Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms

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Summary. An associational plant refuge occurs when a plant that is susceptible to herbivory gains protection from herbivory when it is associated with another plant. In coastal North Carolina, the abundance of the palatable red alga *Gracilaria tikvahiae* is positively correlated with the abundance of the unpalatable brown alga *Sargassum filipendula* during times of increased herbivore activity. To see if grazing by the sea urchin *Arbacia punctulata* could generate this pattern, controlled experiments were conducted in outdoor microcosms and in the laboratory. *Gracilaria* beneath a canopy of *Sargassum* was eaten significantly less than *Gracilaria* alone. When *Arbacia* were excluded, *Gracilaria* alone grew significantly more than *Gracilaria* beneath *Sargassum*, demonstrating that *Sargassum* is a competitor of *Gracilaria*. Experiments investigating *Sargassum*'s deterrent role indicated that *Sargassum* decreased the foraging range of *Arbacia* and the rate at which it fed on *Gracilaria*. Additional experiments with plastic *Sargassum* mimics indicated that the decreased grazing on *Gracilaria* was not a result of *Sargassum* morphology, but was probably attributable to some chemical characteristic of *Sargassum*. The pattern of increased grazing in monocultures (only *Gracilaria* present) versus polycultures (both *Gracilaria* and *Sargassum* present) demonstrated in this study also has been demonstrated for plant-insect interactions in terrestrial communities. In these communities, insect density is higher in monocultures than in polycultures because insects find and immigrate to monocultures more rapidly, and once in a monoculture, they emigrate from them less often than from polycultures. In this study, urchins did not find and immigrate to monocultures more rapidly, nor did they tend to stay in them once they were found; in fact, they emigrated from monocultures of *Gracilaria* more rapidly than from *Gracilaria* and *Sargassum* polycultures. Increased grazing in *Gracilaria* monocultures resulted from increased rates of movement and feeding of individual herbivores, not from increased herbivore density as has been reported for terrestrial systems.

Key words: *Arbacia punctulata* – Associational refuges – Competition – Plant-herbivore interactions – Seaweeds

Characteristics of seaweeds that permit them to escape and deter herbivores have been extensively studied. These in-

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clude: 1) morphological defenses (Hay 1981 b; Steneck and Watling 1982; Littler et al. 1983), 2) chemical defenses (Geiselman and McConnell 1981; Norris and Fenical 1982, 1986; Targett and McConnell 1982; Bertness et al. 1983; Paul and Fenical 1983; Steinberg 1984, 1985, 1986; Targett et al. 1986; Hay et al. 1987a, b), 3) the ability to grow rapidly, allowing productivity to surpass consumption (Littler and Littler 1980), 4) temporal or seasonal escapes (Lubchenco and Cubit 1980; Slocum 1980; Dethier 1981), 5) spatial escapes (Littler and Littler 1980; Hay 1981a, 1984, 1985; Hay et al. 1983; Taylor et al. 1986), and 6) associational refuges or associational resistance (Hay 1985, 1986; Littler et al. 1986).

In this study, we define a spatial refuge as a location where an organism's fitness is high relative to other locations because of the non-uniform impact of mortality agents. This definition follows that of Buss (1978). An associational plant refuge occurs when a plant that is susceptible to herbivory gains protection from herbivores when it is associated with another plant (Tahvanainen and Root 1972; Root 1973, 1974; Atsatt and O'Dowd 1976). In this study, an unpalatable alga decreases herbivory on an associated palatable alga. A similar phenomenon has been referred to as an "associational resistance" by Tahvanainen and Root (1972), Root (1974), and Brown and Ewel (1987). Associational plant refuge is a more accurate descriptor of the situation we studied since palatable plants did not appear actively to resist grazing when associated with other plants; they appeared merely to have escaped in space.

Associational plant refuges have received relatively little attention in the marine ecological literature, perhaps due to an experimental emphasis on negative interactions such as competition and predation. Previous studies of associational refuges in the marine realm have focused on the effect of feeding by highly mobile, visual herbivores such as fishes (Hay 1985, 1986; Littler et al. 1986). However, it is important to understand how any given defense or refuge affects the diverse array of herbivores that attack most plants. In general, the effectiveness of any given herbivore deterrent or escape should decrease as the diversity of herbivores increases (Lubchenco and Gaines 1981; Hay 1984; Paul and Hay 1986; Hay et al. 1987a). In this study, we examine the effectiveness of an associational plant refuge against the sea urchin, *Arbacia punctulata*. These slow moving, non-visual herbivores differ greatly from fishes in the way they search for, and feed on, algae (Ogden 1976; Gaines and Lubchenco 1982); it is therefore possible that plant associa-

tions would have different effects on urchins than on fishes. Additionally, associational plant refuges can involve important indirect interactions between competitors and can have a significant impact on community organization (Atsatt and O'Dowd 1976; Hay 1986; Littler et al. 1986).

This study was initiated by the observation that the red alga *Gracilaria tikvahiae* is often found in stands of the brown alga *Sargassum filipendula* during those times of year when herbivores are most active. In this investigation, we asked the following questions: 1) Does the sea urchin *Arbacia punctulata* prefer *Gracilaria tikvahiae* over *Sargassum filipendula*? 2) Is *Gracilaria tikvahiae* in the understory of *Sargassum filipendula* less susceptible to grazing by *Arbacia punctulata* than *Gracilaria tikvahiae* not associated with *Sargassum filipendula*? 3) In the absence of herbivory, does competition with *Sargassum filipendula* decrease the growth rate of *Gracilaria tikvahiae*? 4) If *Gracilaria tikvahiae* is protected from herbivory when it is associated with *Sargassum filipendula*, what are the mechanisms responsible for deterring grazing by *Arbacia punctulata*? and 5) Are patterns of associational plant refuges documented in marine systems caused by mechanisms similar to those documented in terrestrial systems? We address these questions using both outdoor microcosm and laboratory experiments. We then relate findings from these experiments to patterns documented in the field.

Methods and results

Urchin feeding preference

To test whether *Arbacia* prefer the red alga, *Gracilaria tikvahiae* over the brown alga, *Sargassum filipendula*, both algae were presented to a single urchin in a 3.8 l jar that contained 1.3 l of aerated seawater. Each jar contained 1 g of each alga that was inserted into a slit in two suctioned rubber discs (35–40 cm^2 area) and secured to the bottom within 10 cm of each other. This procedure was replicated 15 times. Eight identical setups contained algae but no urchins. These controlled for change in algal mass unrelated to grazing. The mean change in mass of these controls was used to correct the initial masses of the algae in jars with urchins so that changes related to different rates of respiration would not be confused with changes related to selective grazing by the urchins. Further references to this procedure will state only that initial algal mass was corrected with the mean change in the controls; however, the explanation for this procedure is as discussed above. The assay ran for 46 h. All algae were collected from Radio Island jetty, NC (32°42′N, 76°41′W) several days prior to the experiment. Before and after each experiment, each alga was spun for 10 revolutions (at approximately 120 rpm) in a salad spinner to remove excess water and the spun-wet-mass of each plant was recorded. Subsequent references to spun-wet-mass will refer to this procedure.

In most feeding assays, the mean change in algal mass in the controls (without urchins) was used to correct the initial mass of the algae in corresponding treatments that contained urchins. This causes two potential problems. Firstly, control treatments are not as well replicated and means may not adequately describe the changes in these treatments. Thus, systematically changing all the initial masses in treatments with urchins could have biased these data. Secondly, it is likely that algae in controls will not
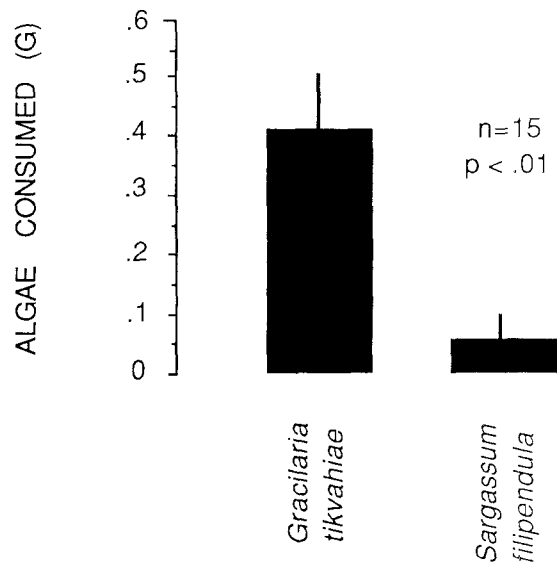

Fig. 1. Feeding preference of *Arbacia punctulata* when offered paired 1 g portions of *Gracilaria* and *Sargassum*. Assays ran 51.5 h, vertical bars through the histograms show +1 standard error, and the *P*-value is by the Wilcoxon Paired-Sample Test

change equally in various treatments, or that various species of algae will show nonequivalent changes in both controls and treatments. This could mask the effect of urchin grazing, or alternatively, produce a differential change in algal mass that would be attributed to urchin grazing. We address these problems with the following analyses: 1) analyses disregarding these possible biases with all control data incorporated, 2) analyses of equality of control treatments, and 3) analyses with control data eliminated, to see if results are consistent with 1) above. Data from most of the feeding assays could be appropriately analyzed by 2-factor ANOVA in which controls and treatments are both included and analyzed together. In such a test it is the interaction effect that addresses whether herbivory varied with treatment. This analysis has the advantage of using the variability among replicates in the control data; this variability is not utilized in the way we construct a single correction factor from each control data set. The disadvantage of this approach is that the interaction test is low in power and it is sensitive to the transformations that are chosen. For these reasons and because in all our tests there were no significant differences between controls, we chose to analyze only the experimentals, both with and without correction constants, as our test of the impact of grazing. In all experiments we used parametric statistical procedures when the assumption of homogeneity of variances was met and nonparametric procedures when this assumption was violated. We rejected a null hypothesis of equality of variances at the p < 0.01 level as suggested by Underwood (1981).

Arbacia consumed 8 times more *Gracilaria* than *Sargassum* (Fig. 1, $P = 0.02$, $n = 15$, Wilcoxon Paired-Sample Test). *Gracilaria* controls showed a change of $+52 \pm 15$ mg ($\bar{x} \pm$ 1SE, $n = 8$); *Sargassum* controls changed by $+159 \pm 24$ mg. There was no difference in the mean change in these controls ($0.10 > P > 0.05$, Paired-Sample *t*-Test). When control data were omitted, *Gracilaria* was still consumed significantly more than *Sargassum* ($P < 0.05$, $n = 15$, Wilcoxon's Paired-Sample Test).

The pattern of association

The spun-wet-mass of all macroalgal species in 17×24 cm quadrats at Radio Island jetty, NC was assessed on 5–7 April ($n = 16$) and 3 Oct 1986 ($n = 25$). The jetty is a man-made structure located in Bogue Sound near the Beaufort Inlet. It extends to a depth of approximately 10 m, but both surveys were conducted between 0.5–1.5 m below mean low water on the eastern side of the southern end of the jetty. A random collection of algae was made by running a 60 m tape along the jetty and collecting all algae within quadrats at locations that corresponded to selections from a random numbers table. The algae within these quadrats were scraped off the rock and placed into separate plastic bags; in the laboratory, the collection from each quadrat was sorted to species and a spun-wet-mass for each species was determined.

The April 1986 quadrats showed no significant correlation between the mass of *Gracilaria* and the mass of *Sargassum* ($r = -0.192$, $0.25 > P > 0.20$, $n = 16$). However, in the October quadrats, there was a significant positive correlation ($r = 0.51$, $P = 0.11$, $n = 25$). During October, the average wet mass of *Gracilaria* in quadrats with *Sargassum* ($\bar{x} \pm$ 1 SE $= 1.003 \pm 0.452$ g) was three times as large as the mass of *Gracilaria* in quadrats with no *Sargassum* (0.316 ± 0.233 g); however, because of the large variance between replicates, this difference was not significant ($P > 0.20$, Mann Whitney U-Test).

We evaluated the abundance of the sea urchin *Arbacia punctulata* near the beginning of the study period (5 May 1986) and near the end of the study period (3 October 1986) in this same location. Urchins were counted in 0.25 m^2 quadrats randomly placed along a 60 m tape transect. In May there were 2.9 ± 0.94 urchins/m^2 ($\bar{x} \pm 1$ SE, $n = 25$); in October there were 2.7 ± 1.3 ($\bar{x} \pm 1$ SE, $n = 25$).

In addition to *Arbacia*, fishes are also important herbivores on some seaweeds at this site (Hay 1986). However, to assess the effectiveness of associational plant refuges against urchins, we needed to eliminate fish grazing. Since this was logistically difficult in the field, we employed microcosm and laboratory experiments to examine the effects of urchins alone.

The effectiveness and the cost of associational refuges

To test if *Arbacia* consume *Gracilaria* that is in the open more readily than *Gracilaria* beneath a canopy of *Sargassum*, several arrangements of these two algae were presented to urchins in outdoor microcosms at Duke University Marine Laboratory (DUML microcosms in subsequent references). The microcosms were cylindrical fiberglass tanks measuring 1.2 m in diameter and 0.6 m in height, with a volume of approximately 560 l. Seawater was pumped in from Taylor's Creek, entered the tanks near the bottom and flowed out at the top of 0.5 m standpipes. Seawater flow averaged 16 l/min. Thus, the entire volume of water in the microcosms was pumped in every 35 min.

Experimental manipulations within each microcosm consisted of three arrangements of algae in the presence or absence of the sea urchin, *Arbacia*. The three arrangements of algae were as follows: 1) 5 plants of *Gracilaria* totaling 5.0 g (spun-wet-mass), 2) 8 plants of *Sargassum* totaling 234.0 g, and 3) both *Gracilaria* and *Sargassum* in the amounts listed above (these amounts mimicked natural
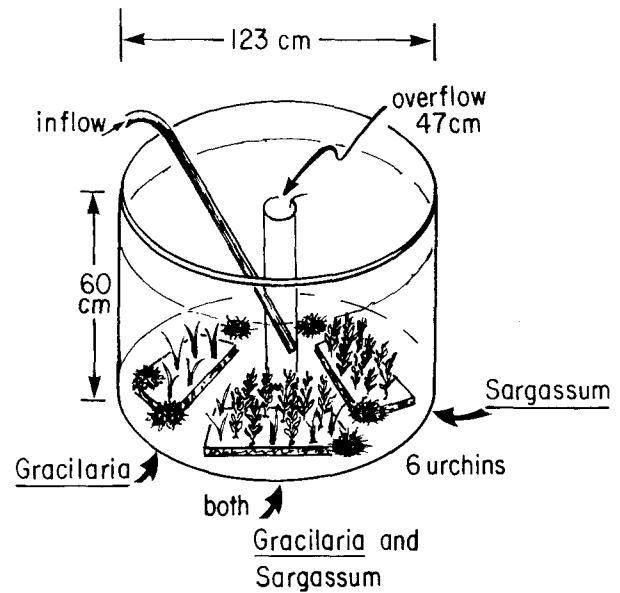

Fig. 2. Diagram of a representative microcosm at the Duke University Marine Laboratory (DUML) showing the arrangements of algae on grids. A continuous flow of seawater was maintained

abundances of these species – see below). We measured the percent change in algal spun-wet-mass in these three arrangements, both in the presence and absence of urchins. Each algal arrangement was fastened to three separate plastic mesh grids (30×40 cm). The plants were inserted approximately 1 cm through the mesh and held by clothespins on the underside of the grid. The grids were anchored equidistant from each other in the microcosms.

The amount of algae on the grids was similar to the amount found in 10 17×24 cm quadrats placed in stands of *Sargassum* at Radio Island Jetty between 26–28 August 1985. To make this collection as random as possible, a 60 m transect line was laid out along the jetty in the same location described earlier. Ten random numbers dictated where on the meter transect the collection was made. However, because we were interested in how much *Gracilaria* occurred beneath *Sargassum* canopies, we placed the quadrat in the *Sargassum* stand closest to the location indicated by the random number. The wet mass of both *Gracilaria* and *Sargassum* in these 10 samples was averaged, and these amounts were extrapolated to an area of 30×40 cm, the size of the grid to which the algae were attached. *Arbacia* were collected from Radio Island jetty and starved for one week prior to the experiment. Six urchins were placed in half of the microcosms ($n = 13$). An equal number of microcosms did not have urchins ($n = 13$), and served as controls for gain or loss in algal biomass in the absence of urchins. Figure 2 shows a microcosm and the various arrangements of algae.

The algae were collected two days prior to the experiment from either Radio Island jetty or from the outdoor seawater system at the University of North Carolina at Chapel Hill's Institute of Marine Sciences in Morehead City, NC. A spun-wet-mass of the algae was obtained before the experiment started and again when the experiment was terminated. The experiment was terminated when it appeared that half of the *Gracilaria* on any one of the grids in any of the microcosms was consumed. Since repeated

Table 1. Results of a Multivariate Analysis of Variance (MANOVA) on the change in *Gracilaria* and *Sargassum* mass when these algae were alone and combined together, both in the presence and absence of urchins. This experiment was performed in the DUML microcosms; the data are graphed in Fig. 3

H_o	F	P
1. Presence of urchins = absence of urchins	32.7	<0.001
2. Change in algal biomass is equal between treatments	13.8	<0.001
a. Difference in algal treatments without urchins is equal	1.6	=0.23
b. Difference in algal treatments with urchins is equal	28.5	<0.001
3. There is no interaction between algal treatments and urchins	16.3	<0.001

Fig. 3. The percent change in algal wet mass in varying associations of *Gracilaria* and *Sargassum* (experiment is pictured in Fig. 2), both with and without *Arbacia*. The four histograms on the left represent means of *Gracilaria;* the four on the right represent *Sargassum*. Vertical bars are +1 standard error. All data were analyzed with a MANOVA and Multivariate Repeated Measures Analysis. The latter analysis provided the *P* values

determinations of spun-wet-mass for algae varies by as much as 3–5%, we excluded results from any urchin enclosure tank where the percent change in algal spun-wet-mass was less than 5.0%. We also randomly excluded the results of one control tank to maintain equal replication and facilitate data analysis. This resulted in $n=12$ for both urchin enclosures and controls. Since only 4 to 6 microcosms were available at once, we had to repeat this experiment several times. All 13 replicates lasted between 4 and 6 days and were performed between 26 October and 13 December 1985.

The data from this experiment were analyzed with a Multivariate Analysis of Variance (MANOVA) and a Multivariate Repeated Measures Analysis. These analyses were chosen because the more commonly used Analysis of Variance (ANOVA) is not applicable here. ANOVA assumes independence of treatments; and, in this case, *Arbacia* have a choice of algal arrangements to graze. Any choice *Arbacia* make will be dependent upon alternative prey items, and will preclude simultaneous grazing on another treatment. Thus, because the algal treatments are clustered in the same microcosm, they need to be considered dependent variables (Winer 1971; McCall and Appelbaum 1973; Bock 1975; Gurevitch and Chester 1986). The presence or absence of urchins was the independent variable. The percent changes in algal wet mass for each algal association, in the presence or absence of urchins, were the dependent variables. A test of the main effect of urchins indicated a highly significant difference between the change in algal wet mass in the presence and absence of urchins ($P<0.001$, Table 1). This simply indicates that urchins are eating algae. A test of whether there is a difference in the various algal treatments, was significant when both the treatments with and without urchins were pooled ($P<0.001$, Table 1). A test of the interaction term was also significant ($P<0.001$, Table 1), but this interaction was caused solely by the presence of urchins ($P<0.001$, Table 1) and not by the exclusion of urchins. Since the interaction term has been partitioned, multiple comparisons can still be computed for algal treatments in the presence of urchins (Morrison 1976).

In the presence of urchins, there are two comparisons that address associational refuges (Fig. 3): a comparison of *Sargassum* alone versus *Sargassum* with *Gracilaria* in the presence of urchins, and a comparison of *Gracilaria* alone versus *Gracilaria* with *Sargassum* in the presence of urchins. The first comparison answers the question: is *Sar-*
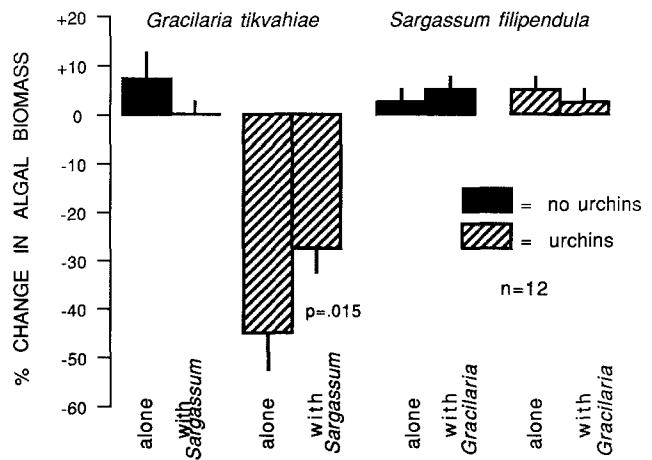
gassum with *Gracilaria* more prone to grazing by urchins than *Sargassum* alone? However, since our repeated determinations of algal spun-wet-mass varies as much as 3–5% and the mean change in *Sargassum* mass did not exceed this, we are not able to analyze this comparison. The second comparison answers the question: is *Gracilaria* with *Sargassum* less susceptible to urchins than *Gracilaria* alone? *Gracilaria* alone ($\bar{x} \pm 1$ SE $= -44.3\% \pm 7.4\%$) is consumed significantly more ($0.02 > P > 0.01$, $n=12$) than *Gracilaria* with *Sargassum* ($\bar{x} \pm 1$ SE $= -28.8\% \pm 5.4\%$). This represents a reduction in grazing of 35% for *Gracilaria* when it is associated with *Sargassum*. Thus the palatable red alga *Gracilaria* appears to gain protection from *Arbacia* grazing when it is associated with the unpalatable brown alga, *Sargassum*.

It is possible, however, that this repeated measures analysis leads to an artificially increased variance within each microcosm, ultimately inflating the F-statistic for a within microcosm effect and increasing the likelihood of a type I error. The within microcosm variation is the sum of the squared deviations of the amount of each alga consumed about the mean consumption for that microcosm (Winer 1971). If we assume that there is a finite amount the urchins can consume in each microcosm, high grazing rates on one alga might result in low grazing on another alga. As a way of reducing this variance, while still testing the equality of algal treatments, we alternately excluded the treatment with *Sargassum* alone and *Sargassum* with *Gracilaria* from the repeated measures analyses. Eliminating these dependent variables had no effect on the p value ($P<0.001$), but the F-statistics were slightly higher (F = 19.54 when *Sargassum* alone was excluded; F = 19.02 when *Sargassum* with *Gracilaria* was excluded). Additionally, the result of the analysis of a treatment difference between *Gracilaria* alone and *Gracilaria* with *Sargassum* in the presence of urchins was unchanged, since this comparison is based only on the means and standard deviations of these two groups. To further assure that these results were accurate, we again tested whether *Gracilaria* with *Sargassum* is less susceptible to urchins than *Gracilaria* alone with a Wilcoxin paired
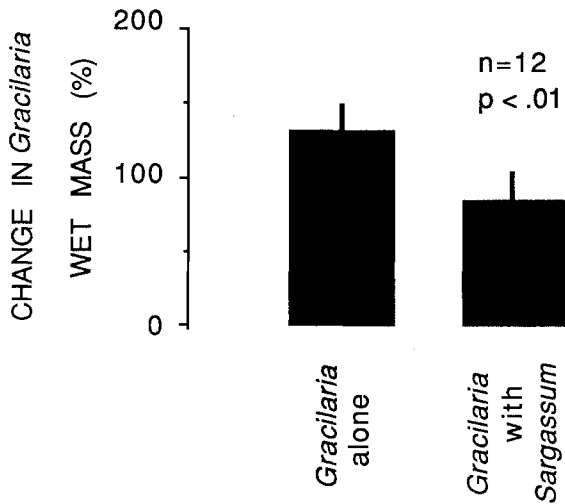
Fig. 4. The growth of *Gracilaria* alone versus the growth of *Gracilaria* with *Sargassum* in microcosms with wave-generating buckets. Plotted are means + 1 standard error; *P*-value was determined with a Paired-sample *t*-test

sample test $(0.05 > P > 0.02)$. Thus, each of our analyses indicated that *Gracilaria* gains protection from *Arbacia* grazing when it is associated with the unpalatable brown alga, *Sargassum*.

We designed a second assay to examine how *Sargassum* and *Gracilaria* interact competitively in the absence of herbivory. This assay was performed in 8 outdoor microcosms located at the Institute of Marine Sciences, Morehead City, NC. These 5000 l tanks employ 60 l wave generating buckets that dump at least once per min. This experiment was performed to supplement the experiment in the DUML microcosms because these wave generating buckets afforded more natural water motion that was more conducive to algal growth. Grids that held either *Gracilaria* alone or *Gracilaria* with *Sargassum* were secured to the bottom of each of these tanks. These grids were identical to those used in the DUML microcosms. A spun-wet-mass was obtained for the algae both before and after the 10 day experiment. This was replicated 12 times between 4 and 25 April 1986. *Gracilaria* alone grew 56% more than the adjacent *Gracilaria* with *Sargassum* (Fig. 4, $P < 0.01$, $n = 12$, Paired t-test). *Gracilaria* alone increased by 131% ± 15% ($\bar{x} \pm 1$ SE), while *Gracilaria* beneath *Sargassum* increased by only 84% ± 13%.

Mechanisms of associational refuges

Chemosensory abilities of urchins. To assess if urchins are preferentially attracted to *Gracilaria* alone, *Gracilaria* with *Sargassum*, or *Sargassum* alone, algal arrangements identical to those used in the DUML microcosms were enclosed in double-walled plastic mesh cages (30 cm diameter × 30 cm length) so that the algae could not be contacted by the urchins. This allowed us to test for chemosensory attraction as opposed to response following contact. The three arrangements of algae were attached to three separate grids (30 × 40 cm) in the same manner as described previously, except that the grids were then rolled up to enclose the algae, and the roll was placed lengthwise inside the cages. The cages with the rolled grids enclosed were then placed equidistant around the perimeter of the microcosms and anchored with a brick inside each cage to eliminate movement of the cages. Since *Arbacia* are negatively phototactic and often seek shade during daylight (Sharp and Gray 1962), assays were run at night by placing 12 urchins (starved for one week) in the center of the microcosms. Hourly observations throughout one night indicated that the urchins do not immediately go to one cage and stay; rather, they move throughout the night. Their positions relative to the three cages were recorded just prior to sunrise. This was repeated 14 times during two nights (1 and 3 May 1986); different urchins were used in each replicate.

The number of urchins found on the caged grids and in the vicinity of the cages (designated as one-third the area of a tank) after 7–8 h of darkness did not differ significantly among any of the three algal treatments. The number of urchins in the vicinity of the cages just prior to sunrise was not significantly different ($\chi^2 = 0.81$, 2 df, $0.75 > P > 0.50$, $n = 14$). There were 45 urchins associated with *Gracilaria* alone, 52 with *Gracilaria* and *Sargassum* together, and 44 with *Sargassum* alone. In addition, if the numbers of urchins directly on the cages are compared, there is still no significant difference between the three algal treatments ($\chi^2 = 2.28$, 2 df, $0.5 > P > 0.25$).

To assess whether or not *Arbacia* have the ability to detect food items at a short distance (40 cm) under controlled laboratory conditions, a Y-tube was constructed with 4 inch diameter PVC pipe and placed in a running seawater trough. Water flowed out of two holes at the bottom of a 51.5 l reservoir and into a perforated section of 1/4 inch plastic mesh at the end of each arm of the Y-tube. The water entered each section at a rate of 62.5 ml/sec and flowed into each 40 cm arm of the Y-tube. Ten grams of the alga (either *Sargassum* or *Gracilaria*) were placed onto the perforated section of one arm, while the other arm remained empty. An urchin was placed at the juncture of the 2 arms. After 20 min the position of the urchin was recorded, and algae and urchin were changed. In addition, the arm that contained the algae was switched for each trial, and the tube was scrubbed with a brush between every trial. All trials were done at night (2100–0530 h) since preliminary assays indicated that *Arbacia* fed more at night and so that light would not influence *Arbacia*'s movements (Sharp and Gray 1962). There were 23 trials for *Gracilaria* and 19 for *Sargassum*.

Arbacia showed no ability to sense algae from a distance of 40 cm. When 10 g of *Gracilaria* were placed in one arm of the Y-tube and the other was left empty, *Arbacia* moved toward *Gracilaria* 11 times, toward the empty arm 10 times, and exhibited no response twice. Similarily, when given a choice of 10 g of *Sargassum* versus an empty tube, *Arbacia* moved toward *Sargassum* 12 times, toward the empty arm 7 times, and exhibited no response 7 times. Although both of these assays show no significant differences with a χ^2 test ($0.95 > P > 0.90$ and $0.50 > P > 0.25$, respectively), increased replication might better document *Arbacia*'s response to *Sargassum*. If *Arbacia* move toward *Sargassum* (as suggested by Hay et al. 1986), it does not explain why *Gracilaria* gains protection when it is with *Sargassum*. A limited number of trials (8) tested *Arbacia*'s response to the bryozoan *Bugula neritina*. Although *B. neritina* has been found in the guts of *Arbacia* (personal observation), and Karlson (1978) noted the decrease of *B. neritina* when the abundance of *Arbacia* increased, there was no obvious che-

Table 2. *Arbacia* movement when placed singly on grids in the DUML microcosms. Urchins were allowed 3 h to respond. All trials were done in darkness. The distribution of *Arbacia* on these grids differed significantly from a distribution where *Arbacia* moved off of all grids with equal frequency ($\chi^2 = 13.74$, $0.005 > P > 0.001$)

	Gracilaria only	*Sargassum* only	*Gracilaria* and *Sargassum*
Moved off of grid	19 (68%)	0 (32%)	6 (21%)
Stayed on grid	9 (32%)	19 (68%)	22 (79%)

motactic response by *Arbacia; Arbacia* moved toward *B. neritina* 3 times, toward the empty arm 3 times, and exhibited no response twice ($\chi^2 = 0.25$, $0.90 > P > 0.75$).

Is Sargassum a deterrent to urchin grazing? To test the hypothesis that *Sargassum* is in some capacity a "repellent plant" (Atsatt and O'Dowd 1976), we placed urchins in the middle of grids with *Gracilaria* alone, *Gracilaria* and *Sargassum*, or *Sargassum* alone and monitored subsequent activity. The grid design, algal abundances, and use of the DUML microcosms were as described in the previous experiments. During nighttime hours one urchin was placed in the middle of each of the 3 grids in each tank, and their movements from grids were monitored for 3 h. This was repeated 7 times in 4 separate tanks with 84 separate urchins between 11 and 16 May 1986. This resulted in $n = 28$ for each type of grid.

Nineteen *Arbacia* left grids with *Gracilaria* only, 9 left grids with *Sargassum* only, and 6 left grids with *Sargassum* and *Gracilaria*. This distribution differed significantly from a distribution where *Arbacia* moved off of all grids with equal frequency ($\chi^2 = 13.74$, $P < 0.005$, Table 2). If grids with only *Sargassum* and those with *Gracilaria* and *Sargassum* are pooled and compared with *Gracilaria* only, the distribution still differs from one where *Arbacia* moves off of all grids with equal frequency ($\chi^2 = 13.07$, $P < 0.001$). Thus, over short time periods of hours, urchins are less likely to move off of grids with *Sargassum*.

To test whether *Sargassum* inhibited *Arbacia* movement, we placed a single urchin between adjacent grids of *Gracilaria* alone and *Gracilaria* with *Sargassum*, and recorded which grid the urchin moved onto after 1 h. This was repeated 48 times with separate urchins. Algal abundance was as described above for each grid and all algae were changed after each experiment in order to assure independence between all replicates.

The urchins initially moved onto both grids in equal numbers; 23 of the urchins moved onto the grids with only *Gracilaria* and 23 moved onto the grids with *Gracilaria* and *Sargassum*. Movement at least half-way across the grid was considered a criterion for penetrating the grid, since this required that urchins move through the algae. Thirteen urchins penetrated the grid with only *Gracilaria* while only 2 urchins penetrated the grid with *Gracilaria* and *Sargassum*. This difference is significant ($P < 0.005$, χ^2 analysis). Thus, there is no difference in the initial choice urchins make regarding which algal association to move onto; nevertheless, they almost always stop once they encounter *Sargassum* plants. These analyses of *Arbacia*'s movements indicate that *Sargassum* somehow inhibits urchin movement,
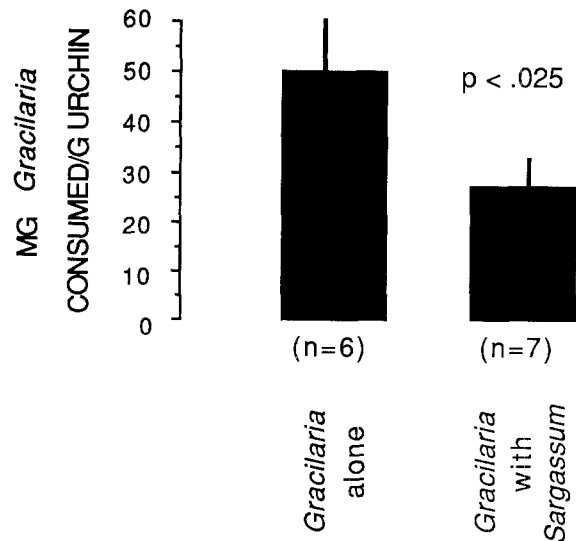

Fig. 5. The rate of *Gracilaria* consumption when alone and when with *Sargassum*. Unlike previous experiments, these two arrangements were separated in laboratory aquaria, and urchins could not choose between types of foraging sites. Means + 1 standard error are plotted; *P*-value was determined with a Two-sample *t*-test

decreasing the range over which *Arbacia* forages. *Sargassum* also seems to increase the time it takes *Arbacia* to find and consume a palatable prey item. *Arbacia* are relatively sedentary on grids with *Sargassum*, but more mobile and actively grazing on grids with only *Gracilaria*.

In all previous tests of *Arbacia*'s grazing on *Gracilaria* alone versus *Gracilaria* with *Sargassum*, urchins had a choice of moving to either type of habitat. To see how *Arbacia*'s grazing would be affected in the absence of such a choice, we placed either *Gracilaria* alone or *Gracilaria* with *Sargassum* separately into aerated 38 l laboratory aquaria, each with a single urchin. The 17×24 cm grids holding the algae were the same size as the quadrat used to sample in the field; therefore, the mass of algae secured to the grids was the average mass of *Gracilaria* (3.5 g) and *Sargassum* (159.3 g) found at Radio Island Jetty during August 1985. For both algal treatments, there were 4 control aquaria with no urchins to correct for the change in algal mass that was not a result of urchin consumption. The initial spun-wet-mass of algae in aquaria with urchins was corrected with the mean change in these controls.

Gracilaria alone was consumed at a rate of 50.1 ± 8.2 mg/g urchin/30.5 h ($\bar{x} \pm 1$ SE), as compared to a rate of 27.3 ± 4.5 when *Gracilaria* was with *Sargassum*. This was a significant (46.7%) reduction in the rate at which *Gracilaria* was consumed when it was with *Sargassum* (Fig. 5, $0.025 > P > 0.01$, $n = 6$ and $n = 7$, Two-sample t-Test). Controls for the *Gracilaria* alone treatment showed a change of -52 ± 58 mg/30.5 h ($\bar{x} \pm 1$ SE, $n = 4$); those for *Gracilaria* with *Sargassum*, $+125 \pm 102$ mg/30.5 h ($\bar{x} \pm 1$ SE, $n = 4$). These control treatments did not differ ($P > 0.50$, Two-Sample t-Test). When the control data were omitted, *Gracilaria* alone is still consumed significantly more than *Gracilaria* with *Sargassum* ($0.05 > P > 0.025$, Two-Sample t-Test).

To test if the physical structure of *Sargassum* could deter urchins from consuming *Gracilaria*, the previously described experiment was repeated using two types of plastic

Table 3. The rate at which *Gracilaria* was consumed by *Arbacia* when *Gracilaria* was associated with real *Sargassum* plants and with different types of *Sargassum* mimics. Experiments lasted 24–32 h in laboratory aquaria. Data were analyzed with Two-sample t-Tests. The results of F-tests for homogeneity of variance are given in the text

	Rate of *Gracilaria* consumption ($\bar{x}$ mg *Gracilaria* eaten/g urchin $\pm$ 1 SE)		
	Gracilaria alone	*Gracilaria* with *Sargassum*	P
Real *Sargassum* plants	51 ± 8 ($n=6$)	27 ± 5 ($n=7$)	$0.025 > P > 0.01$
Sargassum mimics made of monofilament line and flexible plastic leaves	45 ± 13 ($n=10$)	84 ± 10 ($n=11$)	$0.05 > P > 0.02$
Sargassum mimics made of stiff pre-molded plastic (urchins starved 1 week)	35 ± 7 ($n=14$)	47 ± 7 ($n=14$)	$0.50 > P > 0.20$
Sargassum mimics made of stiff pre-molded plastic (urchins starved 2 weeks)	61 ± 11 ($n=15$)	70 ± 15 ($n=15$)	$P > 0.50$

Sargassum mimics. The same plastic mesh grids (17 × 24 cm) were placed in aerated 38 l aquaria, with either 3.5 g of *Gracilaria* alone or 3.5 g of *Gracilaria* interspersed with 6 *Sargassum* mimics (the mean number in the experiment with real *Sargassum*). The first of these experiments employed *Sargassum* mimics that were constructed with frond-shaped sheet plastic threaded onto monofilament fishing line. To keep these "plants" upright like real *Sargassum* plants, they were buoyed by a cork. For this experiment, *Gracilaria* alone had $n=10$, *Gracilaria* with *Sargassum* mimics had $n=11$, and controls were $n=3$ for each treatment. The initial spun-wet-mass of *Gracilaria* in both treatments was corrected with the mean change in *Gracilaria* spun-wet-mass in controls.

Although real *Sargassum* plants significantly decreased the rate of consumption of *Gracilaria*, plastic *Sargassum* mimics did not (Table 3). *Gracilaria* beneath these *Sargassum* mimics was consumed at a rate of 84.3 ± 10.0 mg/g urchin ($\bar{x} \pm 1$ SE), while *Gracilaria* alone was consumed at a rate of 44.9 ± 12.8 mg/g urchin. Thus, in this test, artificial *Sargassum* significantly stimulated, rather than deterred, grazing (Two-sample t-Test, $0.05 > P > 0.02$, $n=11$ and $n=10$). Controls for the *Gracilaria* alone treatment showed a change in spun-wet-mass of -34 ± 40 mg ($\bar{x} + 1$ SE, $n=6$); *Gracilaria* with *Sargassum* controls showed a change of -42 ± 26 mg ($\bar{x} \pm 1$ SE, $n=6$). These control treatments did not differ ($P > 0.50$, Two-sample t-Test), and this pattern of *Gracilaria* grazing was the same when control data were omitted ($0.05 > P > 0.01$, Two-Sample t-Test).

A second experiment used plastic aquarium plants that

more closely resembled *Sargassum*. These were thought to be an improvement on the monofilament and plastic mimics because they more closely resembled the morphology, toughness, and rigidity of *Sargassum*. These black plastic plants were 23–28 cm in height and had thick plastic leaves. This experiment using tough plastic mimics was repeated twice, once with urchins that had been starved for 1 week (for both with and without mimic treatments, $n=14$; there were 4 control tanks without urchins) and once with urchins that had been starved for 2 weeks (both treatments, $n=15$; controls, $n=6$).

There was no significant difference between the amount of *Gracilaria* consumed alone and the amount of *Gracilaria* consumed with *Sargassum* mimics, regardless of whether urchins were starved for 1 or 2 weeks prior to the experiment (Table 3). When urchins were starved for 1 week, the controls for *Gracilaria* alone and *Gracilaria* with *Sargassum* showed a change of 10 ± 37 mg and 100 ± 24 mg respectively ($\bar{x} \pm 1$ SE, $n=6$). There was no significant difference between control treatments ($0.10 > P > 0.05$, Two-sample t-Test). If control data were omitted, there was still no difference in *Gracilaria* consumption when alone or with *Sargassum* mimics ($0.50 > P > 0.20$, Two-Sample t-Test). When urchins were starved for 2 weeks, the controls for *Gracilaria* alone and *Gracilaria* with *Sargassum* showed a change of -50 ± 28 mg and -60 ± 28 mg ($\bar{x} \pm 1$ SE, $n=8$). These controls treatments did not significantly differ ($P > 0.50$, Two-Sample t-Test). Again, the omission of the control data did not change the results of *Gracilaria* consumption; *Gracilaria* alone and *Gracilaria* with *Sargassum* mimics were consumed at equal rates ($P > 0.50$, Two-Sample t-Test).

The morphologies of *Gracilaria* and *Sargassum* differ; *Gracilaria* has a softer, less rigid thallus than the tougher *Sargassum*. Such differences in toughness are thought to have important effects on herbivore preferences (Littler and Littler 1980; Steneck and Watling 1982; but see Padilla 1985). To see if something other than morphology caused *Arbacia* to distinguish between the two species, both algae were collected from the field and held in seawater until homogenized in a blender and presented to an urchin in identical 5 cm diameter agar disks. Forty grams (spun-wet-mass) of either *Gracilaria* or *Sargassum* were homogenized in a blender with 50 ml of seawater and added to a 2% agar/seawater mixture, resulting in an agar mixture that was 8% alga by wet mass. The average mass of an agar disk was 19.434 ± 0.380 g ($\bar{x} \pm 1$ SE, $n=49$). Since agar is an algal-derived product, disks consisting of the same agar/seawater mixture used above, but with no added algal material were also presented to *Arbacia*. These allowed me to determine if *Gracilaria* or *Sargassum* either stimulated or deterred feeding when compared to discs of agar alone.

In the first of the two feeding assays, the three varieties of agar disks were presented separately to individual urchins. Individual *Arbacia* were weighed and placed into 3.8 l aerated jars with 1.3 l seawater. Either a *Gracilaria* ($n=12$), a *Sargassum* ($n=12$), or a plain ($n=11$) agar disk was placed in each jar. All disks were individually weighed prior to the start of the experiment and again after 24 h with the urchins. Similar jars without urchins ($n=3$) were run simultaneously for all types of agar disks to control for changes unrelated to urchin grazing. The mean change in these controls were used to correct the initial mass of agar disks.
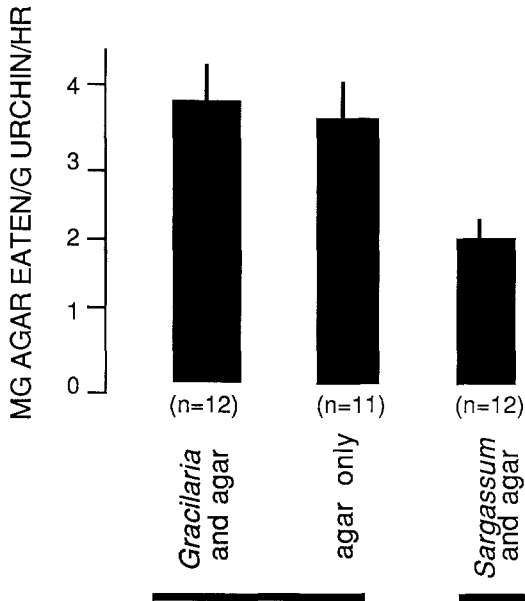
Urchins consumed significantly more of the agar with

Fig. 6. The mean rate of consumption of algal flavored agar disks (+1 SE) by *Arbacia* when the 3 varieties were presented separately. Dark bars beneath the histograms connect disk types that did not differ significantly ($P<0.05$, Kruskal-Wallis Test and a nonparametric Student Newman-Keuls multiple comparison test)

Fig. 7. The mean rate of consumption of agar disks (+1 SE) by *Arbacia* when presented a choice of both *Gracilaria* homogenate in agar and *Sargassum* homogenate in agar. P-value was determined with a Wilcoxon Paired-Sample test, $P=0.001$

Gracilaria ($\bar{x}\pm1$ SE = 3.9 ± 0.5 mg/g urchin/hr) and the agar alone (3.6 ± 0.7) than the agar with *Sargassum* (1.9 ± 0.3). This was tested with a Kruskal-Wallis Test and a nonparametric Student-Newman-Keuls Test (Zar 1974; $P=0.023$, Fig. 6). Controls for disks with *Gracilaria* homogenate with agar, *Sargassum* homogenate with agar, and agar only showed a change in wet mass of -287 ± 43 mg, -202 ± 20 mg, and -241 ± 46 mg, respectively ($\bar{x}\pm1$ SE, $n=3$). These control treatments did not significantly differ ($P=0.35$, ANOVA). When the control data were omitted, there was still a significant difference in the consumption of the three types of agar disks ($P<0.001$, Kruskal-Wallis Test; Cochran's test for homogeneity of variance: $F=0.54$, $P<0.01$). However, there was a significant difference between all three types of agar disks ($P<0.05$, nonparametric Student-Newman-Keuls Test; Zar 1974).

The second assay was performed to determine what *Arbacia*'s response would be when offered a simultaneous choice of both *Sargassum*- and *Gracilaria*-flavored agar disks. Both types of agar disks were placed in the same jar with an urchin for 24 h ($n=13$); controls were run simultaneously ($n=3$). The same methods used in the previous experiment were also used for this second assay.

Agar disks with *Gracilaria* homogenate were eaten significantly more than agar disks with *Sargassum* homogenate (Fig. 7; $\bar{x}\pm1$ SE=9.4 ± 1.3 mg/g urchin/h and 1.6 ± 0.3, respectively; $P<0.001$, Wilcoxon's Paired Sample Test, $n=13$). Controls for disks of *Gracilaria* homogenate with agar and *Sargassum* homogenate with agar showed a change in wet mass of -758 ± 119 mg and -382 ± 63 mg respectively ($\bar{x}\pm1$ SE, $n=3$). These control treatments did not differ ($0.50>P>0.20$, Paired-Sample t-Test). When these control data are omitted, *Gracilaria* homogenate with agar is still consumed significantly more than *Sargassum* homogenate with agar ($P=0.001$, Wilcoxon's Paired-Sample Test). Thus, two separate assays with agar and algal homogenate demonstrate the pattern of decreased con-

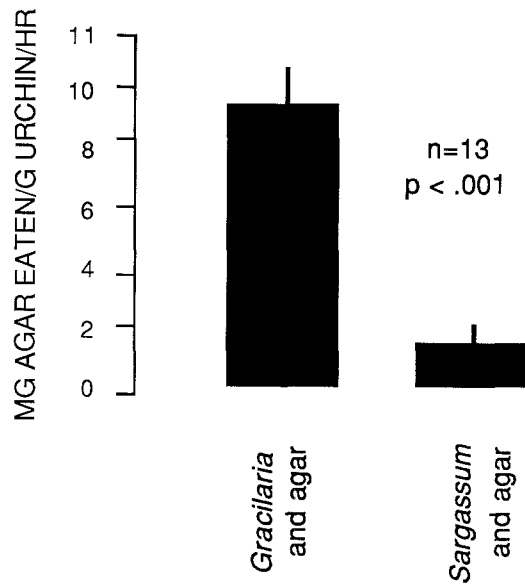sumption of *Sargassum*-flavored agar disks compared with *Gracilaria*-flavored agar disks.

Discussion

Associational plant refuges in marine communities

The amount of *Gracilaria* in *Sargassum* stands varies seasonally and appears to be correlated with the activity and abundance of the major herbivores. In spring when urchins are less active (Karlson 1978) and when common fishes have been absent for preceeding months and newly recruiting juveniles are consuming small invertebrates instead of algae (Adams 1976; Darcy 1985a, b), there is no correlation between the mass of *Gracilaria* and the mass of *Sargassum*. Conversely, in late summer-early fall, these dominant herbivores have been active and abundant (Hay 1986), and there is a sigificant positive correlation between the mass of *Gracilaria* and *Sargassum*.

All available evidence indicates that the process generating this seasonal change in the association of *Gracilaria* and *Sargassum* is herbivory: *Gracilaria* gained protection from urchin grazing when it was associated with the low preference alga *Sargassum* (Figs. 3 and 5). In addition, *Sargassum* significantly decreased the growth of *Gracilaria* when *Arbacia* were excluded (Fig. 4), indicating that *Sargassum* is a competitor of *Gracilaria*. Thus, in the presence of *Arbacia*, *Sargassum* has a net positive effect on *Gracilaria*; in the absence of *Arbacia*, *Sargassum* is a competitor and decreases the growth of *Gracilaria*.

The mechanisms by which *Sargassum* deters *Arbacia* are varied. *Sargassum* inhibits movement, and therefore foraging range and feeding time. The decrease in urchin feeding on *Gracilaria* in stands of *Sargassum* is not a result of *Sargassum* morphology, since grazing on *Gracilaria* was the same or increased when *Gracilaria* was placed among

plastic *Sargassum* mimics (Table 3). There was no evidence that urchins employ preferential chemotaxis to avoid areas with *Sargassum*. Rather, some property of *Sargassum* deters *Arbacia* at close range.

Associational plant refuges in the marine realm have been investigated by Hay (1985, 1986) and Littler et al. (1986). Hay (1986) demonstrated that the palatable algae *Hypnea musciformis* and *Spyridea hypnoides* were less susceptible to grazing fishes when they grew as epiphytes on *Sargassum* than when they occurred 5 cm away from a *Sargassum* plant. However, fish grazing was not reduced when *Hypnea musciformis* was placed beneath two isolated *Sargassum* plants. Littler et al.'s (1986) tropical study showed that a single *Stypopodium zonale* plant reduced fish grazing on nearby palatable algae attached to primary substrate. Several edible algae that occurred almost exclusively within a 10 cm radius of a *Stypopodium* plant were rapidly consumed by fishes when the *Stypopodium* plant was removed. In addition, consumption of the palatable alga, *Acanthophora spicifera* was highest when it was 30–60 cm from *Stypopodium*, intermediate adjacent to plastic *Stypopodium* mimics, and lowest adjacent to real *Stypopodium*. These differences were significant. Thus, in Littler et al.'s (1986) study, *Stypopodium* morphology alone appeared to account for some, but not all, of the reduced herbivory on associated plants. Since *Stypopodium* produces a secondary metabolite that is slowly released into the water and that significantly reduces consumption by reef fishes (Hay et al. 1987b), some portion of *Stypopodium*'s deterrent effects are probably chemical.

In contrast to Littler et al. (1986), I found no evidence that urchin grazing was decreased by the presence of *Sargassum* mimics (Table 3). Thus, *Stypopodium* and *Sargassum* seem to function somewhat differently in deterring grazing, and this difference may be due to the feeding modes of the herbivores studied.

Marine herbivores feed in different ways (Ogden 1976; Steneck and Watling 1982; Vadas 1985), and several studies suggest that plant defenses will decrease in effectiveness as the diversity of herbivore types increases (Lubchenco and Gaines 1981; Hay 1984; Gaines 1985; Paul and Hay 1986; Hay et al. 1987a). For example, although Littler et al. (1986) demonstrated that *Stypopodium* deters fish grazing on edible species associated with it, Littler et al. (1983) showed that the sea urchin *Diadema antillarum* readily grazes on *Stypopodium*. Their study also showed that *Diadema* are often more likely than fishes to feed on algae suspected of being chemically defended. However, *Sargassum* provides a site of decreased herbivory by both fishes (Hay 1986) and urchins. These two herbivores differ dramatically in the ways they forage and they are the dominant macroherbivores at this site.

Marine and terrestrial communities compared

The theory behind associational plant refuges has its origins in the literature of plant-insect interactions (Tahvanainen and Root 1972; Root 1973, 1974; Cromartie 1975; Atsatt and O'Dowd 1976; Risch 1980; Karieva 1982; Turchin 1986; Brown and Ewel 1987). Most of these studies concentrate on the varying effect of plant monocultures and polycultures on insect numbers and diversity (Turchin 1986), as well as how these mono- and polycultures affect insect foraging and reproduction (Bach 1980; Kareiva 1982; Turchin 1986). In addition to plant-insect interactions, Fuentes

et al. (1986) and McAuliffe (1986) documented cases of plant associations that provide refuges from small mammalian herbivores. In both studies, the survival of palatable seedlings was increased under the canopy of a shrub or tree. McNaughton (1978) demonstrated that ungulate grazing in the Serengeti resulted in a plant defense guild that resembled the results shown here; a palatable grass species gained protection from herbivory when it was associated with less palatable species.

Root (1973) proposed two hypotheses as explanations for the increased number of herbivores in collard monocultures versus the more diverse meadow vegetation that was located nearby. The "enemies hypothesis" states that diverse habitats support denser populations of parasitoids and predators that lower the density of herbivores. The "resource concentration hypothesis" asserts that herbivore density is higher in host monocultures because herbivores can more easily find hosts that are in a dense, concentrated assemblage. Building upon Root's (1973) studies, Atsatt and O'Dowd (1976) advanced the concept of the plant defense guild (sensu Root 1967), where different species of plants are dependent on one another for herbivore deterrence. They suggested that plant guilds resist herbivores in three ways: 1) by maintaining parasites and predators (i.e. Root's (1973) enemies hypothesis), 2) by containing some repellent plants that interfere with the herbivore's ability to detect other plants, or 3) by containing attractant-decoy plants that serve as alternate prey.

Root's (1973) enemies hypothesis has been shown to be unimportant in the terrestrial agricultural communities where experimental studies have been conducted (Tahvanainen and Root 1972; Bach 1980); additionally, there is no evidence supporting the enemies hypothesis in this study. The major urchin predators in coastal North Carolina appear to be large fishes which move over extensive areas, and are not restricted to patches of *Sargassum*. In addition, Hay et al. (1986) suggested that *Arbacia* may actually be attracted to the understory of *Sargassum*, since these plants may provide cover from visually searching fishes.

Additionally, the resource concentration hypothesis (Root 1973) does not explain the patterns documented here. In terrestrial habitats, monocultures of host plants are more affected by insect herbivores than are polycultures that contain some non-host plants because insects immigrate to monocultures more rapidly, remain in them longer, and experience higher reproductive output while they are there (Tahvanainen and Root 1972; Bach 1980; Karieva 1982). In contrast, urchins do not migrate to *Gracilaria* monocultures more rapidly than to mixtures of *Gracilaria* and *Sargassum*, and they do not tend to stay in monocultures of *Gracilaria* longer than in mixtures of *Gracilaria* and *Sargassum*. In fact, they are significantly more likely to emigrate from monocultures of the preferred plant (Table 2). When immigration, emigration, and residence times in monocultures versus polycultures are held constant by confining urchins in aquaria with only one of these habitat types, urchins still feed more on *Gracilaria* alone than on *Gracilaria* with *Sargassum* (Fig. 5). The increase in herbivory in areas with *Gracilaria* only appears to be a result of increased urchin mobility and feeding rate in these areas. It is not due to an increased density of herbivores as is the case for terrestrial studies of herbivorous insects (Tahvanainen and Root 1972; Root 1973; Bach 1980; Risch 1980).

Tahvanainen and Root (1972) showed that non-host plant species interspersed with the host plant give off chemi-

cal stimuli that interfere with the insect's ability to find and feed on the host plant. However, *Arbacia* were not differentially attracted to stands of *Gracilaria* alone versus stands of *Gracilaria* with *Sargassum*. Additionally, *Arbacia* exhibited no chemosensory abilities at a distance of 40 cm in a Y-tube. Thus, if interfering chemical cues are causing the patterns documented in this study, then they must be important at a distance of only a few centimeters.

Atsatt and O'Dowd's (1976) repellent plant hypothesis appears to be most applicable to this study. Although the specific aspect of *Sargassum* that makes it a repellent plant has not been identified, the following experimental results indicate that *Arbacia* avoid consuming *Sargassum* and reduce their foraging rate when *Sargassum* is nearby. Firstly, when the algae are homogenized and added to agar, *Arbacia* selectively consume agar alone, or agar with *Gracilaria* over agar with *Sargassum* (Figs. 6 and 7). Secondly, *Arbacia* traverse grids with *Sargassum* and *Gracilaria* significantly less than grids with *Gracilaria* only. Thirdly, *Arbacia* consume *Gracilaria* alone at a rate that is significantly more than the rate at which *Gracilaria* is consumed when it is with *Sargassum* (Figs. 3 and 5). These results, combined with the fact that *Sargassum* mimics either did not change or increased the rate at which *Gracilaria* was consumed (Table 3), suggest that *Sargassum* chemically deters feeding on nearby algae. A relatively high concentration of phenolics has been found in some temperate *Sargassum* species (Steinberg 1986), and it is possible that similar defenses are important here.

The role of urchin chemoreception

This study indicates that *Arbacia* move without regard to distant prey items, exhibiting preference at close range, perhaps only within the radius of the tube feet. These results are counter to most other published accounts of urchin feeding behavior and chemosensory abilities. The ability of urchins to detect prey from a distance has been demonstrated for *Strongylocentrotus droebachiensis* by Vadas (1977) and Larson et al. (1980), and for *Echinus acutus* and *Echinus esculentus* by Bonsdorff and Vahl (1982). All of these studies employed Y-tube experiments. Similarly, Mann et al. (1984) have noted that *Strongylocentrotus droebachiensis* preferentially move toward *Laminaria longicruris* and other urchins feeding on the kelp, and move away from water containing lobsters or crabs. Additionally, other researchers have noted urchin feeding fronts and feeding aggregations in response to algal prey items (Himmelman and Steele 1971; Garnick 1978; Dean et al. 1984; Mann et al. 1984; Vadas et al. 1986; personal observation).

The chemosensory results obtained with *Arbacia* most closely resemble the results of Klinger and Lawrence (1985). They concluded that *Lytechinus variegatus* was unable to locate prey items at a distance of more than 3 to 8 cm. Similar close range chemosensory abilities might explain why Hay et al. (1986) found that *Arbacia* was chemotactic when offered a number of algae in a round pool, where urchins could nearly contact the algae, while our Y-tube assessment of distance chemotaxis yielded negative results.

The generality and consequences of associational refuges

The diversity of habitats in which associational refuges are reported to play a role further testifies to the potential importance and ubiquity of this process. In addition to benthic marine examples (Hay 1985, 1986; Littler et al. 1986), studies include habitats such as the Serengeti grasslands in Africa (McNaughton 1978), Sonoran desert tree communities (McAuliffe 1986), the Chilean mattoral (Fuentes 1986), coastal marine plankton communities (Egloff 1986), and a variety of natural and cultivated habitats where plant-insect interactions are important (Atsatt and O'Dowd 1976; Brown and Ewel 1987).

The question of what maintains species diversity has been a popular one in ecology (Hutchinson 1959; Connell and Orias 1964; Pianka 1966, 1967, 1969; Menge and Sutherland 1976; Connell 1978; Lubchenco 1978; Hay 1981a, 1985, 1986; Ricklefs 1987), and it has been demonstrated that intermediate rates or intensities of disturbance, including predation and herbivory, can facilitate higher numbers of species because they preclude competitive dominance by any one organism (Paine 1966; Dayton 1971; Connell 1978; Sousa 1979; Carpenter 1981; Hixon and Brostoff 1983; Morin 1983; Dethier 1984; Grubb 1986). However, if the competitive subordinate is preferred by the predator, species diversity will be decreased (Lubchenco 1978). In this study, as in Hay (1986) and Littler et al. (1986), associational plant refuges provide a mechanism for maintaining high species numbers, since palatable, relatively undefended algae can avoid local extinction when associated with unpalatable competitors. Thus, a palatable alga can either be in the open, susceptible to herbivory which often causes local extinction (Hay 1981a, 1986; Lewis 1986), or it can be with a competitor, which, although deleterious to growth, often is not fatal (Peterson 1979, 1982).

Conclusions

Although many studies have examined the relative importance of competition and herbivory (predation) in macroalgal communities (Dayton 1975; Foster 1975; Lubchenco 1978, 1983, 1986; Underwood 1980; Hay 1981a, b, 1984, 1985, 1986; Paine 1984; Lewis 1985, 1986), few demonstrate the important indirect effects that may occur when one competitor aids another (see Dethier and Duggins 1984; Hay 1986). During periods of low herbivory, *Gracilaria* should have an increased growth in open stands; during periods of high herbivory, the cost of competition may be less than the benefit of decreased grazing losses, and the fitness of *Gracilaria* should increase when it is closely associated with *Sargassum*. Thus, the effect of *Sargassum* on the fitness of *Gracilaria* is dependent upon the complex interaction of competition and herbivory.

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