

ASSOCIATIONAL PLANT DEFENSES AND THE MAINTENANCE OF SPECIES DIVERSITY: TURNING COMPETITORS INTO ACCOMPLICES

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Experimental field ecologists, especially marine ecologists, have been impressively successful in demonstrating the importance of predation and physical disturbances in maintaining species diversity (Paine 1966, 1979; Dayton 1971; Connell 1975, 1978; Lubchenco 1978; Sousa 1979; Ayling 1981; Hay 1981*a*; Porter et al. 1981; Hixon and Brostoff 1983; Dethier 1984). In many communities it is clear that the number of coexisting species would decrease considerably if predation or physical disturbances did not differentially affect competitively or numerically dominant species, thus freeing resources for use by less abundant species. In some communities, however, natural levels of predation may decrease species diversity because (1) species that would not have been excluded by competition are excluded by predation (Addicott 1974; Lubchenco 1978; Hay 1981*a*, 1985; Sammarco 1982; Hixon and Brostoff 1983; Lewis 1986) or (2) selective predation on poorly defended species and competition from predator-resistant species combine to cause local extinctions (Lubchenco 1980). In many instances the effects of predation or physical disturbance can be predicted if their magnitude and frequency are known. Intermediate levels of predation or physical disturbance tend to promote the highest diversity (Connell 1978; Hixon and Brostoff 1983) in communities where competition causes mortality. This pattern may be less important, or absent, in communities where competition affects growth rate but not mortality (Peterson 1982).

In this paper I argue that the obvious successes achieved by studies focusing primarily on competition and predation may have caused ecologists to overlook more indirect commensal, or mutualistic, interactions that also may play a significant role in community organization (see also O'Dowd and Williamson 1979; Dayton and Oliver 1980; Vandermeer 1980; Dethier and Duggins 1984). More specifically, I show that one competitor may have a strong *positive* effect on another if the first significantly reduces the probability that the second will be excluded from the community through high rates of predation. In the seaweed community I investigate, an increasing abundance of the two most common species is associated with an increased, not a decreased, number of other species.

This occurs even though the growth rates of the less common seaweeds are significantly depressed by the presence of the more common ones (i.e., they are competitors). This pattern occurs because the most abundant species are relatively unpalatable to local herbivores and by their presence create microsites of lowered herbivory where the most palatable species can successfully establish. In the absence of the unpalatable species, the palatable seaweeds are driven locally extinct by consumers. Thus, the competitive costs of being associated with another plant may be much less than the costs of increased herbivory in the absence of that plant.

This type of associational defense can provide an unappreciated mechanism for maintaining species richness within a community (the number of species as opposed to the evenness with which individuals are distributed among species), since increases in the most abundant competitor can lead to increases, instead of decreases, in the number of other species present (see also O'Dowd and Williamson 1979).

In this investigation, I ask the following questions. First, can palatable seaweeds decrease their losses to herbivory by growing in close association with unpalatable seaweeds? Second, in the absence of major herbivores, how does each species affect the growth of the other? Third, must palatable plants be relatively rare in order to gain protection from herbivores by associating with unpalatable plants? Finally, how does an increasing abundance of unpalatable plants affect the establishment of palatable species and the species richness of the plant community in general?

STUDY SITE AND ORGANISMS

Fieldwork was conducted on Radio Island Jetty near Beaufort, North Carolina (34°42' N, 76°41' W). The jetty runs from the surface to a depth of approximately 10 m, but all field experiments were conducted in shallow areas at a depth of 0.5–1.5 m. The jetty is man-made, but the fish fauna and algal flora of the jetty are similar to natural hard-substrate areas that occur offshore at a depth of 20–30 m (Richardson 1978; Link 1980; Peckol 1980). The large brown seaweed *Sargassum filipendula* is the most common seaweed on the jetty, making up approximately 85% of total algal mass during the summer. It and another common brown seaweed, *Padina vickersiae*, are relatively unpalatable to a mixture of three local omnivorous fishes (table 1).

Various palatable seaweeds, including *Hypnea musciformis*, *Chondria* spp., *Ulva* spp., *Enteromorpha* spp., and *Gracilaria* spp., are relatively common on the jetty throughout much of the year but appear to decrease sharply in abundance during midsummer, when omnivorous fishes are most common. Additionally, during spring and late fall when fishes are rare or are feeding on amphipods instead of algae (Adams 1976c; Stoner and Livingston 1984), most of these palatable seaweeds are abundant on primary substrate. In midsummer, when fishes abound and feed primarily on algae, the palatable seaweeds occur almost exclusively as epiphytes on unpalatable species such as *Sargassum* and *Padina*.

Common herbivorous or omnivorous fishes include spottail pinfish (*Diplodus holbrooki*), pinfish (*Lagodon rhomboides*), and planehead filefish (*Monocanthus*

TABLE 1
CHANGE IN WET MASS OF PORTIONS OF ADULT PLANTS IN FISH-INCLUSION OR FISH-EXCLUSION TREATMENTS IN MICROCOSMS

SPECIES	CHANGE IN WET MASS (%), $\bar{x} \pm 1$ SE)		
	Fish Present	Fish Excluded	P
<i>Sargassum filipendula</i>	6.0 \pm 1.7	6.0 \pm 0.9	>> 0.50
<i>Padina vickersiae</i>	8.5 \pm 2.3	7.5 \pm 3.2	>> 0.50
<i>Gracilaria verrucosa</i>	-54.5 \pm 18.1	9.9 \pm 1.2	< 0.01
<i>Chondria dasyphylla</i>	-75.4 \pm 10.0	-2.5 \pm 6.9	< 0.001
<i>Hypnea musciformis</i>	-78.5 \pm 9.3	-8.0 \pm 1.8	< 0.001
<i>Spyridia hypnoides</i>	-84.2 \pm 11.0	3.5 \pm 3.0	< 0.001
<i>Enteromorpha linza</i>	-100.0 \pm 0.0	-16.2 \pm 12.2	< 0.001
<i>Ulva</i> spp.	-78.0 \pm 15.2	43.5 \pm 6.2	< 0.001

NOTE.— $N = 8$ paired samples; the assay ran for 48 h. Fish densities in the inclusion treatment were eight *Diplodus holbrooki*, one *Lagodon rhomboides*, and one *Monocanthus hispidus* per square meter. This approximates field densities in midsummer. P values were calculated by the paired-sample t -test.

hispidus). These fishes are abundant in near-shore waters during the spring, summer, and fall, but most individuals move offshore during colder periods of the year (Adams 1976a,b). Numerous studies are available on the feeding habits of these fishes (Carr and Adams 1973; Adams 1976c; Stoner 1980; Stoner and Livingston 1984). As juveniles, they eat primarily zooplankton and small benthic crustaceans; with increasing size they become more herbivorous, and by early summer most individuals are almost completely herbivorous.

In addition to the field experiments, several experiments were conducted in eight large microcosms (5000 liters) adjacent to Bogue Sound, behind the Institute of Marine Sciences. The microcosms were made of stainless steel and measured 4.27 m long by 1.22 m wide by 0.6 m deep. Unfiltered seawater was continuously pumped into each microcosm at a rate of 60–120 liters per min. The water entered through a wave generator, which provided turbulence similar to that encountered on the shallow jetty. Since the microcosms were located outside and were directly adjacent to the sound, physical conditions such as light, temperature, and water clarity varied in accordance with local weather conditions.

In most bioassays of associational defense, *Sargassum* was used as the unpalatable host and either *Hypnea musciformis* or *Spyridia hypnoides* was used as the palatable epiphyte. Both of these palatable species have hooklike terminal tips that facilitate their attachment to other seaweeds (see Taylor 1960, figs. 71, 73). These plants could be attached easily to *Sargassum* plants by pulling them down the main axis until their tips hooked securely around the areas where blades or branchlets emerged from the main axis.

METHODS

Fish Density and Algal Abundance on the Jetty

During mid-July 1984, three scuba divers placed quadrats of 0.5 m by 0.5 m (0.25 m²) at haphazard intervals along the jetty, between depths of 0.5 m and 1.5

m. The small quadrat size was necessitated by the poor visibility on the jetty, which was often only 1–2 m. Every 10 s for 40 s, the diver would count the number of fish and record the species composition of all fish over the quadrat at that instant. The four counts were then averaged for each quadrat. Small floats were tied at each corner of the quadrat in order to help determine if a fish was actually above or just near the quadrat. Quadrats were moved to a new location after each set of four counts. Counts were conducted on three separate days until a total of 100 quadrats had been counted. Spottail pinfish did not appear to be affected by the presence of the diver or quadrat; pinfish and filefish often appeared to avoid the quadrat, but the limited visibility compromised our ability to assess fish behavior with regard to diver or quadrat presence. Pinfish and filefish were commonly seen in the area, but seldom occurred in our quadrats. In January and February 1985, fish counts were made by swimming along the jetty for three 1-h periods and counting all the fishes seen. Since no fish were seen on the jetty during this time, I did not bother to use the quadrat method.

During mid-July 1984 and mid-February 1985, I collected all seaweeds within quadrats of 17 cm by 24 cm located at random intervals along a 60-m transect running at a depth of 0.5–1.5 m on the north end of Radio Island Jetty ($N = 38$ –40). Each quadrat was bagged separately, as were individuals that occurred on primary substrate versus those growing as epiphytes on other seaweeds. Algae from all quadrats were sorted in the laboratory, and the wet mass of each species was determined after spinning in a salad spinner to remove excess water.

Microcosm Feeding Assays

The susceptibility of eight common seaweeds to fish grazing was assessed in the eight 5000-liter microcosms. Within each microcosm, two parallel areas of 1 m² (0.6 m × 1.68 m) were established using plastic mesh fences with attached bottoms. Because the fences extended above water level (≈40 cm deep), no top was needed to confine the eight spottail pinfish, one pinfish, and one filefish that were placed in one side of each microcosm. This density of fishes approximated that found on Radio Island Jetty during midsummer of 1984. The other side of each microcosm contained no fishes and served as a control. In order to mimic the natural seaweed community, I added to both sides of each microcosm the mean wet mass of each common seaweed per square meter on Radio Island Jetty (as determined in mid-July 1984 from 20 randomly located quadrats of 24 cm × 17 cm). The following genera were added to the microcosms: *Codium*, *Ulva*, *Sargassum*, *Dictyota*, *Padina*, *Hypnea*, *Neogardhiella*, *Rhodymenia*, *Gracilaria*, *Gelidium*, *Grinnellia*, *Lomentaria*, *Gymnogongrus*, and *Chondria*.

Seaweed species used in the herbivory assay were *Sargassum filipendula*, *Padina vickersiae*, *Gracilaria verrucosa*, *Chondria dasyphylla*, *Hypnea musciformis*, *Spyridia hypnoides*, *Enteromorpha linza*, and *Ulva* sp. Small pieces of each of these species were spun in a salad spinner to remove excess water before their wet mass was determined. One weighed piece of each species was then placed between the strands of a three-strand rope in such a way that each rope held one piece of all eight species. The position of each species along the rope was assigned haphazardly. Two of these ropes were then anchored securely at both ends in

each side of each microcosm. After 48 h, each alga was reweighed; the two ropes within each side of each microcosm were pooled to give eight paired samples for each algal species.

Field Assays of Associational Defenses

The consequences of placing herbivore-susceptible and herbivore-resistant seaweeds together were assessed in the presence and absence of herbivorous fishes by placing algae inside or outside of cages on Radio Island Jetty. Since the palatable species *Hypnea musciformis* often grows epiphytically on the unpalatable species *Sargassum filipendula*, I used these two species in this experiment. Three-strand ropes held preweighed pieces of *Hypnea* alone (100–150 mg), *Hypnea* (100–150 mg) placed on *Sargassum* (1000–1500 mg), and *Sargassum* alone (1000–1500 mg). On each rope, *Hypnea* alone, *Hypnea* on *Sargassum*, and *Sargassum* alone were separated by about 5 cm. On July 18, 1984, 10 of the ropes were placed inside cages 34 cm long by 30 cm in diameter (6-mm mesh) that were suspended 15 cm above the substrate on steel rods in order to minimize invasion by small nonswimming invertebrates. Cages were separated from each other by about 4 m. An uncaged rope was placed within 2 m of each cage and suspended 15 cm above the substrate by placing it on a thin steel rod. Suspending ropes above the bottom prevented grazing by urchins and other nonswimming herbivores. Urchin distribution is very patchy in coastal North Carolina; urchins would, therefore, be important herbivores in some areas and have no effect in others. In this study, I concentrated on grazing by fishes since herbivory by temperate fishes has been studied so much less than herbivory by urchins and since urchins were absent from large areas on the jetty I studied. Effects of associational defenses on herbivory by urchins is being assessed in a separate study (C. Pfister and Hay, unpubl. data); results available to date suggest that fish and urchins are affected in similar ways.

Preliminary field experiments showed that fishes avoided open-sided cages; for this reason I did not attempt to use these as cage controls. All cages and suspended ropes were on the lee side of the north end of Radio Island Jetty at a depth of 0.5–1 m. Uncaged ropes were visually monitored every 6–12 h and were removed after 32 h since almost all *Hypnea* that was not on *Sargassum* had been consumed by that time. Caged algae remained in the field for 152 h in order to allow a more accurate assessment of differences between the growth rates of *Hypnea* and *Sargassum* alone and the growth of each when they occurred together. This experiment was repeated on July 30, 1984, with both caged and uncaged ropes remaining in the field for 92 h. In order to eliminate the possibility that changes in algal wet mass on the ropes were related to some artifact of caging instead of fish grazing, similar enclosure and exclosure experiments were also conducted in the microcosms where caging conditions were identical. These experiments are described below.

It is possible that presenting *Hypnea* alone, *Sargassum* alone, and *Hypnea* on *Sargassum* all on the same rope could bias the results relative to those that would be obtained if each was presented separately. This was tested by placing each algal treatment on a separate rope and interspersing these along the leeward side

of the north end of the jetty. Sample size for each treatment was 30 and all ropes remained in the field for 27 h.

To assess *Hypnea* consumption when it grows beneath the canopy of *Sargassum*, as opposed to growing on *Sargassum*, I placed 40 preweighed pieces (100–150 mg) of *Hypnea* in numbered sections of three-strand ropes. On 20 of these ropes, I placed large *Sargassum* plants about 6 cm on either side of the *Hypnea* plant; the other 20 ropes contained *Hypnea* alone. These ropes were interspersed at 1-m intervals along the lee side of the jetty (0.5–1.0 m deep) and remained in the field for 25 h.

To determine how the efficiency of the associational defense changed with an increasing relative abundance of the palatable species, I added varying masses of *Hypnea* to 1.0–1.5-g pieces of *Sargassum*. Five preweighed combinations of *Hypnea* and *Sargassum* were placed in each of 19 sections of three-strand rope. *Hypnea* was added as 5%, 10%, 20%, 50%, or 100% of the wet mass of the *Sargassum* plant. On July 26, 1984, these ropes were placed on the lee side of the jetty at its northern end and collected and reweighed after 19 h. On July 31, 1984, this procedure was repeated with 30 ropes. Attempts to place some ropes inside cages as a control for loss that was unrelated to grazing were unsuccessful. The treatments with a high ratio of *Hypnea* to *Sargassum* had many recurved *Hypnea* tips that were not hooked onto the limited amount of *Sargassum* available. These tips became hooked onto the cages themselves and would thus often pull loose from the ropes. To see if turbulence and wave force alone would cause differential loss of *Hypnea* or *Sargassum* from the uncaged ropes, 17 ropes were prepared as described above and placed near the wave generators in the microcosms. The portions of the microcosms used were devoid of macro-herbivores, and the ropes were placed in the microcosms for 10 h during the dark period between dusk and sunrise. This procedure eliminated changes in mass related to either herbivory or production. Three or four ropes were placed in each of five microcosms. After 10 h, each alga was reweighed to determine change in mass as a function of each treatment. Replicates within a microcosm were pooled since these could not be considered independent. Loss patterns from this microcosm assessment were compared to those from the field to see if water motion alone might have generated patterns seen in the field. Waves in the microcosms are generated by rapidly dropping about 60 liters of water from a height of 0.5 m into water with a depth of only 0.4 m. This occurs every 30–60 s. The turbulence created in the microcosms is clearly greater than that occurring on the lee side of the jetty.

Microcosm Assays of Associational Defenses

Field caging studies usually had to be completed during the weekdays in order to avoid the disturbances and cage losses associated with weekend use of the jetty by fishermen. During periods of overcast weather, fishing activity decreased and studies could sometimes run for longer periods; however, attempts to conduct long-term caging studies resulted in an unacceptably large loss of cages. Use of microcosms for these studies alleviated this problem, allowed greater control of herbivore density, and eliminated potential biases from cage effects in the field studies, where caged plants were compared with plants placed in the open.

Microcosms were used to replicate the field assays under more-controlled conditions and to monitor longer-term settlement and growth of benthic organisms when exposed to, and protected from, fish grazing. For these tests the microcosms were set up as follows. Seawater was continuously pumped through the microcosms for 2 mo before any experimental work began. This allowed the sides of the tanks and the plastic mesh fences that separated adjacent 1.0-m² areas of the tanks to become covered with various species of algae and marine invertebrates that colonized through the unfiltered seawater system. During the second week of August 1984, the mean wet mass per square meter of each common algal species from Radio Island Jetty was added to the two enclosed areas in each tank. Eight spottail pinfish, 1 pinfish, and 1 filefish were added to one side of each tank. Five new cinder blocks were added to each side of each tank and an area 17 cm by 24 cm on top of each was monitored every 2–4 wk to determine the presence and percent cover of each species present. Percent cover was determined using a quadrat with 100 monofilament cross hairs. Cross hairs were made by running 10 strands of monofilament across the length of the quadrat, and 10 across the width, using a stratified random procedure for determining the location of each strand.

On August 16, 1984, the field methods used to assess the effects of associational defenses were repeated in the microcosms. This test alleviated the potential problem of cage artifacts in the field experiments since portions of the microcosm enclosing or excluding fishes were identical. Additionally, the potential suite of herbivore species was limited to the three fish species enclosed in the microcosm. In this assay, each three-strand rope held preweighed plants of *Sargassum filipendula* (1000–1500 mg), *Hypnea musciformis* (100–150 mg), and *Spyridia hypnoides* (100–150 mg) that were not touching other plants, as well as a *Hypnea* plant and a *Spyridia* plant that were each placed on a separate *Sargassum* plant. As in the field experiments, the palatable species (*Hypnea* and *Spyridia*) were added to the unpalatable species (*Sargassum*) in a wet-mass ratio of 1 part palatable plant to 10 parts unpalatable plant. Five of these ropes were placed in the fish-inclusion and five in the fish-exclusion side of each microcosm by wiring each to the top of a cinder block. After 24 h, each alga on each block was visually censused and recorded as still present or completely missing. After 8 days (192 h), all ropes were collected and each plant was reweighed. This method produced eight paired samples (one per microcosm), with each sample consisting of five subsamples.

Laboratory Feeding Assay

Since fishes were so numerous and appeared to be responsible for most plant removal, I performed only limited laboratory assays on how grazing by the local sea urchin *Arbacia punctulata* and a mixed-species assemblage of local amphipods might be affected by associational defenses. I placed 20 urchins in separate 3.8-liter containers. A 1-g piece of *Sargassum* alone, a 1-g piece of *Sargassum* entwined with a 0.1-g piece of *Hypnea*, and a 0.1-g piece of *Hypnea* alone were held in each container by placing their bases through small slits in a rubber disk that rested on the bottom of each container. Algae were placed in five additional containers that did not hold urchins. These containers allowed an

assessment of changes in algal wet mass that were unrelated to urchin grazing. After 5 days, all algae were reweighed and changes in algal mass in the containers with urchins were corrected according to changes that had occurred in the control containers. All containers were constantly aerated and water was changed once daily.

To assess how small herbivores might affect associational defenses, a mixed-species assemblage of amphipods was collected from *Sargassum* and *Hypnea* growing on Radio Island Jetty. Ten amphipods (most were *Ampithoe longimana*) were placed in each of 10 separate 20-cm-diameter dishes that contained 1 liter of seawater. To each dish, I added a 50-mg piece of *Hypnea* alone, a 50-mg piece of *Hypnea* entwined with a 250–300-mg piece of *Sargassum*, and a 250–300-mg piece of *Sargassum* alone. Five additional dishes, with algae but without amphipods, served as controls. Alga position was randomized within each dish, and all algae or algal combinations were separated by about 8 cm. After 75 h, all algae were reweighed and changes in algal mass corrected according to changes in controls.

RESULTS

Seasonal Changes in Herbivore Abundance and Plant Associations

During mid-July 1984, the density of the spottail pinfish on the shallow portion (0.5–1.5 m deep) of Radio Island Jetty was $1.91 (\pm 0.20)$ per 0.25 m^2 ($\bar{x} \pm 1 \text{ SE}$, $N = 100$), or 7 to 8 individuals per square meter. Pinfish (*Lagodon rhomboides*) and filefish (*Monocanthus hispidus*) were also common at this time, but few came close enough to divers to be reliably counted in our small quadrats. During three separate 1-h dives in January and February 1985, no herbivorous fishes of any kind were seen on the jetty. Adams (1976a,b) documented similar patterns in nearby seagrass-bed communities. Thus, herbivorous fishes are abundant during the summer and absent, or very rare, during the winter.

The effect of fish grazing on adult portions of eight common seaweeds is shown in table 1. *Sargassum* and *Padina* were not consumed by the assemblage of fishes in the microcosms ($P > 0.50$), whereas *Gracilaria*, *Chondria*, *Hypnea*, *Spyridia*, *Enteromorpha*, and *Ulva* showed large and significant losses in the presence of these fishes (paired-sample *t*-test, $P < 0.01$). These feeding assays, coupled with the algal seasonality patterns described below suggest that these temperate fishes play a significant role in selecting for algal associations that decrease losses to herbivores.

During summer collections from the jetty, *Hypnea* was present in 81% of the 22 quadrats that contained *Sargassum* or *Padina* but was completely absent from all 19 quadrats that did not contain these common, unpalatable seaweeds (fig. 1A). Other palatable species, such as *Chondria*, *Ulva*, and *Enteromorpha*, showed similar patterns during the summer. All palatable species were completely absent from quadrats without *Sargassum* or *Padina* but were present in 33% to 81% of the quadrats that contained *Sargassum* or *Padina*. For each of the palatable

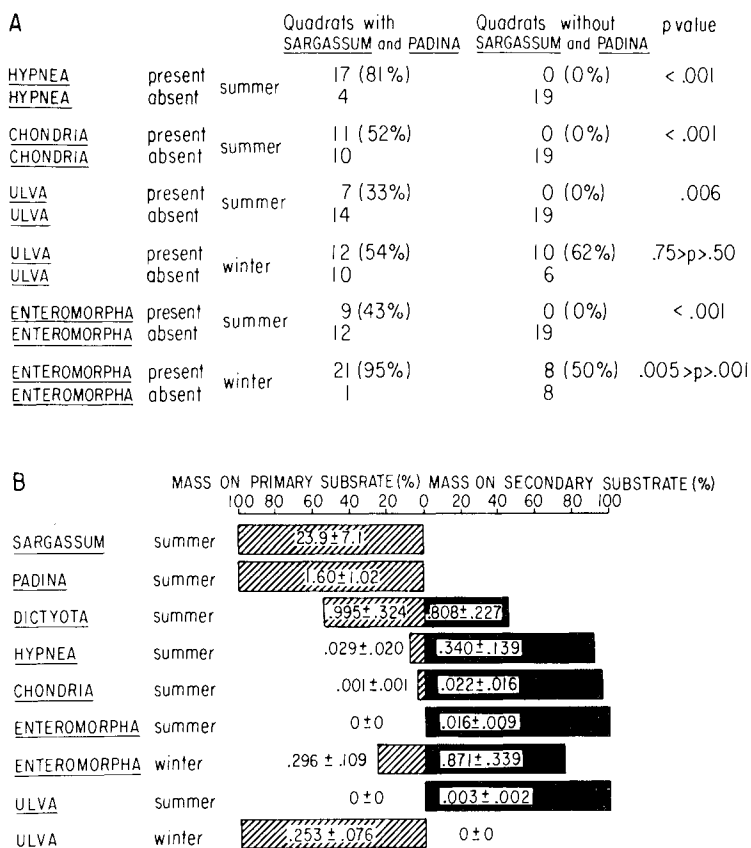


FIG. 1.—A, The effect of the presence of *Sargassum* and *Padina* on the frequency of occurrence of common palatable species on Radio Island Jetty. Collections were made from quadrats measuring 17 cm by 24 cm: 40 in the summer (mid-July); and 38 from the same area in the winter (mid-February). *P* values are by Fisher's exact test or contingency-table analysis if cell sizes were sufficiently large. B, The relative proportion of each species' wet mass occurring on primary rather than secondary substrate. Numbers within, or beside, each histogram give the mean wet mass per quadrat \pm 1 SE. A correlation analysis of the wet mass of unpalatable versus palatable species (as defined by patterns shown in table 1) showed that the abundances of palatable and unpalatable plants were positively correlated in the summer ($r = 0.50$, $P < 0.001$) and were unrelated during the winter ($r = 0.05$, $P > 0.50$).

species, the frequency of occurrence increased significantly in quadrats with *Sargassum* or *Padina* compared with quadrats without these unpalatable seaweeds (Fisher's exact test, $P \leq 0.006$; fig. 1A).

Additionally, the palatable species occurred almost exclusively as epiphytes on the unpalatable species (fig. 1B). During the summer, *Ulva* and *Enteromorpha* occurred exclusively as epiphytes, and 96% of the *Chondria* mass and 92% of the *Hypnea* mass were epiphytic. This epiphytic habit was not simply a result of all primary substrate being occupied by other species; 18 of the 40 quadrats collected

during the summer contained no macrophytes and appeared to be available for colonization.

Ulva and *Enteromorpha* were the only palatable seaweeds that occurred frequently in both summer and winter collections. *Hypnea* and *Chondria* were absent during the winter. *Ulva* abundance was dramatically higher during the winter (0.003 g per quadrat in summer vs. 0.253 g per quadrat in winter, fig. 1B), and it occurred with almost equal frequency in quadrats with or without unpalatable species (fig. 1A). *Ulva* also occurred almost exclusively on primary, rather than secondary, substrate during this season (fig. 1B). *Enteromorpha* showed a similar, although less dramatic, shift, exhibiting a significant winter increase in its occurrence in quadrats without *Sargassum* or *Padina* (Fisher's exact test, $P = 0.006$), although it still occurred significantly more often in quadrats with those species (fig. 1A). *Enteromorpha* abundance also was dramatically higher in the winter and an appreciable portion of its mass occurred on primary substrate (fig. 1B). The appearance of *Enteromorpha* was strikingly different between summer and winter. During the summer, I saw no *Enteromorpha* while making the field collections. It was restricted to the denser portions of the *Sargassum* plants and could usually be seen only after several of the *Sargassum* blades had been removed as samples were sorted in the laboratory. During the winter, I could often see *Enteromorpha* on *Sargassum* even when I was still several meters from the plant. It not only grew on the more protected central portions of *Sargassum* plants but also occurred as long strands extending many centimeters beyond the margins of its host. Thus, when herbivorous fishes were common on the jetty, palatable species occurred almost exclusively as small, cryptic plants that grew epiphytically on the much larger and more common unpalatable plants. During the winter when herbivorous fishes were absent, palatable species became more apparent and significantly increased their use of both primary substrate and quadrats in which the unpalatable species did not occur. This seasonal change in abundance and habitat use of palatable species was not caused by seasonal changes in the total abundance of the unpalatable species. Neither the combined mean wet mass of *Sargassum* and *Padina* per quadrat ($\bar{x} \pm 1 \text{ SE} = 39.4 \pm 11.3 \text{ g}$ in winter, and $25.5 \pm 7.1 \text{ g}$ in summer; t -test, $0.50 > P > 0.25$) nor the proportion of quadrats occupied by at least one of the species (23 of 38 quadrats in winter, and 21 of 40 quadrats in summer; χ^2 test, $0.50 > P > 0.25$) changed between seasons. Although palatable plants growing on unpalatable hosts were restricted to a small size during the summer (figs. 1, 6), several reproductive plants were present in the collections. Therefore, small size apparently does not preclude reaching sexual maturity.

For the summer collection, the wet mass of unpalatable species per quadrat correlated positively with the wet mass of palatable species per quadrat ($r = 0.50$, $P < 0.001$, $N = 40$). During the winter when herbivorous fishes were not in the area, no such correlation existed ($r = 0.05$, $P > 0.50$, $N = 38$). All of these findings are consistent with the hypothesis that palatable species would be excluded from the jetty by herbivores during the summer if not for the presence of unpalatable competitors providing microsites of reduced herbivory (fig. 1). The following procedures tested this hypothesis.

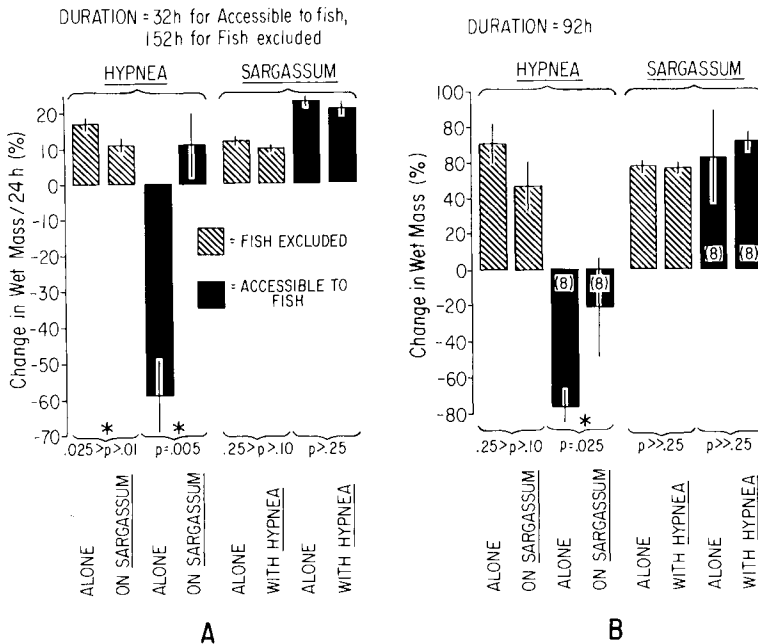


FIG. 2.—Effect of fish grazing on change in wet mass of *Hypnea* and *Sargassum* when grown together or separately in the field. $N = 8-10$; vertical bars through each histogram show ± 1 SE. A, B, Results from experiments conducted on two separate dates. Asterisks, Significant differences ($P < 0.05$) by the Wilcoxon paired-sample test. For each replicate, *Hypnea* alone, *Hypnea* on *Sargassum*, and *Sargassum* alone were separated by approximately 5 cm.

Interactions among Fishes, Palatable Seaweeds, and Unpalatable Seaweeds

The interactions that occur in the field among fishes, *Hypnea*, and *Sargassum* are shown in figure 2. In the first set of field experiments (fig. 2A), *Hypnea* grew equally well either inside or outside of cages when it was placed on *Sargassum* (Mann-Whitney U -test, $P > 0.20$). However, *Hypnea* was rapidly consumed (-59% per day) when it occurred outside of cages and was not placed on *Sargassum*. *Hypnea* that was not on *Sargassum* grew well in fish exclosures ($+17\%$ per day). These dramatic differences in *Hypnea* consumption occurred even though plants on *Sargassum* were separated by only 5 cm from plants that were considered to be growing alone. Immediately after placing these transplants on the jetty, I often observed spottail pinfish grazing on *Hypnea* plants that occurred alone; I rarely saw them consume *Hypnea* plants that had been placed on *Sargassum*. When fishes were excluded by cages, *Hypnea* placed on *Sargassum* grew significantly more slowly than *Hypnea* separated from *Sargassum* by a distance of 5 cm (Wilcoxon paired-sample test, $0.025 > P > 0.01$). In both the field and microcosm studies, when *Hypnea* or *Spyridia* was placed on *Sargassum* in a ratio of approximately 1 part *Hypnea* or *Spyridia* to 10 parts *Sargassum* (measured as wet mass), neither *Hypnea* nor *Spyridia* significantly affected the growth

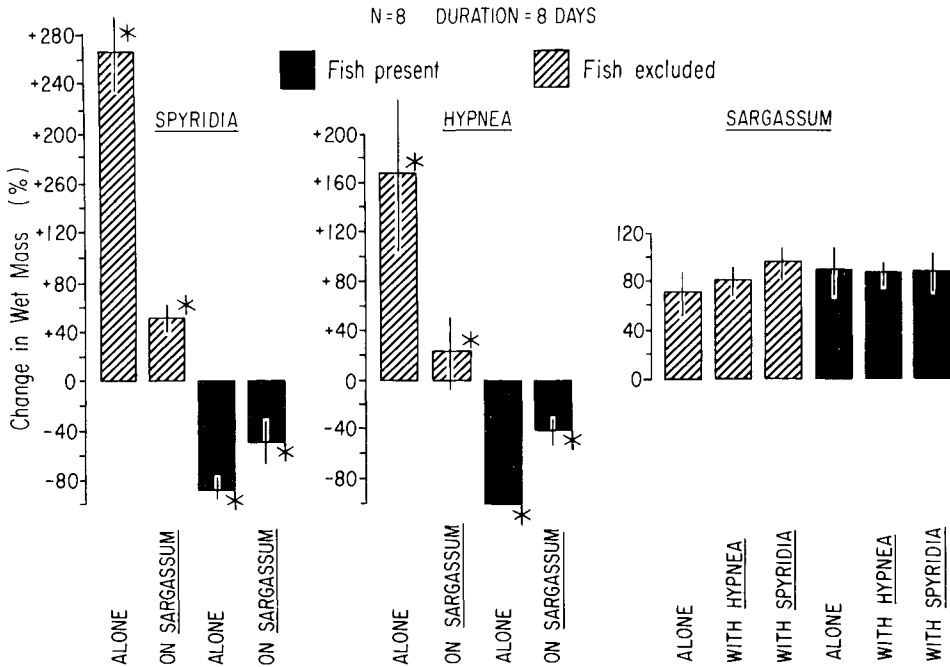


FIG. 3.—Effect of grazing by fish on change in wet mass of *Spyridia*, *Hypnea*, and *Sargassum* when these are grown separately or together in eight outdoor 5000-liter microcosms. Asterisks, Treatments that differ significantly from all others for that species (Kruskal-Wallis test and a nonparametric parallel of the Student-Newman-Keuls test, $P < 0.05$). *Sargassum* showed no significant differences between any treatments. Other symbols are the same as for figure 2.

rate of *Sargassum*, regardless of the presence or absence of fishes (figs. 2A,B, 3). Thus, when palatable species like *Hypnea* and *Spyridia* grow on *Sargassum* and their mass is 10% or less of the mass of the *Sargassum*, the herbivore defense advantage that accrues to the palatable species does not necessarily cost the unpalatable host any measurable growth rate on account of increased competition for light or nutrients.

In the first field experiment (fig. 2A), both *Sargassum* treatments inside of cages grew significantly more slowly than treatments outside of cages (Kruskal-Wallis test and a nonparametric parallel of the Student-Newman-Keuls test, $P < 0.001$; see Zar 1974). This appeared to be a result of the cages' reducing light levels below saturation intensity during this experiment. This significant cage effect was not observed in the field when the experiment was repeated (fig. 2B) during a period when light intensities appeared to be higher (i.e., fewer rainy, overcast days). Additionally, it was not observed in the microcosm trials where neither fish-exclusion nor fish-inclusion treatments were subject to artificial shading by cage tops (fig. 3). During the second field experiment (fig. 2B), *Hypnea* again benefited from its association with *Sargassum* when fishes were present. When fishes were excluded by cages, *Hypnea* alone appeared to increase its wet mass more than

Hypnea placed on *Sargassum*; however, this trial was of shorter duration (92 h as opposed to 152 h) and the difference was not significant (fig. 2B).

Field experiments were also conducted to determine if palatable plants placed beneath *Sargassum* canopies, rather than placed directly on *Sargassum*, would be grazed less than plants placed about 0.5 m away from any *Sargassum* plant. Percent change in wet mass of *Hypnea* placed beneath two *Sargassum* plants was not significantly less than the change in *Hypnea* plants placed in the open. In open microhabitats, *Hypnea* wet mass decreased by $39\% \pm 13\%$ ($\bar{x} \pm 1$ SE, $N = 14$). Beneath the *Sargassum* plants, *Hypnea* decreased by $53\% \pm 12\%$ ($N = 19$; Mann-Whitney U -test, $P > 0.20$). Since seas were calm and all plants were on the lee side of the jetty, it is very unlikely that whiplash of *Sargassum* plants contributed to *Hypnea* losses. Thus, in order to decrease losses to herbivores, it appears that palatable species may need to grow on, not merely near, unpalatable species. Recent work by C. Pfister (pers. comm.) shows that some individuals on primary substrate beneath *Sargassum* may experience lower rates of urchin grazing than those growing at some distance from *Sargassum*.

Results from the microcosm experiments were similar to those seen in the field. In fish-exclusion treatments, palatable species growing alone accumulated five to seven times as much biomass as those same species growing on *Sargassum* (fig. 3). In the presence of omnivorous fishes, however, palatable species occurring alone were consumed at a significantly greater rate than those occurring on *Sargassum*. For both *Hypnea* and *Spyridia*, each treatment was significantly different from all others (Kruskal-Wallis test and a nonparametric parallel of the Student-Newman-Keuls test, $P < 0.05$). The effectiveness of this associational defense is even more pronounced when the fate of individuals over shorter periods of time is considered. When *Hypnea* and *Spyridia* occurred alone, 90% and 85%, respectively, of all individuals were completely consumed within 24 h. Only 10% of the *Hypnea* individuals and 32% of the *Spyridia* individuals on *Sargassum* were consumed within this same time period.

In most of the assays discussed previously, a single three-strand rope held *Sargassum* alone, the palatable species alone, and the palatable species on *Sargassum*. Because all of these treatments are separated by only a few centimeters, it is possible that each affects the other in ways that would not adequately mimic field conditions where individuals represented by these treatments might be separated by several meters. Figure 4 shows results from a field assay in which each rope held only one of the three treatments and all ropes were separated by 1–2 m. As in all of the previous experiments, when *Hypnea* occurred alone it was eaten at a significantly greater rate than when it occurred as an epiphyte on *Sargassum* (Mann-Whitney U -test, $P < 0.001$). In contrast to the results of previous experiments, *Sargassum* alone accumulated significantly more biomass than *Sargassum* entwined with *Hypnea* (Mann-Whitney U -test, $0.05 > P > 0.025$). This could be caused either by competition with *Hypnea* or by the presence of the palatable *Hypnea* increasing the rate of grazing on *Sargassum*. An analysis of the 30 ropes with *Hypnea* growing on *Sargassum* suggests the latter. On ropes where *Hypnea* had increased in mass (i.e., had not been heavily grazed), *Sargassum* grew well ($\bar{x} \pm 1$ SE = $10\% \pm 2\%$, $N = 13$). On ropes where *Hypnea* had decreased in mass

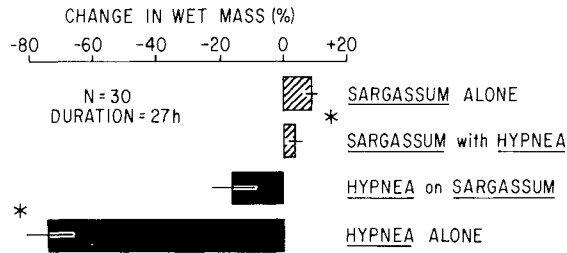


FIG. 4.—The effect of grazing by fish on *Hypnea* and *Sargassum* when these were presented intermixed or alone in the field. Unlike the data presented in figures 2 and 3, each type of treatment was placed on a separate rope and all replicates were separated from others by at least 1–2 m. Asterisks, Significant differences (Mann-Whitney *U*-test, $P < 0.05$).

(i.e., grazing exceeded production), *Sargassum* plants experienced no net increase in biomass ($0\% \pm 4\%$, $N = 17$). These differences are significant (Mann-Whitney *U*-test, $0.025 > P > 0.01$). The significant negative effect of *Hypnea* on *Sargassum* seen in this experiment appears to occur only infrequently. This result was not seen in previous field experiments (fig. 2) or in microcosm experiments (fig. 3).

The most obvious, nonswimming herbivore at the study site was the sea urchin *Arbacia punctulata*. When these urchins were offered the various combinations of *Hypnea* and *Sargassum* in the laboratory, they consumed significantly more *Hypnea* when it was alone than when it was on *Sargassum* (fig. 5). Their consumption of *Sargassum* was not significantly affected by the presence or absence of *Hypnea*.

Grazing by the less obvious amphipod herbivores was not affected by plant associations. *Hypnea* growing alone and *Hypnea* growing on *Sargassum* were consumed at identical rates ($\bar{x} \pm 1 \text{ SE} = -4 \pm 2 \text{ mg per 75 h}$; $N = 10$; paired-sample *t*-test, $P > 0.50$). *Sargassum* alone lost $17 \pm 6 \text{ mg per 75 h}$ and *Sargassum* entwined with *Hypnea* lost $24 \pm 5 \text{ mg per 75 h}$ ($N = 10$; paired-sample *t*-test, $0.50 > P > 0.20$). In these laboratory assays, amphipods consumed about five times as

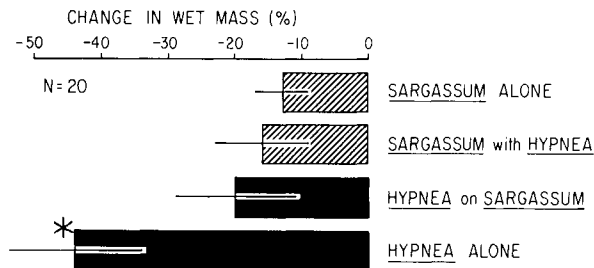


FIG. 5.—Laboratory assays on how the presence of *Hypnea* and *Sargassum* alone or in an interwoven mixture affects their consumption by the sea urchin *Arbacia punctulata*. Other symbols are as for previous figures. Duration was 5 days. Asterisks, Significant differences between treatments for a species (Wilcoxon paired-sample test, $P < 0.05$).

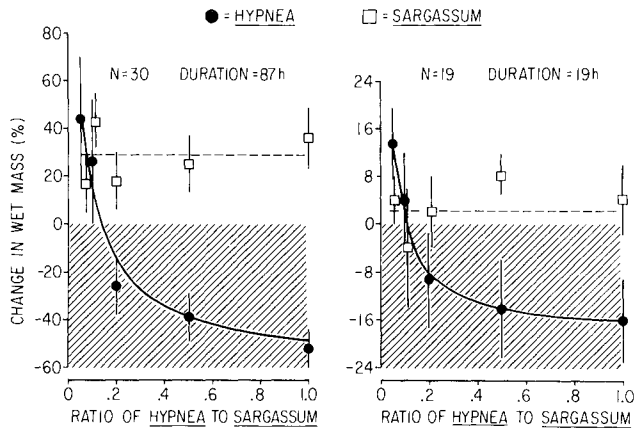


FIG. 6.—Loss of *Hypnea* and *Sargassum* in the field as a function of the initial *Hypnea*-to-*Sargassum* wet-mass ratios. Vertical bars indicate ± 1 SE. Lines through the points were drawn by eye.

much *Sargassum* as *Hypnea*. Since *Sargassum* mass in these tests was five to six times the mass of the *Hypnea*, this suggests that each was eaten indiscriminately in proportion to its abundance.

In the field, the effectiveness with which growing on *Sargassum* protects *Hypnea* from herbivores diminishes as *Hypnea* abundance increases relative to the abundance of the unpalatable host. *Hypnea* grows faster than it is consumed only so long as its mass does not exceed about 10%–15% of the mass of the *Sargassum* on which it grows (fig. 6). Problems of developing appropriate controls for this experiment were discussed in the Methods section. However, losses caused by turbulence do not appear to be capable of generating this pattern. When ropes and algae were arranged like those used in the field and were placed near the wave generators in the microcosms for 10 h during the night, the 0.05 ratio treatment lost significantly more *Hypnea* biomass than any of the other treatments (ANOVA and Student-Newman-Keuls test, $P < 0.05$). No other treatments differed significantly. Percent changes in wet mass for each treatment were as follows ($\bar{x} \pm 1$ SE): 0.05, -16 ± 5 ; 0.10, 0 ± 2 ; 0.20, -4 ± 4 ; 0.50, -3 ± 2 ; 1.0, -3 ± 3 . The greatest loss of *Hypnea* biomass from the treatment with the smallest ratio of *Hypnea* to *Sargassum* would prejudice against the pattern shown in figure 6. This suggests that the increased loss of *Hypnea* as it increases in abundance relative to *Sargassum* is a result of its greater apparency to grazing fishes and not an artifact caused by wave motion.

Additionally, this field assay (fig. 6) can be used to test the possibility that fishes in the earlier assays (figs. 2, 3, 4) were responding to between-treatment differences in the size of algal clumps instead of differences between plant associations. If fishes selectively avoided large clumps of algae, then treatments of *Hypnea* or *Spyridia* not associated with *Sargassum* would have been grazed more heavily than treatments of *Hypnea* or *Spyridia* on *Sargassum* simply because of differences in clump size. This is clearly not the case since fishes in this assay grazed most intensively on the large algal clumps (fig. 6).

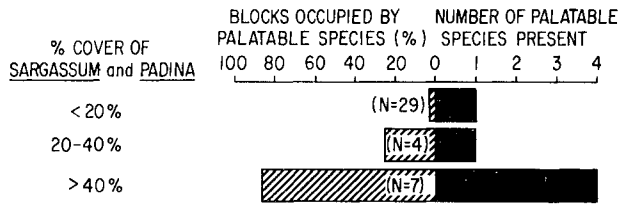


FIG. 7.—The relationship between percent cover of *Sargassum* plus *Padina*, the colonizations of blocks by palatable species, and the number of different palatable species on these blocks. All data are from the fish-inclusion treatments in the microcosms during mid-October. Numbers in parentheses show the number of blocks in each *Sargassum* and *Padina* abundance category. Blocks with more than 40% cover of *Sargassum* and *Padina* were significantly more likely to support palatable species than blocks with less than 20% cover of *Sargassum* and *Padina* (Fisher's exact test, $P < 0.001$). Mean number of palatable species per block was significantly higher on blocks with greater than 40% cover of *Sargassum* and *Padina* than on blocks with less than 20% cover (Mann-Whitney U -test, $P < 0.001$).

Effects of Associational Defenses on Species Richness

Colonization of cinder-block settling surfaces placed in portions of the microcosms containing herbivorous fishes showed that establishment of palatable species depended on the abundance of the unpalatable forms. After approximately 2 mo in the fish-inclusion treatments, 6 of the 7 blocks that had developed greater than 40% cover of *Padina* and *Sargassum* were also colonized by palatable species, while only 1 of the 29 blocks with less than 20% cover of *Sargassum* and *Padina* had been colonized by a palatable species (Fisher's exact test, $P < 0.001$; fig. 7). In addition, the 7 blocks with greater than 40% cover of *Sargassum* and *Padina* had been colonized by four palatable species (*Hypnea*, *Spyridia*, *Enteromorpha*, and *Gracilaria verrucosa*), while the 33 blocks with less than 40% cover of the unpalatable species had been colonized by only one palatable species (*Enteromorpha*).

Additionally, using data from the late October sample, a correlation analysis for the percent cover of *Sargassum* and *Padina* on each block with the total number of other macrophyte species (both palatable and unpalatable) on each block showed a weak but significant positive interaction ($r = 0.488$, $P < 0.005$). Thus, blocks dominated by *Sargassum* and *Padina* tended to have more, not fewer, of the other species. (Cover of *Sargassum* and *Padina* ranged from 0% to 104%; 14 of the 40 blocks had greater than 50% cover, and 6 had greater than 90% cover.) This suggests that species added because of the effects of associational defenses more than compensate for the number of species lost (if any) as a result of competitive exclusion.

Figure 8 shows the time course of invasion by *Enteromorpha* (the most frequently occurring palatable species in the microcosms) in fish-inclusion versus fish-exclusion treatments. In the treatments from which fish were excluded, *Enteromorpha* colonized 92% (37 of 40) of the blocks after only 1 mo and retained a high frequency of occurrence throughout the experiment. In the treatment with fish present, colonization by *Enteromorpha* was delayed by approximately 2 mo and occurred only after *Sargassum* and *Padina* became abundant and provided

microsites of decreased herbivory. *Enteromorpha* plants in the fish-exclusion treatments were almost exclusively attached to primary substrate and by late September had a mean cover of approximately 12%. In the fish-inclusion treatments, *Enteromorpha* occurred exclusively on, or among, dense aggregations of *Sargassum* or *Padina* and never reached a mean cover of more than 0.3%.

DISCUSSION

Associational Defenses

Most previous work on associational resistance has focused primarily on how specialized insect herbivores forage, reproduce, and disperse in monocultures of their host plant versus polycultures that include some non-host species. These studies have consistently shown that insect density per host plant is significantly higher if plants are grown in monocultures rather than polycultures (Tahvanainen and Root 1972; Root 1973; Cromartie 1975; Bach 1980; Risch 1980, 1981; Kareiva 1982). Root (1973) advanced two hypotheses to explain the increased abundance of pests in monocultures. First, the enemies hypothesis suggested that more-diverse plant communities might harbor larger and more-diverse populations of predators and parasites and that these would regulate herbivore populations and prevent outbreaks. Second, the resource-concentration hypothesis stipulated that herbivores were more likely to find and remain on hosts growing in dense and nearly pure stands. Atsatt and O'Dowd (1976) extended these hypotheses by suggesting (1) that other plants might act as repellent plants, either directly or indirectly causing the herbivore to fail to locate or reject its normal prey (similar to Root's resource-concentration hypothesis) or (2) that other plants might serve as attractant-decoy plants, causing the herbivore to feed on alternative prey.

Recent work has shown that rates of predation and parasitism on herbivores are not higher in polycultures (Tahvanainen and Root 1972; Root 1973; Bach 1980; Risch 1981). Insect herbivores are more abundant in host monocultures because they experience increased reproduction (Bach 1980), they colonize monocultures more rapidly, and they are less likely to emigrate from them (Bach 1980; Risch 1981; Kareiva 1982).

The associational defenses demonstrated for the seaweeds studied here bear little resemblance to the previous studies of insects and terrestrial plants. The herbivores studied here are not relatively immobile specialists; they are generalist feeders that consume a wide variety of both plant and animal species (Carr and Adams 1973; Adams 1976c; Stoner 1980; Stoner and Livingston 1984) and move rapidly over large areas and among many plants. Thus, dispersal to an appropriate host plant will not be an important component of their life history; for specialist insects, dispersal to an appropriate host may represent the primary challenge to herbivore success (Kareiva 1982). Although differing from the previous studies on associational defenses against insects, the patterns documented here for fishes and seaweeds are in some respects similar to those claimed for generalist ungulates consuming grasses on the Serengeti Plain in eastern Africa (McNaughton 1978).

Neither the enemies hypothesis nor the resource-concentration hypothesis are applicable to the field situations tested here. Palatable species were never presented in large monospecific patches; palatable individuals alone and those on *Sargassum* were separated by only a few centimeters. In both microcosm and field assays, all plants were presented against a background of the natural species-rich community. That palatable species gained significant protection from unpalatable species only so long as they grew *on* and not merely near or under them (figs. 1, 2, 3) suggests that the repellent-plant hypothesis (Atsatt and O'Dowd 1976) best explains the data presented here. I interpret the repellent-plant hypothesis to include any of a wide variety of chemical or physical characteristics of the unpalatable plant that interfere with an herbivore's ability to locate or utilize the palatable plant.

Lowered consumption of palatable species associated with *Sargassum* may have been a result of increased crypsis. During the summer when fishes were numerous, palatable epiphytes were commonly found only among the densest portion of *Sargassum* plants where they were very cryptic. During the winter, palatable plants were larger and less cryptic on their hosts and also grew on primary substrate (fig. 1). When favored food items are cryptic and occur at low density (as in the summer), both laboratory tests and theoretical considerations of optimal foraging suggest that these items may be excluded from the diet (Hughes 1979; Erichsen et al. 1980). The importance of crypsis is further suggested by the pattern shown in figure 6. *Hypnea* gains significant protection from *Sargassum* only so long as its wet mass is less than 10%–15% of *Sargassum*'s wet mass. As *Hypnea* becomes more visually apparent, it is consumed more rapidly. A portion of the crypsis provided by unpalatable plants like *Sargassum* also could be olfactory. In terrestrial plant communities, olfactory stimuli from nearby non-host plants can apparently confuse herbivores and decrease feeding on host plants (Tahvanainen and Root 1972; Altieri et al. 1977; Perrin 1977). Potential interference with olfactory feeding cues has not been assessed for marine plants and herbivores.

The Positive Effect of Competitors

In the absence of herbivorous fishes and urchins, *Hypnea* growing on *Sargassum* in the field accumulates 34%–35% less wet mass than *Hypnea* that is not attached to *Sargassum* (fig. 2). In longer, and better-controlled, experiments in the microcosms, growth of *Hypnea* decreased by 86% and *Spyridia* by 81% when the plants were growing on, rather than near, *Sargassum* (fig. 3). I interpret these large growth-rate differences to be a consequence of competition with *Sargassum*. *Sargassum* growth was not significantly affected by the presence of *Hypnea* or *Spyridia* in a ratio of approximately 1 part *Hypnea* or *Spyridia* to 10 parts *Sargassum* (figs. 2, 3). Since herbivores in the field usually limit the abundance of *Hypnea* or *Sargassum* to approximately this ratio (fig. 6), *Sargassum* will rarely suffer negative consequences from competition with epiphytic *Hypnea*. In situations where epiphytes become more abundant, however, they may significantly depress the growth of host plants (Caine 1980; Brawley and Adey 1981; Howard 1982; Orth and Van Montfrans 1984). Thus, under the conditions used in these

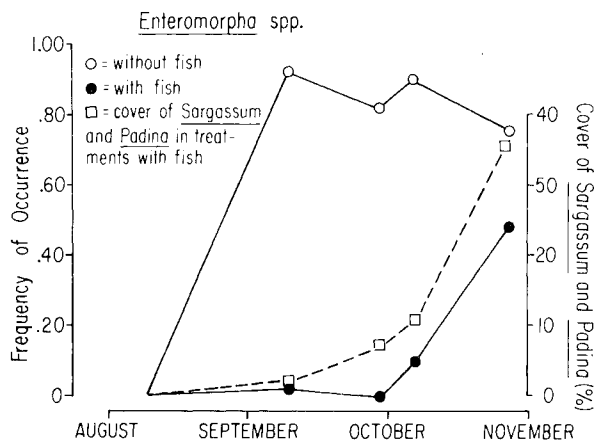


FIG. 8.—Frequency of occurrence of *Enteromorpha* species on blocks in the fish-inclusion and fish-exclusion portions of the microcosms. *Enteromorpha* colonized immediately in the fish-exclusion treatment. In the fish-inclusion treatment, *Enteromorpha* colonization did not occur until after *Sargassum* and *Padina* became common and provided microsites of reduced herbivory.

tests, *Sargassum* significantly reduced the growth of *Hypnea* and *Spyridia*, but these palatable species had no significant effect on *Sargassum* (figs. 2, 3).

When herbivorous fishes are added to the system, it becomes apparent that the competitive costs experienced by *Hypnea* and *Spyridia* growing on *Sargassum* are much less than the costs of increased predation in the absence of *Sargassum* (figs. 2, 3). For palatable species, the overall consequence of growing intermixed with unpalatable competitors can be positive (figs. 1–5, 7, 8).

The absence of a competitive effect of *Hypnea* on *Sargassum* and the presence of a large negative effect of *Sargassum* on *Hypnea* may be due primarily to the way that *Hypnea* was placed on *Sargassum*. *Hypnea* was wound closely around the central stipe of the *Sargassum* plant. Thus, *Hypnea* shaded *Sargassum* blades only slightly, while *Sargassum* blades shaded almost the entire *Hypnea* plant. During the summer months when these studies were conducted, this placement of *Hypnea* on *Sargassum* closely mimicked the way that *Hypnea* was distributed on *Sargassum* in the field. *Hypnea* occurred primarily as small plants entangled among or attached to the center portion of *Sargassum* plants. During spring and early summer when omnivorous fishes were small and feeding primarily on invertebrates (Carr and Adams 1973; Stoner 1980; Stoner and Livingston 1984) and during late fall after most fishes had migrated from the jetty, *Hypnea* often grew in loose aggregations that extended over and beyond the *Sargassum* blades. At these times it is likely that *Hypnea* exerts a greater competitive effect on *Sargassum*.

Until very recently most ecologists focused primarily on the direct and negative effects of competition and predation. However, indirect commensalisms like those described here could be both common and important factors structuring many communities (Dayton and Oliver 1980; Vandermeer 1980; Osman and Haugsness 1981; Dethier and Duggins 1984). Some possible examples from marine communities are listed below.

In the equatorial eastern Pacific, branching pocilloporid corals compete for space and light with more massive corals such as *Gardineroseris planulata*. *Pocillopora* species are resistant to attack by the predatory sea star *Acanthaster* because of the coral's nematocysts (Barnes et al. 1970) and symbiotic crustacean guards that attack and repel sea stars (Glynn 1976, 1983). The massive corals like *Gardineroseris* are favored prey of *Acanthaster*. The 1982–1983 El Niño event caused the death of most *Pocillopora* species in the eastern Pacific (Glynn 1984), and many of these species had been completely encircling large colonies (up to 192 yr old) of *Gardineroseris* (Glynn 1985). Once *Gardineroseris* was no longer surrounded by competing *Pocillopora* colonies, *Acanthaster* crossed over the dead *Pocillopora* and consumed *Gardineroseris* (Glynn 1985). In a situation more similar to the one reported here, young kelp plants suffer less fish grazing if they are intermixed within aggregations of small, early-successional algae than when they occur by themselves (Harris et al. 1984). Additionally, limited studies on coral-reef seaweeds (Hay 1985; Littler et al. 1986) and Sonoran Desert trees (McAuliffe 1986) show that palatable species appear to be protected from herbivores by growing intertwined with relatively unpalatable forms.

These examples suggest that indirect commensalisms between competitors may be common and widespread. Some of these interactions could be mutualistic (see Osman and Haugness 1981) instead of commensal, but this has yet to be investigated. An important component of these types of interactions is that they all appear to be relatively opportunistic. If so, then associational defenses could be very common in many different types of communities since they would not require the long history of interaction and coevolution that appears necessary for the development of most mutualisms (Vermeij 1983).

Epiphytism as an Herbivore Escape

Growing epiphytically has been viewed primarily as a competitive strategy that facilitates invasion of areas where most primary substrate is already occupied (Hay 1981a,b; Hawkins and Harkin 1985). Patterns of herbivory documented in this study suggest that herbivores also may select for the ability to grow epiphytically (figs. 2–5). Most seaweed epiphytes are capable of growing equally well on primary substrate and are not physiologically dependent on a host (Taylor 1960). There are also limited data suggesting that palatable species, more commonly than unpalatable ones, occur as epiphytes (Hay 1981b). Since several seaweeds produce spores that disperse only a few meters from the parent plant (Dayton 1973; Dayton et al. 1984; Sousa 1984), the ability to grow as a cryptic epiphyte during seasonal periods of intense herbivory may allow some seaweeds to remain predictable components of communities that they would be unable to reinvade if all adults were removed.

Effects on the Maintenance of Species Richness and Patterns of Succession

The maintenance of numerous similar species within a community often depends on predation or physical disturbances that selectively remove numerical or competitive dominants and free limiting resources for less common species (Paine 1966, 1979; Connell 1978; Sousa 1979; Porter et al. 1981). If the accumulation of

numerical dominants goes unchecked, one or a few species may eventually control most resources and other species may be excluded from the community by competition. This basic pattern has been documented in numerous field studies (e.g., Paine 1966; Lubchenco 1978; Sousa 1979; Hixon and Brostoff 1983) but may not occur in those communities where competition affects growth but not mortality rates (Peterson 1979, 1982).

The data presented here show that an increased abundance of one, or a few, species does not necessarily lead to decreased species richness within the community. During the summer when fish were common, a high abundance of *Sargassum* and *Padina* was associated with an increased, not decreased, frequency of other species (fig. 1). Similar patterns occurred in the microcosm experiments (figs. 7, 8). In the fish-inclusion treatments, there was a significant positive correlation ($r = 0.45$, $P < 0.005$) between the cover of *Sargassum* and *Padina* and the number of other species present. Thus, species richness increased as the community became dominated by *Sargassum* and *Padina*. This increase appeared to result from the common, unpalatable species' creating microhabitats of lowered herbivory that facilitated the invasion of palatable species, which were excluded by herbivores if these refuges were not available. Associational defenses may thus contribute significantly to the maintenance of species numbers or richness. Associational defenses cannot significantly increase species evenness since unpalatable hosts must remain much more abundant than their palatable epiphytes; this should result in species-rich communities that are dominated by a few unpalatable species. Recent analyses of numerous marine communities have pointed out that there is a significant tendency for numerical dominance of common species to be greater in species-rich than in species-poor communities (Birch 1981). This contradicts an earlier hypothesis that species-rich communities would have more-equal distributions of relative abundance than species-poor communities (MacArthur 1969), but this is the pattern expected if associational defenses are common in these communities.

Most investigations of succession have concentrated on processes affecting the colonization and growth of species that become relatively abundant. Timing of establishment and subsequent growth of rare species have attracted less attention. Drury and Nisbet (1973) and Connell and Slatyer (1977) pointed out that under most conditions early-successional species should inhibit rather than facilitate the establishment of later-successional forms. This interaction was clearly demonstrated by Sousa (1979). Instances of early-successional species facilitating the invasion of later-successional forms have been documented (Turner 1983; Harris et al. 1984) but these cases appear to be relatively rare. In the seaweed community studied here, when herbivores are present, late-successional species like *Sargassum* and *Padina* clearly facilitate the invasion of early-successional species like *Enteromorpha* and *Ulva*. During the first 8 wk of the microcosm experiments, nine species of seaweeds rapidly colonized the fish-exclusion treatments but not the fish-inclusion treatments. However, as *Sargassum* and *Padina* became abundant ($> 20\%$ cover) on some blocks in the inclusion treatments, several of these palatable species were then able to colonize (figs. 7, 8). Therefore, in communities where associational defenses are important, increasing dominance by a few un-

palatable species can lead to increases instead of decreases in species richness and to retention instead of exclusion of early-successional forms. These findings conflict with several tenets of present ecological theory, suggesting that present theory is inadequate when applied to communities where associational defenses are common.

SUMMARY

The palatable plants investigated in this study gained significant protection from herbivores by associating with abundant competitors that were less susceptible to herbivory. When herbivores were excluded, palatable species associated with unpalatable ones grew at only 14%–19% of the rate of palatable plants separated from unpalatable ones. When herbivores were present, however, palatable species appeared to depend completely on unpalatable competitors to provide microsites of reduced herbivory to prevent grazers from causing local extinction of the preferred species. For the species studied here, the cost of being associated with a larger, unpalatable competitor was much less than the cost of increased consumption in the absence of that competitor. Under these conditions, one competitor can have a strong positive effect on another. Associational defenses can provide an unappreciated mechanism for maintaining species richness within communities that are dominated by one or a few major species. In this community, increases in the abundance of common late-successional competitors led to increases, not decreases, in the abundance and number of other species and to retention, not exclusion, of early-successional species.

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