithoiaes incurvaria when offered four species of brown seaweeds in the family Dictyotaceae. Data for fishes were analyzed by a 2 × 4 contingency table using a G test. Data for amphipods (shown as means ± 1 SE) were analyzed by Kruskal-Wallis and Student-Newman-Keuls tests. Heavy lines beneath the histogram connect species that do not differ significantly ($P \leq .05$).

domicile building behavior of Pseudamphithoides was directly responsive to algal defensive chemistry as evidenced by the significantly increased probability of amphipods building domiciles from the green seaweed Ulva if it was treated with increasing concentrations of pachydictyol-A (Fig. 4). In laboratory feeding assays Pseudamphithoides also selectively consumed dictyotalean seaweeds containing pachydictyol-A or the closely related dictyol-B acetate; the amphipods fed very little, if at all, on dictyotalean species that lacked these compounds (Fig. 5). Feeding patterns of reef fishes were opposite those of the amphipods.

When amphipods collected from the field were presented to the common wrasse Thalassoma bifasciatum, individuals removed from their domiciles were invariably consumed while ones in domiciles were consumed in only 2 of 20 presentations. In numerous cases,

fish took the domicile into their mouths but invariably spit these out. The rejection of amphipods in domiciles was not a simple result of the physical presence of a domicile, since domiciles built from the green alga *Ulva* did not provide protection to amphipods while domiciles built from *Dictyota* were very effective defenses.

Although *Pseudamphithoides* selectively consumes algae that are chemically defended from the fishes, they do not appear to metabolically sequester the algal metabolites and thus lower their acceptability as prey. Like *Pseudamphithoides,* the tube-building amphipod *Ampithoe longimana* and the free-living amphipod *Hyale macrodactyla* selectively consume brown algae that are chemically defended from fishes, and they also do not sequester algal metabolites; they may however experience reduced predation due to their close association with seaweeds that are less often visited by fishes (Hay et al. 1987*a,* 1988*b,* Duffy and Hay, *in press*). Similar interactions occur in terrestrial communities where an insect may selectively forage on a low-quality food that provides the insect with some escape from its natural enemies (Damman 1987).

The amphipods *Hyale macrodactyla, Ampithoe longimana,* and *Pseudamphithoides incurvaria* can be viewed as occupying different positions along a gradient of increasing host-plant specialization. Most plant-eating amphipods appear to be very generalized feeders consuming detritus and a wide variety of microalgae, small filamentous seaweeds, and at times larger macrophytes (Martin 1966, Nelson 1979*a,* Zimmerman et al. 1979, Smith et al. 1982). *H. macrodactyla,* like other members of the genus, may be less generalized in that it appears to feed primarily on plant material and to live primarily among aggregations of seaweed thalli in the lower intertidal (Moore 1977, McBane and Croker 1983, Hay et al. 1988*b*). Although it is predictably associated with seaweeds, it is free-living and does not build tubes or other domiciles. Data on its feeding habits are limited, but when offered several species of seaweeds, it selectively consumed the brown alga *Dictyopteris delicatula* and the red alga *Halymenia duchassaignii,* both of which were of low to intermediate preference for reef fishes (Hay et al. 1988*b*). The C_{11} hydrocarbons dictyopterene A and B from *D. delicatula* deterred feeding by fishes but did not affect feeding by *Hyale.* Feeding by *H. macrodactyla* also was unaffected by an unrelated red algal terpene that deterred fishes (Paul et al. 1987). Although *Hyale* was resistant to seaweed chemical defenses and was hypothesized to experience less predation when associated with seaweeds that were deterrent to fishes, it could be found on a wide variety of unrelated seaweeds and was not specialized to a particular host plant (Hay et al. 1988*b*).

The association between *Ampithoe longimana* and its host plants is somewhat more intimate in that it lives in a fixed, mucilaginous tube built directly on its host. However, it occurs in diverse types of habitats,

and uses a wide variety of unrelated host plants (Bousfield 1973, Nelson 1979*a,* 1980, Stoner 1980). When offered a range of common macrophytes, *A. longimana* selectively consumed *Dictyota dichotoma* which was a very low-preference food for co-occurring omnivorous fishes; the diterpene alcohols pachydictyol-A and dictyol-E produced by *D. dichotoma* deterred feeding by fishes but either stimulated or did not affect feeding by the amphipod (Hay et al. 1987*a,* 1988*c*). Even though *A. longimana* selectively consumed *Dictyota,* experienced dramatically increased survivorship and thus cohort fecundity when cultured on *Dictyota* vs. other seaweeds (J. E. Duffy and M. E. Hey, *personal observation*), and suffered significantly reduced rates of fish predation when on *Dictyota* compared to a seaweed more palatable to fishes (Duffy and Hay, *in press*), *A. longimana* retains its generalized life style, living on and feeding from a wide variety of seaweeds (Hay et al. 1987*a,* 1988*c,* Duffy and Hay, *in press*).

Pseudamphithoides incurvaria is much more specialized than the other amphipods. Although Just (1977) found *P. incurvaria* in Barbados building domiciles from a species of *Dictyopteris* (a chemically defended alga [Hay et al. 1988*b*] in the Dictyotaceae), our studies in Belize and the Bahamas (Figs. 2, 3, and 5) and those of Lewis and Kensley (1982) in Belize indicated that *P. incurvaria* fed and built domiciles only from certain chemically defended members of the genus *Dictyota.* Differences between Just's observations and the experiments conducted in Belize and the Bahamas could be a result of localized specialization onto different host plants; this often occurs among terrestrial insects (Fox and Morrow 1981).

Within marine communities most specialized herbivores appear to derive some protection from predators as a result of their feeding specialization. The relatively uncommon ascoglossan gastropods are the only group that show a degree of feeding specialization similar to that seen in terrestrial insects. Although their feeding has rarely been studied in a rigorous manner, most ascoglossans appear to feed on a very restricted number of closely related species. Of the 61 herbivorous species listed by Jensen (1980), 82% fed from only one seaweed family, 15% fed from two families, and only 3% fed from three or more families. Most ascoglossans feed only on green seaweeds in the chemically rich (Paul and Fenical 1987) order Caulerpales. Because ascoglossans feed by piercing cells and sucking algal sap, they could feed on the Caulerpales primarily because the absence of cross walls in this order allows more effective feeding. However, since many ascoglossans feed on only a few species within this diverse order, morphology alone does not appear to be an adequate explanation for their feeding specificity. Rigorous documentation of the chemical interactions between these plants and herbivores are rare, but the few studies available indicate that the ascoglossans sequester secondary compounds from their algal food

and use these in their own defense (Paul and Van Alstyne 1988).

Many sea slugs (*Aplysia, Dolabella,* and other genera) also selectively consume chemically rich seaweeds from which they sequester defensive compounds; however, they are not obligately specialized to these foods and will consume a wide variety of other seaweeds if the preferred algae are not available (Carefoot 1987). Additionally, a few shelled gastropods also specialize on particular seaweeds that appear to provide structural refuges from predation (Phillips and Castori 1982, Steneck 1982). A number of other small invertebrate grazers such as amphipods and polychaetes have been hypothesized to experience less predation when associated with chemically rich seaweeds that they selectively consume (Hay et al. 1987a, 1988b, c, Hay and Fenical 1988). However, these grazers are usually very generalized and will readily use other seaweeds when their preferred foods are unavailable. The amphipod we studied here appears to be much more specialized. Even when deprived of all other choices, it rarely ate or built domiciles from anything other than species of *Dictyota* containing dictyol-class diterpenes (Figs. 2 and 5).

Although several amphipods decrease their encounters with predators by boring into seaweeds (Myers 1974), living in cryptic tubes they build on seaweeds (Nagle 1968, Nelson 1979b, but see Stoner 1979), or living in refuges they create by curling fronds (Griffiths 1979), we know of no other amphipod that creates a portable refuge from its chemically defended host plant. The chemical cuing of *Pseudamphithoides'* domicile-building behavior (Fig. 4) suggests that this is "behavioral sequestering" of algal chemical defenses by an organism that does not sequester metabolites metabolically, as is commonly done by sea slugs (Faulkner and Ghiselin 1983, Faulkner 1984, 1986, Carefoot 1987, Paul and Van Alstyne 1988) and terrestrial insects (Brower 1969, Rothschild 1973).

Specialization among terrestrial insect herbivores may arise in part because short-lived adults are equipped primarily for mating, dispersal, and careful placement of eggs (oviposition) on appropriate hosts; less dispersive juveniles are equipped primarily for feeding and growth on the host where they were placed by the adult. Most marine herbivores differ dramatically from insects because the marine organisms disperse widely in the plankton as short-lived juvenile stages that may have very limited ability to settle near particular host plants, and because long-lived adults do most of the feeding and are usually less dispersive than the planktonic juveniles. The relative scarcity of feeding specialization along marine herbivores has been hypothesized to result from the broadly dispersing larval stages, the potential costs of selective settlement, and the inability of adults to search widely and place their young on appropriate host plants without suffering high rates of predation (Hay and Fenical 1988). Protection of *Pseudamphithoides* by the portable domicile, coupled

with the lack of a larval stage (amphipods are brooders), could free this amphipod from these constraints. Since juveniles stay in the parent's domicile for a few days after hatching (Lewis and Kensley 1982), the domicile may increase the ability of the female to migrate among plants and provide juveniles with access to appropriate hosts. This could result in an increased probability of specialization due to local adaptation to specific host plants, and may account for *P. incurvaria's* more specialized feeding and behavior compared with other amphipods, which appear to be very generalized as a group.

LITERATURE CITED

Anderson, R. J., and B. Velimirov. 1982. An experimental investigation of the palatability of kelp bed algae to the sea urchin *Parechinus angulous* Leske. Marine Ecology (Publicazioni della Stazione Zoologica di Napoli I) 3:357–373.

Barbosa, P. 1988. Some thoughts on "the evolution of host range". Ecology 69:912–915.

Barnard, J. L. 1969. Gammaridean Amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. United States National Museum Bulletin 258:1–230.

Bernays, E., and M. Graham 1988. On the evolution of host specificity in phytophagous arthropods. Ecology 69:886–892.

Bousfield, E. L. 1973. Shallow-water Gammaridean Amphipoda of New England. Cornell University Press, Ithaca, New York, USA.

Brower, L. P. 1969. Ecological chemistry. Scientific American 220:22–29.

Carefoot, T. H. 1987. *Aplysia*: its biology and ecology. Oceanography and Marine Biology Annual Review 25:167–284.

Courtney, S. 1988. If it's not coevolution, it must be predation? Ecology 69:910–911.

Damman, H. 1987. Leaf quality and enemy avoidance by the larvae of a pyralid moth. Ecology 68:88–97.

Dayton, P. K., and M. J. Tegner. *In press.* Bottoms below troubled waters: benthic impacts of the 1982–1984 El Nino in the temperate zone. *In:* P. W. Glynn, editor. Global ecological consequences of the 1982–1983 El Nino-Southern Oscillation. Elsevier Oceanography Series, Amsterdam, The Netherlands.

Duffy, J. E., and M. E. Hay. *In press.* Herbivore resistance to seaweed chemical defense: the role of herbivore mobility and susceptibility to predation. Ecology.

Edgar, G. J. 1983a. The ecology of southeast Tasmanian phytal animal communities. II. Seasonal changes in plant and animal populations. Journal of Experimental Marine Biology and Ecology 70:159–179.

————. 1983*b*. The ecology of southeast Tasmanian phytal animal communities. IV. Factors affecting the distribution of ampithoid amphipods among algae. Journal of Experimental Marine Biology and Ecology **70**:205–225.

Ehrlich, P. R., and D. D. Murphy. 1988. Plant chemistry and host range in insect herbivores. Ecology **69**:908–909.

Faulkner, J. D. 1984. Marine natural products: metabolites of marine algae and herbivorous marine molluscs. Natural Products Reports **1**:251–280.

————. 1986. Marine natural products. Natural Products Reports **3**:1–33.

Faulkner, J. D., and M. T. Ghiselin. 1983. Chemical defense and evolutionary ecology of dorid nudibranchs and some other opisthobranch gastropods. Marine Ecology Progress Series **13**:295–301.

Faulkner, J. D., B. N. Ravi, J. Finer, and J. Clady. 1977. Diterpenes from *Dictyota dichotoma*. Phytochemistry **16**:991–993.

Fox, L. R. 1988. Diffuse coevolution within complex communities. Ecology **69**:906–907.

Fox, L. R., and P. A. Morrow. 1981. Specialization: species property or local phenomenon? Science **211**:887–893.

Futuyma, D. J., and F. Gould. 1979. Associations of plants and insects in a deciduous forest. Ecological Monographs **49**:33–50.

Gilbert, L. E., and M. C. Singer. 1975. Butterfly ecology. Annual Review of Ecology and Systematics **6**:365–397.

Griffiths, C. L. 1979. A redescription of the kelp curler *Ampithoe humeralis* (Crustacea, Amphipoda) from South Africa and its relationship to *Macropisthopous*. Annals of the South African Museum **79**:131–138.

Gunnill, F. C. 1985. Growth, morphology, and microherbivore faunas of *Pelvetia fastigiata* (Phaeophyta, Fucaceae) at La Jolla, California, USA. Botanica Marina **28**:187–199.

Hay, M. E. 1984. Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? Oecologia (Berlin) **64**:396–407.

Hay, M. E., J. E. Duffy, and W. Fenical. 1988*a*. Seaweed chemical defenses: among-compound and among-herbivore variance. *In* Proceedings of the Sixth International Coral Reef Congress, Townsville, Australia. James Cook University of North Queensland, Queensland, Australia. *In press*.

Hay, M. E., J. E. Duffy, W. Fenical, and K. Gustafson. 1988*b*. Chemical defense in the seaweed *Dictyopteris delicatula*: differential effects against reef fishes and amphipods. Marine Ecology Progress Series **48**:185–192.

Hay, M. E., J. E. Duffy, C. A. Pfister, and W. Fenical. 1987*a*. Chemical defenses against different marine herbivores: are amphipods insect equivalents? Ecology **68**:1567–1580.

Hay, M. E., and W. Fenical. 1988. Marine plant–herbivore interactions: the ecology of chemical defense. Annual Review of Ecology and Systematics **19**:111–145.

Hay, M. E., W. Fenical, and K. Gustafson. 1987*b*. Chemical defense against diverse coral-reef herbivores. Ecology **68**:1581–1591.

Hay, M. E., P. E. Renaud, and W. Fenical. 1988*c*. Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. Oecologia (Berlin) **75**:246–252.

Holmes, S. J. 1901. Observations of the habitats and natural history of *Ampithoe longimana* Smith. Biological Bulletin **2**:165–193.

Janzen, D. H. 1988. On the broadening of insect–plant research. Ecology **69**:905.

Jensen, K. R. 1980. A review of sacoglossan diets, with comparative notes on radular and buccal anatomy. Malacological Review **13**:55–77.

Jermy, T. 1988. Can predation lead to narrow food specialization in phytophagous insects? Ecology **69**:902–904.

Jones, L. G. 1965. Canopy grazing at southern Point Loma. Pages 62–63 in Kelp habitat improvement project Annual Report 1 February 1964–31 March 1965. W. M. Keck Laboratory of Environmental Health and Engineering. California Institute of Technology, Pasadena, California, USA.

————. 1971. Studies on selected small herbivorous invertebrates inhabiting *Macrocystis* canopies and holdfasts in southern California kelp beds. Pages 343–367 *in* W. J. North, editor. The biology of giant kelp beds (*Macrocystis*) in California. Nova Hedwigia, Supplement **32**.

Just, J. 1977. *Amphyllodomus incurvaria* gen. et sp. n. (Crustacea, Amphipoda), a remarkable leaf-cutting amphipod from the marine shallows of Barbados. Zoologica Scripta **6**:229–232.

Kelcom, A., and V. L. Teixeira. 1988. Dolastane diterpenes from the marine brown alga *Dictyota cervicornis*. Phytochemistry **27**:2907–2909.

Lawrence, J. M. 1975. On the relationship between marine plants and sea urchins. Oceanography and Marine Biology Annual Review **13**:213–286.

Lawton, J. H. 1978. Host-plant influences on insect diversity: the effects of space and time. Pages 105–125 *in* L. A. Mounds and N. Waloff, editors. Diversity of insect faunas. Symposia of the Royal Entomological Society of London, Volume 9. Blackwell, Oxford, England.

Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecological Monographs **56**:183–200.

Lewis, S. M., and B. Kensley. 1982. Notes on the ecology and behaviour of *Pseudamphithoides incurvaria* (Just) (Crustacea, Amphipoda, Amphithoidae). Journal of Natural History **16**:267–274.

Littler, M. M., P. R. Taylor, and D. S. Littler. 1983. Algal resistance to herbivory on a Caribbean barrier reef. Coral Reefs **2**:111–118.

Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant–herbivore interactions. I. Populations and communities. Annual Review of Ecology and Systematics **12**:405–437.

Martin, A. L. 1966. Feeding and digestion in two intertidal gammarids: *Marinogammarus obtusatus* and *M. pirloti*. Journal of Zoology **148**:515–525.

McBane, C. D., and R. A. Croker. 1983. Animal-algal relationships of the amphipod *Hyale nilssoni* (Rathke) in the rocky intertidal. Journal of Crustacean Biology **3**:592–601.

Moore, P. G. 1977. Organization in simple communities: observations on the natural history of *Hyale nilssoni* (Amphipoda) in high littoral seaweeds. Pages 443–451 *in* B. F. Keegan, P. O. Ceidigh, and P. J. S. Boaden, editors. Biology of benthic organisms. 11th European Marine Biology Symposium, Galway, Ireland. Pergamon, Elmsford, New York, USA.

Myers, A. A. 1974. *Amphitholina cuniculus* (Stebbing), a little-known marine amphipod crustacean new to Ireland. Proceedings of the Royal Irish Academy **74**:463–467.

Nagle, J. S. 1968. Distribution of the epibiota of macroepibenthic plants. Contributions of Marine Science **13**:105–144.

Nelson, W. G. 1979*a*. An analysis of structural pattern in an eelgrass (*Zostera marina* L.) amphipod community. Journal of Experimental Marine Biology and Ecology **39**:231–264.

————. 1979*b*. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. Journal of Experimental Marine Biology and Ecology **38**:225–245.

————. 1980. A comparative study of amphipods in seagrasses from Florida to Nova Scotia. Bulletin of Marine Sciences **30**:80–89.

Norris, J. N., and W. Fenical. 1982. Chemical defense in tropical marine algae. Pages 417–431 *in* K. Rutzler and I.

G. Macintyre, editors. Atlantic barrier reef ecosystem Carrie Bow Cay, Belize. 1. Structure and communities. Smithsonian Contributions to the Marine Sciences **12**.

Norris, J. N., and W. Fenical. 1985. Natural products chemistry: uses in ecology and systematics. Pages 121–145 *in* M. M. Littler and D. S. Littler, editors. Handbook of phycological methods. Ecological field methods: macroalgae. Cambridge University Press, Cambridge, England.

Paul, V. J., and W. Fenical. 1987. Natural products chemistry and chemical defense in tropical marine algae of the phylum Chlorophyta. Pages 1–29 *in* P. J. Scheuer, editor. Bioorganic marine chemistry 1. Springer-Verlag, Berlin, West Germany.

Paul, V. J., and M. E. Hay. 1986. Seaweed susceptibility to herbivory: chemical and morphological correlates. Marine Ecology Progress Series **33**:255–264.

Paul, V. J., M. E. Hay, J. E. Duffy, W. Fenical, and K. Gustafson. 1987. Chemical defense in the seaweed *Ochtodes secundiramea* (Montagne) Howe (Rhodophyta): effect of its monoterpenoid components upon diverse coral reef herbivores. Journal of Experimental Marine Biology and Ecology **114**:249–260.

Paul, V. J., and K. L. Van Alstyne. 1988. The use of ingested algal diterpenoids by the ascoglossan opisthobranch *Elysia halimedae* Macnae as antipredator defenses. Journal of Experimental Marine Biology and Ecology **119**:15–29.

Peterson, C. H., and P. E. Renaud. 1989. Analysis of feeding preference experiments. Oecologia (Berlin) **80**:82–86.

Phillips, D. W., and P. Castori. 1982. Defensive responses to predatory seastars by two specialist limpets, *Notoacmea insessa* (Hinds) and *Collisella instabilis* (Gould), associated with marine algae. Journal of Experimental Marine Biology and Ecology **59**:23–30.

Price, P. W. 1983. Hypotheses on organization and evolution in herbivorous insect communities. Pages 559–598 *in* R. F. Denno and M. S. McClure, editors. Variable plants and herbivores in natural and managed systems. Academic Press, New York, New York, USA.

Price, P. W., C. E. Bouton, P. Gross, B. A. McPherson, J. N. Thompson, and A. E. Weiss. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annual Review of Ecology and Systematics **11**:41–65.

Price, P. W., M. Westoby, B. Rice, P. R. Atsatt, R. S. Fritz, J. N. Thompson, and K. Mobley. 1986. Parasite mediation in ecological interactions. Annual Review of Ecology and Systematics **17**:487–505.

Randall, J. E. 1967. Food habits of reef fishes of the West Indies. Studies of Tropical Oceanography **5**:655–897.

Rausher, M. D. 1988. Is coevolution dead? Ecology **69**:898–901.

Rothschild, M. 1973. Secondary plant substances and warning coloration in insects. Royal Entomological Society of London Symposium **6**:59–83.

Schultz, J. C. 1988. Many factors influence the evolution of herbivore diets, but plant chemistry is central. Ecology **69**:896–897.

Smith, G. A., J. S. Nickels, W. M. Davis, R. F. Martz, R. H. Findlay, and D. C. White. 1982. Perturbations in the biomass, metabolic activity, and community structure of the estuarine detrital microbiota: resource partitioning in amphipod grazing. Journal of Experimental Marine Biology and Ecology **64**:125–143.

Steneck, R. S. 1982. A limpet–corallina alga association: adaptations and defenses between a selective herbivore and its prey. Ecology **63**:507–522.

Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. Marine Biology **68**:299–319.

Stoner, A. W. 1979. Species-specific predation on amphipod Crustacea by the pinfish *Lagodon rhomboides*: mediation by macrophyte standing crop. Marine Biology **55**:201–207.

———. 1980. Abundance, reproductive seasonality and habitat preferences of amphipod crustaceans in seagrass meadows of Apalachee Bay, Florida. Contributions in Marine Science **23**:63–77.

Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. Insects on plants: community patterns and mechanisms. Blackwell Scientific, Oxford, England.

Tegner, M. J., and P. K. Dayton. 1987. El Nino effects on southern California kelp forest communities. Advances in Ecological Research **17**:243–279.

Teixeira, V. L., T. Tomassini, B. G. Fleury, and A. Kelacom. 1986a. Dolastane and secodolastane diterpenoids from the marine brown alga *Dictyota cervicornis*. Journal of Natural Products **46**:570–575.

Teixeira, V. L., T. Tomassini, and A. Kelcom. 1986b. Cervicol, a further secodolastane diterpene from the marine brown alga *Dictyota cervicornis* Kutzing (Phaeophyceae, Dictyotacea). Bulletin des Sociétés Chimiques Belges **95**:263–268.

Thompson, J. N. 1988. Coevolution and alternative hypotheses on insect/plant interactions. Ecology **69**:893–895.

Van Dolah, R. F. 1978. Factors regulating the distribution and population dynamics of the amphipod *Gammarus palustria* in an intertidal salt marsh community. Ecological Monographs **48**:191–217.

Vince, S., I. Valiela, N. Backus, and J. M. Teal. 1976. Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. Journal of Experimental Marine Biology and Ecology **23**:255–266.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Zimmerman, R., R. Gibson, and J. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Marine Biology **54**:41–47.

NOTE ADDED IN PROOF

The experiment shown in Fig. 4 was recently repeated at Chub Cay in the Bahamas. *Pseudamphithoides incurvaria* from this location did not respond to pachydictyol-A. A repetition of the experiment in Belize reconfirmed that *P. incurvaria* from Carrie Bow Cay were significantly stimulated by this compound. Although our data suggest that amphipods from both sites build domiciles exclusively from *Dictyota bartayresii,* cuing on pachydictyol-A appears to be a local adaptation of the amphipods in Belize.