

## Plant defense associations in the marine environment

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**Abstract.** In contrast to terrestrial systems, few positive plant-plant associations have been recorded in tropical reef environments. This study, conducted at Carrie Bow Cay, Belize during 28 March–10 April 1984, provides the first documentation of herbivore escapes for natural combinations of palatable and unpalatable marine plants. For example, there was a highly significant association of several macrophyte taxa (*Laurencia poitei*, *Dictyota* spp., *Amphiroa fragilissima*, *Cladophoropsis macromeres*, *Galaxaura cylindrica*, rhodophycean turf) within a 2.0-cm radius of the herbivore-resistant brown alga *Styopodium zonale*. Almost twice as many taxa occurred within 10 cm of *S. zonale* as within 10 cm of an equal number of random *Styopodium*-free points, and there were no algal species negatively associated with *S. zonale*. The association of *A. tribulus*, *L. poitei*, *Digenia simplex*, rhodophycean turf, and *Jania adherens* with *S. zonale* provided them a fourfold greater survivorship per 48 h in the presence of grazing activity by fishes (mainly Acanthuridae and Scaridae). Reduced herbivory by fishes on macroalgae associated with *S. zonale* was not solely a consequence of its structural aspect. Losses of the palatable alga *Acanthophora spicifera* were significantly greater for thalli spatially remote (30 and 60 cm) from either a real or simulated *Styopodium*; however, losses of *A. spicifera* adjacent to actual *Styopodium* plants were significantly less than the losses next to models. The interrelationships studied here, where an abundant and well-defended plant provides a significant refuge habitat for at least five relatively edible macroalgae, clearly facilitates the survival of certain taxa in the reef system and concomitantly enhances the within habitat diversity. Our findings also suggest an interaction counter to the process of competitive exclusion, since the single predominant plant has a positive rather than negative net effect on the abundances of other species that utilize the same general resources (e.g., light, space, nutrients).

### Introduction

Herbivory generally is assumed to be an intense selective force in the evolution of both marine and terrestrial plants and is an important factor in the organization and development of macroalgal communities. Because grazing losses reduce the growth, reproduction and survival of individuals, herbivory is strongly implicated (Littler and Littler 1984) in the evolutionary selection of the morphological, chemical, nutritional, temporal and spatial mechanisms that plants use for defense against, or escape from, herbivorous animals.

Such defenses and escapes have been widely investigated in terrestrial plant communities (e.g., Coley 1983) and are currently receiving considerable attention in marine systems (e.g., Lubchenco and Gaines 1981). An extensive literature concerning the adaptive significance of plant chemical defenses has emanated primarily from an abundance of terrestrial research (e.g., see Rhoades 1979; Rosenthal and Janzen 1979; Fox 1981; Hedin 1983; Futuyma 1983; Denno and McClure 1983); however, comparable marine studies are on the increase (e.g., Geiselman and McConnell 1981; Targett and McConnell 1982; McConnell et al. 1982; Paul and Fenical 1983; Steinberg 1984, 1985). One synthetic theory that has emerged from studies of plant-herbivore interactions (Rhoades 1979; Lubchenco and Gaines 1981) states that the evolution of plant defense mechanisms has occurred in response to (1) an individual's probability of being discovered by a predator, (2) the likelihood of losing biomass (and amount lost) once located, (3) the decrease in fitness caused by the loss of that biomass, and (4) the costs of a given defense.

A prevalent viewpoint (Bakus 1969; Earle 1972; Vermeij 1978; Fenical 1980; Menge and Lubchenco 1981; Sousa et al. 1981; Gaines and Lubchenco 1982) is that the intensity of herbivory in marine systems increases from high latitudes towards the tropics (but see also Choat 1982). The proposed reason is that while invertebrate grazers are common at all latitudes, herbivorous fishes,

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because of their larger size, higher metabolic rates, mobility, orientation behavior, and range of sophisticated sensory cues, become increasingly damaging to macroalgal populations in subtropical to tropical regions. Although studies on certain reef systems have shown the localized importance of grazing by sea urchins (e.g., Ogden et al. 1973; Sammarco et al. 1974; Hay and Taylor 1985; Carpenter 1985), as well as gastropods (Levings and Garrity 1983) and micrograzers (Brawley and Adey 1981), fishes tend to be the predominant herbivores on most natural reef systems (e.g., Stephenson and Searles 1960; Randall 1961; Bakus 1969; Earle 1972; Vermeij 1978; Menge and Lubchenco 1981; Gaines and Lubchenco 1982; Hay 1984a, b). However, there are large spatial variations in grazing intensity on reefs (Hay 1981a, 1984b, 1985; Lewis 1985; Lewis and Wainwright 1985). For example, where access is reduced due to lack of protective cover (e.g., shallow lagoons, extreme landward portions of backreefs, deep reef slopes), fish grazing can be minimal.

Most studies have failed to approach holistically the questions concerning the effects of herbivores in marine benthic communities. Instead, they have focused on direct grazing effects primarily through single plant-herbivore relationships. Fewer investigations have considered interactions at other levels, and those that have, for example herbivore-herbivore [see Stimson (1973) on limpets; Lubchenco (1983) on limpets and barnacles; Hay and Taylor (1985) on fish vs sea urchins] and carnivore-herbivore (e.g., Lubchenco and Menge 1978; Duggins 1980), usually emphasized "negative" effects (i.e., predation and competition). Although requiring more study, one role of micrograzers (Brawley and Adey 1981; Steeneck 1982; Shacklock and Doyle 1983) involves the selective removal of microalgal epiphytes resulting in enhanced macroalgal growth. Such "positive" associations within or between trophic levels in natural marine systems have been largely unexplored (but see Sutherland 1974; Black 1976; Suchanek 1978; Woodin 1978; Osman and Haugsness 1981; Gallagher et al. 1983; Dethier and Duggins 1984; Turner 1985), particularly plant-plant interactions (see Harris et al. 1984); however, numerous positive effects of animals on terrestrial plants have been documented (e.g., Simberloff et al. 1978; Inouye 1982). The goal of this study was to examine the hypothesis that some palatable marine plants show a reduced probability of being discovered or eaten when they occur in close physical proximity to low-preference plants.

The concept of defense associations against herbivores has long been noted in the fields of terrestrial ecology and agriculture (e.g., Phillips and Pfeiffer 1960; Harper et al. 1961; Pimentel 1961; Morris 1963; Smith 1969; Tahvanainen and Root 1972; Root 1973, 1974; Levin 1973; Atsatt and O'Dowd 1976; Kroh and Beaver 1978; Risch 1979; Robinson 1980; Rausher 1981). The term "defense association" as used here characterizes co-occurring, ecologically linked assemblages of plants, with the result that some members show reduced susceptibility

to herbivores. The following questions were examined by several different experiments to test the hypothesis posed above:

(1) Are palatable marine plants spatially associated with non-palatable species? If so, is this a frequent and predictable relationship?

(2) Is the survivorship of a marine alga improved in the vicinity of a specific neighbor? If so, is this a functional dependence mediated by herbivorous fishes?

(3) If the answers to (1) and (2) are positive, is the effect of structural shelter as important as the role of deterrent chemistry in these plant defense associations?

(4) How might functional plant defense associations relate to ecological and evolutionary relationships on biotic reefs?

### Study site

The study was conducted at the Smithsonian Institution's field station on Carrie Bow Cay, Belize (16°48' N, 88°05' W) during 28 March to 10 April 1984. The study site (Fig. 1) is located on the upper fore-reef at the mouth of South Water Cut, the channel between South Water Cay and Carrie Bow Cay, approximately 500 m north of Carrie Bow Cay. An excellent description of the reef system of Carrie Bow Cay may be found in Rützler and Macintyre (1982).

Extensive research near Carrie Bow Cay (Hay 1981a; Littler et al. 1983a, b; Lewis and Wainwright 1985) in all accessible major habitats, including the site studied here, have implicated herbivory by fishes as a major factor controlling macroalgal abundances and patterns of distribution. This condition prevailed both before and after the major die-offs of *Diadema antillarum* Philippi throughout the Caribbean (Lessios et al. 1984).

All of the assessments and experiments were conducted at a depth of approximately 4–6 m in a region with a relatively smooth (e.g., two dimensional) substratum, which consists of a mixture of uniform carbonate "pavement" thinly covered in places by a light layer of calcareous sand. Gorgonians and *Millepora* (averaging about 0.5 m tall), due to their upright three-dimensional structure (spatial heterogeneity), provide shelter for fishes. Tidal-driven current movement in this habitat is consistently moderate (<1–2 knots), as is wave surge. The brown alga *Styopodium zonale* (Lamour.) Papenf. is by far the predominant frondose alga, occurring mostly as individual iridescent plants that are 8–20 cm tall.

### Experimental organism

*Styopodium zonale* is a member of the Dictyotaceae (Phaeophyta) that occurs abundantly throughout the tropical Pacific and Atlantic Oceans even where herbivore pressure is intense. We have collected this plant over a depth range from 0.2 to 81 m, but it appears most conspicuously in open areas several meters deep, frequently reaching 30 cm in height.



Fig. 1. Location of the study area (dark triangle) on the Belize barrier fore-reef

*Styopodium zonale* apparently is not an important food source of either fishes or urchins (Gerwick 1981), although *Diadema antillarum* will consume it at low levels (Littler et al. 1983 b). L. Coen (personal communication) indicates that *S. zonale* is the least preferred alga by herbivorous crabs among the numerous macrophyte species he has tested at Carrie Bow Cay.

This low preference appears to be based largely on chemical defense. Mature individuals of *Styopodium zonale* contain substantial amounts of seven unique  $C_{27}$  compounds as well as two previously known metabolites (Gerwick and Fenical 1981); three are toxic to fish at low levels (stypoldione, stypotriol, epistypodiol), one (stypodiol) causes an instantaneous hyperactive "escape" response, and the remainder produce distinct lethargic behavior and narcosis. For example, when fresh *S. zonale* is maintained in a well-aerated aquarium, the water is rendered extremely toxic to reef-dwelling herbivorous fishes within 10 h (Norris and Fenical 1982) even though the alga remains healthy. Fish placed in such water immediately sense the toxins and attempt to jump out (Gerwick et al. 1979). The avoidance response is quickly followed by erratic behavior, respiratory difficulty, loss of equilibrium, and eventual death.

In addition, some of the unique metabolites also are implicated as antifouling compounds (Gerwick 1981); the only common cases of epiphytism on *Styopodium zonale* (personal observations) are thin crustose corallines and infrequent microalgae on older basal portions of thalli.

### Materials and methods

The types of herbivores and their abundances were assessed in the experimental area by 8 replicate, 2-m wide by 9 to 12-m long transects that were slowly evaluated by a diver (2–3 m from the bottom) throughout a typical day (10 April 1984). Data consisted of counts of surgeonfishes (Acanthuridae) and parrotfishes (Scaridae) since other grazing fishes and sea urchins were not encountered.

To determine whether other macroalgae have distributions that are positively associated with individuals of *Styopodium zonale*, we randomly chose 20 specimens of *S. zonale* along a 50-m long transect in South Water Cut (Fig. 1). For each sample, we recorded all macroalgae within a 10-cm radius from the base of *S. zonale* and measured the distance to the nearest individual of each species. We repeated this same process from 20 points on the open substratum that were at least 30 cm in distance from any individual of *S. zonale*, which had been chosen randomly along the same transect. To test whether the dominant algal taxa were distributed independently of *S. zonale*, we performed a contingency table analysis on the number of sample points [i.e., *Styopodium* ( $n=20$ ) or random open-substratum sites ( $n=20$ )] in which a particular macroalgal taxa was within a given distance of the sample point.

To test whether *Styopodium zonale* afforded neighboring macroalgae any protection from the grazing activity of herbivores, we haphazardly selected 20 additional individuals of *S. zonale*. Each specimen was marked by nailing a numbered tag nearby. Close-up photographs of all algae adjacent to each *S. zonale* were taken using a 1:4 extension tube with fixed framer on a 35-mm Nikonos camera equipped with an electronic flash and Kodachrome 64 transparency film. This yielded 60-cm<sup>2</sup> (6 × 10 cm) quadrats that were used to document the species and cover. A sub-group of 10 individuals of *S. zonale* were assigned randomly to the removal treatment, while the remaining 10 served as controls. In the former, the *S. zonale* were carefully dislodged from the substratum ensuring a minimal disturbance to the region. Care was taken to avoid the loss of other macroalgae and not attract the attention of herbivorous fishes (or wrasses) that might have further disturbed the remaining seaweeds. The removal quadrats were again photographed close-up. The photo-samples were used to document any algal losses due to the mechanical manipulations and also to compare to those taken subsequently. Observations were made by divers at haphazard intervals and confirmed that grazing fish ultimately were the agents of removal of the algal cover. After 48 h, all removal and control quadrats were re-photographed.

The color transparencies for all samples were "scored" in the laboratory to determine the percent cover of every species in each 60-cm<sup>2</sup> quadrat. Scoring was accomplished by projecting the transparencies onto a sheet of white bristol paper containing a pattern of randomly spaced dots. The average density was 2 dots per cm<sup>2</sup> and approximately 300 dots were scored per quadrat. The scoring was repeated for each macrophotograph following blind movement of the dot grid. Reproducibility was high with this method, seldom varying more than ±5% of the previous value for each of the dominant algae. The relative percent loss of algal cover (total and by taxa) was calculated from the differences between measurements before and after 48 h.

A one-way analysis of variance (ANOVA; Sokal and Rohlf 1969) of the initial percent cover of macroalgae in the removal and control quadrats was performed to test the null hypothesis that the two groups were not significantly different. A similar test concerning treatment effects on the loss of algal cover following *Styopodium* removal (before and after 48 h) also was conducted using a one-way ANOVA. In both of these analyses, assumptions of normality and homoscedasticity were tested (Sokal and Rohlf 1969) and met without transforming the percent cover data.

We used another experimental approach to test whether herbivory was reduced as a function of nearness to *Styopodium zonale* and, if so, to discern whether the effect was attributable to the structural aspect of the plant. To accomplish this, 10 representative models, constructed of thin (0.5 mil) brown polyethylene plastic, that were outlined, cut, and clumped together to closely mimic *S. zonale* (i.e., in terms of flexibility, size, density of branching, and color), and 10 freshly collected *S. zonale* specimens were fastened within the twists at the center of 20 1.5-m long, 3-stranded, thin (2 mm) nylon lines. The lines were firmly attached at each end to the solid calcareous substratum with nails. The entire randomly positioned array was left in place for 3 days prior to the comparative experiments so that fish could become acclimated to the associated minor habitat alterations.

At the start of each experimental period, 5-cm long basal segments of unbranched *Acanthophora spicifera* (Vahl) Børg., an alga that has been shown to be highly palatable to a variety of reef fishes (Littler et al. 1983 b; Hay 1984 b; Lewis 1985; Lewis and Wainwright 1985), was attached into the twists of each line approximately 1–2 cm from the base of each living or model *Styopodium*. Four additional segments were fastened on both sides at distances of 30 and 60 cm from the model or experimental plant. The *A. spicifera* was collected within 400 m of the study site, cut by razor blade 24 h prior to use, and maintained in mesh bags suspended from a boat dock.

Feeding on the *Acanthophora* segments by fishes was verified visually at haphazard intervals, and then losses were determined after 8 h by in situ measurements of length to the nearest 0.5 cm. All losses of the securely held thalli were attributable to fish bites and no artificial breakage or fragmentation was detected. The complete experiment was repeated three times between 29 March and 3 April 1984. Differences in the loss of segment length were analyzed using a one-way ANOVA. We

predicted a priori that any "non-structural" deterrent to fish herbivory imposed by *Styopodium* would have to be substantial in order to be separated in our comparison of real *Styopodium* versus the models. We suspected, based on much previous experimentation with fish herbivory throughout the Carrie Bow Cay reef system (e.g., Littler et al. 1983 b), that the structure of the models would itself deter some grazing activity. We have noticed initial caution by herbivorous fishes (acanthurids and scarids) when using artificial substrata during other in situ herbivory studies (see also Steneck 1983). Therefore, any significant reduction of herbivory in the living *Styopodium* treatment versus the models should be a conservative assessment of the actual effects of *Styopodium* as a refuge.

## Results

The study was designed to measure only the relative susceptibility of algal removal by natural mixed assemblages of grazing fishes and did not differentiate among fish species or determine specific preferences for any given species. The surgeonfish *Acanthurus bahianus* was by far the dominant (Table 1) in terms of numbers per 1.0 m<sup>2</sup> of substrata (0.169), whereas three parrotfishes [*Scarus taeniopterus* (0.090), *Sparisoma aurofrenatum* (0.072), *Sparisoma viride* (0.050)] ranked next in abundance. Damsel-fishes were low in species richness and numbers in this habitat.

The contingency table analysis (Table 2) revealed a highly significant association of macrophyte taxa directly related to the presence of *S. zonale* ( $P < 0.01$  at distances of 1, 2 and 5 cm). On a species by species basis, this association was confirmed ( $P < 0.01$  with Yate's correction; Sokal and Rohlf 1969) within the 2-cm distance for *Laurencia poitei*, *Dictyota* spp., *Amphiroa fragilissima*, *Cladophoropsis macromeres*, *Galaxaura cylindrica*, and the rhodophycean turf (predominantly an iridescent *Chondria*). Almost twice as many taxa occurred within 10 cm of *Styopodium* as within 10 cm of an equal

**Table 1.** Fish transect data within the *Styopodium* study site, transects were 9–12 m long by 2-m wide

Fish species	Number · m <sup>-2</sup> of substratum	
	Mean	± SE
<b>Surgeonfishes</b>		
<i>Acanthurus bahianus</i> Castelnau	0.169	±0.024
<i>Acanthurus coeruleus</i> Bloch and Schneider	0.024	±0.018
<i>Acanthurus chirurgus</i> Bloch	0.005	±0.005
Total	0.198	±0.038
<b>Parrotfishes<sup>a</sup></b>		
<i>Scarus taeniopterus</i> Desmarest	0.090	±0.055
<i>Sparisoma aurofrenatum</i> Valenciennes	0.077	±0.014
<i>Sparisoma viride</i> Bonnaterre	0.050	±0.022
<i>Scarus croicensis</i> Bloch	0.030	±0.025
<i>Sparisoma chrysopterus</i> Bloch and Schneider	0.019	±0.014
Total	0.266	±0.088

<sup>a</sup> *Scarus vetula* Bloch and Schneider and *Sparisoma rubripinne* Valenciennes were present in the study area but were not encountered in the transects

**Table 2.** Mean distance (cm) within a 10-cm radius from randomly selected *Styopodium zonale* individuals or randomly selected *Styopodium*-free point locations;  $\pm 1$  SE

Species	<i>Styopodium</i>	Random locations
Rhodophycean turf (mostly <i>Chondria</i> sp.)	1.2 $\pm$ 0.5*	4.8 $\pm$ 1.1
<i>Laurencia poitei</i> (Lamour.) Howe	2.3 $\pm$ 0.8*	6.9 $\pm$ 0.9
<i>Dictyota</i> spp.	2.6 $\pm$ 0.7*	5.4 $\pm$ 0.8
<i>Gelidiella acerosa</i> (Forssk.) Feldm. and Hamel	2.8 $\pm$ 0.8	2.9 $\pm$ 0.9
<i>Amphiroa fragilissima</i> (L.) Lamour.	3.2 $\pm$ 0.8*	8.0 $\pm$ 0.8
<i>Cladophoropsis macromeres</i> Taylor	4.7 $\pm$ 0.9*	8.2 $\pm$ 0.7
<i>Galaxaura cylindrica</i> (Ell. and Sol.) Lamour.	6.2 $\pm$ 1.0*	Absent
<i>Dictyosphaeria cavernosa</i> (Forssk.) Børg.	7.8 $\pm$ 0.8	7.4 $\pm$ 0.7
<i>Amphiroa tribulus</i> (Ell. and Sol.) Lamour.	8.6 $\pm$ 0.8	Absent
<i>Champia parvula</i> (C. Ag.) Harv.	8.7 $\pm$ 0.7	Absent
<i>Halimeda opuntia</i> (L.) Lamour.	8.7 $\pm$ 0.7	Absent
<i>Lobophora variegata</i> (Lamour.) Womersley	8.7 $\pm$ 0.7	Absent
<i>Neomeris annulata</i> Dickie	9.2 $\pm$ 0.6	9.8 $\pm$ 0.2
<i>Digenia simplex</i> (Wulf.) C. Ag.	9.2 $\pm$ 0.6	Absent
<i>Padina jamaicensis</i> (Collins) Papenfuss	9.3 $\pm$ 0.5	Absent
<i>Halimeda incrassata</i> (Ellis) Lamour.	9.5 $\pm$ 0.5	9.9 $\pm$ 0.1
<i>Anadyomene stellata</i> (Wulf.) C. Ag.	9.5 $\pm$ 0.5	Absent
<i>Botryocladia</i> sp.	9.5 $\pm$ 0.5	Absent
<i>Jania adherens</i> Lamour.	9.5 $\pm$ 0.5	9.6 $\pm$ 0.4
<i>Udotea cyathiformis</i> Dec.	9.5 $\pm$ 0.5	Absent
<i>Valonia macrophysa</i> Kütz.	9.6 $\pm$ 0.3	8.3 $\pm$ 0.7

\* Positive association with *S. zonale* at  $P = < 0.01$  (Yates correction)

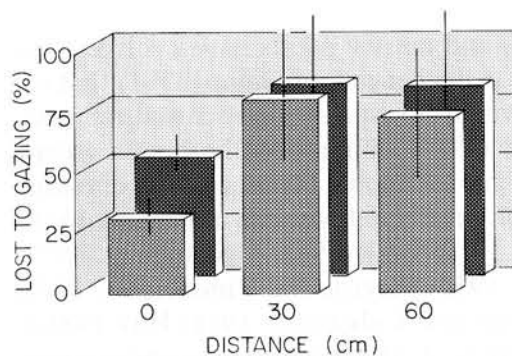
**Table 3.** Losses of major taxa (% cover relative to initial  $\pm 1$  SE) 48 h after the removal of *Styopodium*, compared with controls retaining *S. zonale*

Species	Mean relative cover losses	
	<i>Styopodium</i> removed	<i>Styopodium</i> present
<i>Amphiroa tribulus</i>	75.0* ( $\pm 25.0$ )	15.6 ( $\pm 9.7$ )
<i>Jania adherens</i>	66.5* ( $\pm 11.6$ )	0.0
<i>Laurencia poitei</i>	51.9* ( $\pm 8.9$ )	0.0
<i>Digenia simplex</i>	46.4* ( $\pm 13.6$ )	5.5 ( $\pm 5.5$ )
<i>Galaxaura cylindrica</i>	46.3 ( $\pm 13.3$ )	0.0
Turf	43.2* ( $\pm 8.5$ )	0.0
<i>Dictyota</i> spp.	26.1 ( $\pm 11.0$ )	0.0
<i>Amphiroa fragilissima</i>	23.3 ( $\pm 13.0$ )	0.0

\* Significant reduction at  $P < 0.05$  (ANOVA)

number of random *Styopodium*-free points (Table 2). There were no algal species negatively associated with *S. zonale*.

The association of several macroalgal taxa with *Styopodium zonale* affords them a fourfold greater survivorship per 48 h in the presence of grazing activity by fishes. In the experiment involving the assessment of macrophyte losses to herbivory following the removal of



**Fig. 2.** Percent losses (and standard error bars) for the palatable alga *Acanthophora spicifera* (% thallus length) as a function of distance from *Styopodium zonale* (light columns in front) and polyethylene models of *S. zonale* (dark columns in rear) following 8 h. The two columns at zero distance are significantly different ( $P < 0.05$ , ANOVA, SNK from each other and from all other values)

*S. zonale* (Table 3), comparisons of the initial (pre-manipulation) total absolute macroalgal cover (one-way ANOVA) indicated no differences ( $P = 0.86$ ) between the removal ( $10.7 \pm 2.2\%$ ,  $X \pm SE$ ) and control ( $10.2 \pm 2.4\%$ ) treatments. This similarity of treatments was paralleled in the cover of the individual macroalgal dominants in the region ( $0.07 < P < 0.48$  for *Dictyota* spp., *Amphiroa tribulus*, *Galaxaura cylindrica*, *Amphiroa fragilissima*, *Digenia simplex*, and the rhodophycean turf).

Following the 48-hr experimental period, the removal treatment exhibited significantly greater ( $P < 0.05$ , one-way ANOVA) loss of total macroalgal cover ( $48.1 \pm 9.7\%$ , relative to initial values) than the control group in which *Styopodium zonale* had been left intact ( $12.8 \pm 8.1\%$  loss of relative cover). Significant losses ( $P < 0.05$ ) appeared in five of the 13 species encountered (*Amphiroa tribulus*, *Laurencia poitei*, *Digenia simplex*, *Jania adherens*, and the rhodophycean turf). Three other taxa showed losses exceeding 23% cover relative to pre-removal values (Table 3), contrasted with no losses in the presence of *S. zonale*.

The second grazing experiment (Fig. 2) corroborated the results of the first (Table 3) and further suggested that the reduced herbivory by fishes on macroalgae associated with *Styopodium zonale* is not solely a consequence of its structural aspect. Losses in the *Acanthophora* assay (Fig. 2) were significantly greater for the four thalli spatially removed (30 and 60 cm on opposite sides) from a real or model *Styopodium* than when located within 1–2 cm (ANOVA and Student-Newman-Keuls multiple classification test,  $P < 0.05$ ), suggesting a structural effect. No detectable losses of either *S. zonale* or the models occurred over the duration of the experiments. However, as predicted, the losses of *Acanthophora* adjacent to the actual *Styopodium* plants were significantly less ( $P < 0.05$ , Fig. 2) than the losses next to the models.

## Discussion

Although tropical reefs are heavily grazed (Bakus 1969), herbivory is not uniform (Hay 1981 a, 1984 b; Lewis and

Wainwright 1985) and marine plants have evolved a diversity of escapes (Lubchenco and Gaines 1981) that result in a higher overall floristic abundance and richness. Littler and Littler (1984) summarized herbivore escape mechanisms for algae as follows: (1) occupation of refuge habitats that are physically unfavorable or unavailable to herbivores (Dahl 1972; Earle 1972; Ogden et al. 1973; Adey and Vassar 1975; Parrish and Zimmerman 1977; Brock 1979; Menge and Lubchenco 1981; Hay 1981 a, 1981 b, 1984 b; Hay et al. 1983), (2) cryptic appearances or mimicry (Kraft 1972; Littler et al. 1983 b), (3) unpredictable spatial and temporal distributions (Littler and Littler 1980; Lubchenco and Cubit 1980), (4) rapid growth involving the replacement of vegetative and reproductive tissues while simultaneously satiating the appetites of grazers (Littler and Littler 1980; Borowitzka 1981), (5), close association with unpalatable organisms, (6) nearness to carnivorous predator territories (Randall 1965; Ogden et al. 1973; Hay 1981 a; Hay et al. 1983), (7) location close to highly territorial animals (Brawley and Adey 1977; Montgomery 1980; Hixon and Brostoff 1982; Sammarco 1983), and (8) allocation of materials and energy toward herbivore defenses (e.g., Littler et al. 1983 b; Paul and Fenical 1983; Gaines 1985). The present study provides the first experimental documentation of mechanism (5) above for naturally co-occurring marine algae. Repellent plants such as *Styopodium zonale*, in the vicinity of palatable plants (Table 1 and Fig. 2), cause herbivorous fishes to reject or fail to locate normally palatable prey. This provides a refuge and increases survivorship of otherwise vulnerable macrophytes.

The reciprocal benefit of proximal palatable algae to a repellent plant is difficult to test over ecological time and, consequently, remains speculative. Palatable plants in the vicinity of unpalatable *Styopodium* individuals may dilute the overall herbivore impact on *S. zonale* by drawing off the highly mobile grazing fishes. The benefit to an organism such as *S. zonale* could be to reduce the probability of selection for specialized detoxification adaptations on the part of any single grazer. As stated by Atsatt and O'Dowd (1976), the concept of such hypothetical "gene conservation guilds" adds diversionary and delaying tactics to the adaptation/counter-adaptation view of plant-herbivore coevolution. Therefore, the evolutionary usefulness of deterrent chemicals such as styopodiol could be extended by mechanisms that disrupt genetic specialization by mobile herbivores. *Styopodium zonale* conceivably could retain its characteristic inedibility, not because its "chemical arsenal" represents an evolutionary impasse, but because it lives in an environment that provides acceptable alternative prey options of variable quality. Such variability is exemplified by the associated calcified red alga *Amphiroa tribulus*, the palatable rhodophycean turf species (Montgomery et al. 1980), and algal forms such as *Laurencia* and *Digenia* that also contain some degree of toxic chemistry (Norris and Fenical 1982). If no such alternatives were available, then herbivores would be presented with little or no feeding

choice. Therefore, the defensive nature of this association results from the condition that an individual alga's susceptibility to herbivory depends not only on its own inherent properties, but on the morphological, chemical, distributional, and abundance features of other prey plants as well as non-prey plants. In addition, the inhibition of a coevolutionary relationship between a potential prey plant and grazer may well be influenced by the presence of such an associational unit. This group attribute could not be inferred from a study of the interaction between each macrophyte species and its grazers alone.

We hasten to point out that the association documented here can probably best be interpreted as facultative and not obligate or coevolved (see Vermeij 1983). *Styopodium zonale* ranks among the most toxic of marine plants (Gerwick and Fenical 1981) and, although widely studied, has only one probable specialist herbivore (the sea hare *Petalifera petalifera* Ranger) that may have overcome its chemical toxicity. In the case of other toxic algae such as *Caulerpa* (Jensen 1980) or *Laurencia* (Norris and Fenical 1982), numerous specialist opisthobranch molluscs appear to have evolved detoxification mechanisms on a broader scale. Lack of broad-ranging motility (e.g., in the case of relatively immobile molluscs) would seem to intensify selection for specialization or even coevolution (Steneck 1982) by forcing physiological detoxification adaptations.

Conversely, selection favoring specialization in mobile animals such as herbivorous fishes is probably decreased by the relatively high exposure frequency to prey species with varying levels of palatability (Littler et al. 1983 b; Hay 1984 b). The above mechanism of conserving palatable as well as herbivore resistant plant species takes advantage of herbivore behavioral sensitivity to variations in prey quality (Atsatt and O'Dowd 1976). As mentioned (Littler and Littler 1984), a diversity of plant prey of variable quality is maintained on reefs through a broad spectrum of morphological, chemical, nutritional, temporal and spatial mechanisms. Such diversity of available prey could, hypothetically (Steneck 1982), explain the relative lack of highly specialized fish-plant relationships (Randall 1967; Ogden and Lobel 1978) on tropical reef systems. Sea urchins, because of their drift feeding option, tend to have a relatively broad range of plant diets (Lawrence 1975), while still showing some degree of preference (Littler et al. 1983 b; Hay 1984 a).

Concerning the positive interactive evidence presented in Table 2, one open-ended alternative hypothesis to associational defenses remains unfalsified by our data. It is conceivable that *Styopodium zonale* and its associated flora are simultaneously responding to some physical microhabitat feature and that the areas surrounding these plants are not suitable for their growth. However, the removal experiments (Table 3), coupled with the subsequent direct observations of fish grazing, argue strongly against this unlikely possibility.

The system studied here, where an abundant and well-defended plant provides a significant refuge habitat

for at least five relatively edible macroalgae, facilitates the survival of certain taxa in the reef system and concomitantly enhances the within-habitat diversity. Connell and Slatyer (1977) found little evidence for facilitative succession in their review and, although we can draw no conclusions, our data indicate that this mechanism may be more common than suspected. Facilitation in regard to the settlement of seeds of the seagrass *Phyllospadix*, which is enhanced by the presence of turf algae, similarly has been demonstrated (Turner 1985), but the mechanism is strictly physical. Our findings also suggests an interaction counter to the process of competitive exclusion, since the single predominant organism has a positive rather than negative overall effect on the abundances of other species that utilize the same general resources (e.g., light, space, nutrients). Positive interactions such as documented here may be quite widespread, particularly on tropical reefs. Recognition of plant (and animal) defense associations and their role in ecological succession, as well as in other aspects of community ecology, should prove to be a fertile area for future research.

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## References

- Adey WH, Vassar JM (1975) Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). *Phycologia* 14:55-69
- Atsatt PR, O'Dowd DJ (1976) Plant defense guilds. *Science* 193:24-29
- Bakus GJ (1969) Energetics and feeding in shallow marine waters. *Int Rev Gen Exp Zool* 4:275-369
- Black R (1976) The effects of grazing by the limpet, *Acmaea insessa*, on the kelp, *Egregia laevigata*, in the intertidal zone. *Ecology* 57:265-277
- Borowitzka MA (1981) Algae and grazing in coral reef ecosystems. *Endeavour* 5:99-106
- Brawley SH, Adey WH (1977) Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. *Environ Biol Fishes* 2:45-51
- Brawley SH, Adey WH (1981) The effect of micrograzers on algal community structure in a coral reef microcosm. *Mar Biol* 61:167-177
- Brock RE (1979) An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Mar Biol* 51:381-388
- Carpenter RC (1985) Sea urchin mass-mortality: effects on reef algal abundance, species composition, and metabolism and other coral reef herbivores. *Proc 5th Int Coral Reef Symp* 2:66
- Choat JH (1982) Fish feeding and the structure of benthic communities in temperate waters. *Annu Rev Ecol Syst* 13:423-449
- Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol Monogr* 53:209-233
- Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am Nat* 111:1119-1144
- Dahl AL (1972) Ecology and community structure of some tropical reef algae in Samoa. In: Nisizawa K (ed) *Proceedings of the 7th International Seaweed Symposium*. University of Tokyo Press, Tokyo, pp 36-39
- Dethier MN, Duggins DO (1984) An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. *Am Nat* 124:205-219
- Denno RF, McClure MS (eds) (1983) *Variable plants and herbivores in natural and managed systems*. Academic, New York
- Duggins DO (1980) Kelp beds and sea otters: an experimental approach. *Ecology* 61:447-453
- Earle SA (1972) The influence of herbivores on the marine plants of Great Lameshur Bay. *Los Angeles County Nat Hist Mus Sci Bull* 14:17-44
- Fenical W (1980) Distributional and taxonomic features of toxin-producing marine algae. In: Abbott IA, Foster MS, Eklund LF (eds) *Pacific seaweed aquaculture*. California Sea Grant College Program, Institute of Marine Resources, University of California, La Jolla, Calif, pp 144-151
- Fox LR (1981) Defense and dynamics in plant-herbivore systems. *Am Zool* 21:853-864
- Futuyma DJ (1983) Evolutionary interactions among herbivorous insects and plants. In: Futuyma DJ, Slatkin M (eds) *Coevolution*. Sinauer, Sunderland, Mass, pp 207-231
- Gaines SD (1985) Herbivory and between-habitat diversity: the differential effectiveness of defenses in a marine plant. *Ecology* 66:473-485
- Gaines SD, Lubchenco J (1982) A unified approach to marine plant-herbivore interactions. II. Biogeography. *Annu Rev Ecol Syst* 13:111-138
- Gallagher ED, Jumars PA, Trueblood DD (1983) Facilitation of soft-bottom benthic succession by tube builders. *Ecology* 64:1200-1216
- Geiselman JA, McConnell OJ (1981) Polyphenols in brown algae *Fucus vesiculosus* and *Ascophyllum nodosum*: chemical defenses against the marine herbivorous snail, *Littorina littorea*. *J Chem Ecol* 7:1115-1133
- Gerwick WH (1981) The natural products chemistry of the Dictyotaceae. PhD dissertation, University of California, San Diego, Calif
- Gerwick WH, Fenical W (1981) Ichthyotoxic and cytotoxic metabolites of the brown alga, *Styopodium zonale*. *J Org Chem* 46:22-27
- Gerwick WH, Fenical W, Fritsch N, Clardy J (1979) Stypotriol and stypoldione; ichthyotoxins of mixed biogenesis from the marine alga *Styopodium zonale*. *Tetrahedron Lett* 1979:145-148
- Harper JL, Clatworthy JN, McNaughton IH, Sagar GR (1961) The evolution and ecology of closely related species living in the same area. *Evolution* 15:209-227
- Harris LG, Ebeling AW, Laur DR, Rowley RJ (1984) Community recovery after storm damage: a case of facilitation in primary succession. *Science* 224:1336-1338
- Hay ME (1981 a) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aqua Bot* 11:97-109
- Hay ME (1981 b) Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *Am Nat* 118:520-540
- Hay ME (1984 a) Patterns of fish and urchin grazing on Caribbean barrier reefs: are previous results typical? *Ecology* 65:446-454
- Hay ME (1984 b) Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia* 64:396-407
- Hay ME (1985) Spatial patterns of herbivore impact and their importance in maintaining algal species richness. *Proc 5th Int Coral Reef Symp* 4:29-34
- Hay ME, Taylor PR (1985) Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia* 65:591-598
- Hay ME, Colburn T, Downing D (1983) Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia* 58:299-308
- Hedin PA (ed) (1983) *Plant resistance to insects*. American Chemical Society Symposium Series 208, American Chemical Society, Washington, DC
- Hixon MA, Brostoff WN (1982) Differential fish grazing and benthic community structure on Hawaiian reefs. In: Cailliet GM, Simenstad CA (eds) *Fish food habit studies*. *Proceedings of the 3rd Pacific*

- Workshop. Washington Sea Grant Program, University of Washington, Seattle, Wash, pp 249–257
- Inouye DW (1982) The consequences of herbivory: a mixed blessing for *Jurinea mollis* (Asteraceae). *Oikos* 39:269–272
- Jensen KR (1980) A review of sacoglossan diets, with comparative notes on radular and buccal anatomy. *Malacol Rev* 13:55–77
- Kraft GT (1972) Preliminary studies of Philippine *Eucheuma* species (Rhodophyta). Part 1, taxonomy and ecology of *Eucheuma arnoldii* Weber-van Bosse. *Pac Sci* 26:318–334
- Kroh GC, Beaver DL (1978) Insect response to mixture and monoculture patches of Michigan old-field annual herbs. *Oecologia* 31:269–275
- Lawrence JM (1975) On the relationships between marine plants and sea urchins. *Oceanogr Mar Biol Annu Rev* 13:213–286
- Lessios HA, Robertson DR, Cubitt JD (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* 226:335–337
- Levin DA (1973) The role of trichomes in plant defense. *Q Rev Biol* 48:3–15
- Levings SC, Garrity SD (1983) Diel and tidal movement of two co-occurring neritid snails; differences in grazing patterns on a tropical rocky shore. *J Exp Mar Biol Ecol* 67:261–278
- Lewis SM (1985) Herbivory on coral reefs: algal susceptibility to herbivorous fishes. *Oecologia* 65:370–375
- Lewis SM, Wainwright P (1985) Herbivore abundance and grazing intensity on a Caribbean coral reef. *J Exp Mar Biol Ecol* 87:215–228
- Littler MM, Littler DS (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am Nat* 116:25–44
- Littler MM, Littler DS (1984) Models of tropical reef biogenesis: the contribution of macroalgae. In: Round FE, Chapman DJ (eds) *Progress in phycological research*, vol 3. Biopress, Bristol, England, pp 232–364
- Littler MM, Littler DS, Taylor PR (1983 a) Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J Phycol* 19:229–237
- Littler MM, Taylor PR, Littler DS (1983 b) Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2:111–118
- Lubchenco J (1983) *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64:1116–1123
- Lubchenco J, Cubitt J (1980) Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61:676–687
- Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annu Rev Ecol Syst* 12:405–437
- Lubchenco J, Menge BA (1978) Community development and persistence in a low rocky intertidal zone. *Ecol Monogr* 48:67–94
- McConnell OJ, Hughes PA, Targett NM, Daley J (1982) Effects of secondary metabolites from marine algae on feeding by the sea urchin, *Lytechinus variegatus*. *J Chem Ecol* 8:1437–1453
- Menge BA, Lubchenco J (1981) Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol Monogr* 51:429–450
- Montgomery WL (1980) Comparative feeding ecology of two herbivorous damselfishes (Pomacentridae: Teleostei) from the Gulf of California, Mexico. *J Exp Biol Ecol* 47:9–24
- Montgomery WL, Gerrodette T, Marshall LD (1980) Effects of grazing by the yellowtail surgeonfish, *Prionurus punctatus*, on algal communities in the Gulf of California, Mexico. *Bull Mar Sci* 30:901–908
- Morris RF (ed) (1963) The dynamics of epidemic spruce budworm populations, no 31. *Memoirs of the Entomological Society of Canada*, Ottawa
- Norris JN, Fenical W (1982) Chemical defense in tropical marine algae. In: Rützler K, Macintyre IG (eds) *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities*. Smithsonian Contrib Mar Sci 12:417–431
- Ogden JC, Lobel PS (1978) The role of herbivorous fishes and urchins in coral reef communities. *Environ Biol Fish* 3:49–63
- Ogden JC, Brown RA, Salesky N (1973) Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science* 182:715–717
- Osman RW, Haugsness JA (1981) Mutualism among sessile invertebrates: a mediator of competition and predation. *Science* 211:846–848
- Parrish JD, Zimmerman RJ (1977) Utilization by fishes of space and food resources on an offshore Puerto Rican coral reef and its surroundings. *Proc 3rd Int Coral Reef Symp* 1:297–303
- Paul VJ, Fenical W (1983) Isolation of halimedatrial: chemical defense adaptation in the calcareous reef-building alga *Halimeda*. *Science* 221:747–749
- Phillips JD, Pfeiffer RK (1960) An example of the relation between palatability of pastures and selective buttercup control. In: *Proceedings of the 4th British Weed Control Conference*. Society of Chemical Industry, London, pp 15–16
- Pimentel D (1961) Species diversity and insect population outbreaks. *Ann Entomol Soc Am* 54:76–86
- Randall JE (1961) Overgrazing of algae by herbivorous marine fishes. *Ecology* 42:812
- Randall JE (1965) Grazing effect on seagrasses by herbivorous reef fishes in the West Indies. *Ecology* 46:255–260
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Stud Trop Oceanogr Miami* 5:665–847
- Rausher MD (1981) The effect of native vegetation on the susceptibility of *Aristolochia reticulata* (Aristolochiaceae) to herbivore attack. *Ecology* 62:1187–1195
- Rhoades DF (1979) Evolution of plant chemical defense against herbivores. In: Rosenthal GA, Janzen DH (eds) *Herbivores: their interaction with secondary plant metabolites*. Academic, New York, pp 3–54
- Risch SJ (1979) A comparison, by sweep sampling, of the insect fauna from corn and sweet potato monocultures and dicultures in Costa Rica. *Oecologia* 42:195–212
- Robinson T (1980) The organic constituents of higher plants: their chemistry and interrelationships. Burgess, Minneapolis, Minn
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). *Ecol Monogr* 43:95–124
- Root RB (1974) Some consequences of ecosystem texture. In: Levin SA (ed) *Ecosystem analysis and prediction*. Proceedings of a Conference on Ecosystems, Alta, Utah, pp 83–97
- Rosenthal GA, Janzen DH (1979) *Herbivores: their interaction with secondary plant metabolites*. Academic, New York
- Rützler K, Macintyre IG (eds) (1982) *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I. Structure and communities*. Smithsonian Contrib Mar Sci 12:1–539
- Sammarco PW (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. *Mar Ecol Prog Ser* 13:1–14
- Sammarco PW, Levinton JS, Ogden JC (1974) Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. *J Mar Res* 32:47–53
- Shacklock PF, Doyle RW (1983) Control of epiphytes in seaweed cultures using grazers. *Aquaculture* 31:141–151
- Simberloff D, Brown BJ, Lowrie S (1978) Isopod and insect root borers may benefit Florida mangroves. *Science* 201:630–632
- Smith JG (1969) Some effects of crop background on populations of aphids and their natural enemies on Brussels sprouts. *Ann Appl Biol* 63:326–329
- Sokal RR, Rohlf FJ (1969) *Biometry*. Freeman, San Francisco, Calif
- Sousa WP, Schroeter SC, Gaines SD (1981) Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia* 48:297–307
- Steinberg PD (1984) Algal chemical defense against herbivores: allocation of phenolic compounds in the kelp *Alaria marginata*. *Science* 223:405–407
- Steinberg PD (1985) Feeding preferences of *Tegula funebris* and chemical defenses in marine brown algae. *Ecol Monogr* 55:333–349



- Steneck RS (1982) A limpet-coralline alga association: adaptations and defenses between a selective herbivore and its prey. *Ecology* 63:507–522
- Steneck RS (1983) Quantifying herbivory on coral reefs: just scratching the surface or still biting off more than we can chew. In: Reaka ML (ed) *The ecology of deep and shallow coral reefs*. NOAA's Undersea Research Program, vol 1, no 1, National Oceanic and Atmospheric Administration, US Department of Commerce, Washington, DC, pp 103–111
- Stephenson W, Searles RB (1960) Experimental studies on the ecology of intertidal environments at Heron Island. *Aust J Mar Freshwater Res* 11:241–267
- Stimson J (1973) The role of the territory in the ecology of the intertidal limpet *Lottia gigantea* (Gray). *Ecology* 54:1020–1030
- Suchanek TH (1978) The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. *J Exp Mar Biol Ecol* 31:105–120
- Sutherland JP (1974) Multiple stable points in natural communities. *Am Nat* 108:859–873
- Tahvanainen JO, Root RB (1972) The influence of vegetational diversity on the population ecology of specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10:321–346
- Targett NM, McConnell OJ (1982) Detection of secondary metabolites in marine macrophytes using the marsh periwinkle, *Littorina irrorata* Sya, as an indicator organism. *J Chem Ecol* 8:115–124
- Turner T (1985) Stability of rocky intertidal surfgrass beds: persistence, preemption, and recovery. *Ecology* 66:83–92
- Vermeij GJ (1978) *Biogeography and adaptation*. Harvard University Press, Cambridge, England
- Vermeij GJ (1983) Intimate associations and coevolution in the sea. In: Futuyma DJ, Slatkin M (eds) *Coevolution*. Sinauer, Sunderland, Mass, pp 311–327
- Woodin SA (1978) Refuges, disturbance, and community structure: a marine soft-bottom example. *Ecology* 59:274–284