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Animal–plant defense associations: effects on the distribution and abundance of tropical reef macrophytes*

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Abstract: This study, conducted at Carrie Bow Cay, Belize during 2–24 April 1985, documents a refuge from predation afforded a group of marine algae by the purple sea fan, *Gorgonia ventalina* Linnaeus, and the fire coral, *Millepora alcicornis* Lamarck. There was a highly significant ($P < 0.05$) association of *Galaxaura cylindrica* (Ell. & Sol.) Lamour., *Dictyota* spp., *Laurencia poitei* (Lamour.) Howe, *Lobophora variegata* (Lamour.) Womersley, *Chondria* sp., and *Amphiroa rigida* Lamour. within 2 cm of the base of *Gorgonia ventalina*. Species positively associated (within 2 cm) with *Millepora alcicornis* were *Galaxaura cylindrica*, *Dictyota* spp., *Laurencia poitei*, and *Amphiroa fragilissima* (L.) Lamour. Only the diminutive turf-form of *Digenia simplex* (Wulf.) C. Ag. was negatively associated with the sessile animals within the 5-cm zones ($P < 0.01$). However, we observed that the upright frondose form of *D. simplex*, on the average, was restricted to within 6.0 cm of either *Gorgonia ventalina* or *Millepora alcicornis*. Almost twice as many taxa occurred within 9 cm of *Gorgonia ventalina* and *Millepora alcicornis* as within 9 cm of an equal number of random points lacking *Gorgonia* and *Millepora alcicornis*, and seven species were found in samples only near (within 10 cm) the two invertebrates. The association of 11 macroalgal taxa with either *Gorgonia ventalina* or *Millepora alcicornis* resulted in considerably greater survivorship over 66 h in the presence of grazing activity by fishes (mainly Acanthuridae and Scaridae). Also, only half as much of the palatable alga *Acanthophora spicifera* (Vahl) Boerg. was eaten when experimentally placed near (5 cm) either *Gorgonia ventalina* or *Millepora alcicornis* than when located 30 cm away. About half of the losses occurred within the first 1.5 h and were entirely due to herbivorous fishes, as evidenced by direct observations and grazing scars. The interrelationships studied here, where abundant sessile animals provide a significant refuge from predation for at least 11 relatively edible macroalgae, clearly augment the abundances of certain taxa in microhabitats throughout the reef system. These findings document a type of interaction among sessile organisms that may be important in the development and organization of communities in predation-mediated systems.

Key words: Herbivory; Refuge; Reef; Algae; Defense associations

INTRODUCTION

Although herbivory on tropical reefs is not uniform either temporally or spatially (Hay, 1981a,b, 1984; Lewis & Wainwright, 1985), it is particularly important in the organization and development of macroalgal communities (Bakus, 1969). In

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response, macroalgae have evolved a diverse array of mechanisms that they employ for defense against, or escape from, grazers and, consequently, show a broad range of susceptibility to herbivory. Intrinsic organismic properties exist (e.g., Borowitzka, 1981; Paul & Fenical, 1983; Littler & Littler, 1984) that ameliorate the damage caused by herbivores. Similarly, temporal refuges from herbivory (e.g., Lubchenco & Cubit, 1980) result from the ability of algal prey to displace their occurrences from those of their predators. Physical abiotic features of environmental heterogeneity can limit the access of grazers (e.g., Dahl, 1972; Ogden *et al.*, 1973; Menge & Lubchenco, 1981; Hay, 1981a; Taylor *et al.*, 1986) to their prey. Biologically generated aspects of heterogeneity that are superimposed on the physical habitat have been noted (e.g., Randall, 1965; Ogden *et al.*, 1973; Hay *et al.*, 1983; Hixon & Brostoff, 1983; Littler *et al.*, 1986; Hay, in press) to deter grazing and can be regarded as "defense associations". Defense associations are defined as co-occurring groups of organisms, where some members show reduced susceptibility to predators due to the presence of one or more of the other members. While refuges from grazers related to such defense associations have not received much study in the marine environment, the concept of defensive associations against herbivores has long been noted by terrestrial ecologists and agronomists (e.g., see reviews by Harper *et al.*, 1961; Root, 1974; Atsatt & O'Dowd, 1976; Robinson, 1980; Rausher, 1981).

In this paper, we investigate the role of sessile animal–plant defense associations on a portion of the Belizean barrier reef. We have studied this system extensively since March 1984, during which time we observed algal distributional patterns correlated with the presence of large conspicuous plants such as *Stypopodium zonale* (Littler *et al.*, 1986) and two sessile animals, the purple sea fan *Gorgonia ventalina* and the stinging fire coral *Millepora alcicornis*, that dominate the biomass in some habitats (see Muzik, 1982). These observations led us to examine the general concept that some palatable marine plants show a reduced probability of being discovered or eaten when they occur in close physical proximity to large, sessile, predation-resistant animals. The following questions were addressed.

(1) On a spatial basis, are palatable marine plants frequently and predictably associated with predator-resistant sessile animal species?

(2) Is the survivorship of certain marine algae improved in the vicinity of conspicuous, predation-resistant animals? If so, is this functionally dependent on herbivorous fishes?

(3) Do defense associations augment algal abundances within microhabitats?

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

STUDY SITE

The research was carried out near the Smithsonian Institution's field station on Carrie Bow Cay, Belize (16°48′N: 88°05′W) during 2–24 April 1985. The study site (Fig. 1) was located within the upper fore-reef zone (see Ruetzler & Macintyre, 1982 for

details) near the mouth of South Water Cut (the channel between South Water Cay and Carrie Bow Cay) ≈ 500 m north of Carrie Bow Cay. The community composition and zonation of the Carrie Bow Cay portion of the Belizean barrier reef, despite some
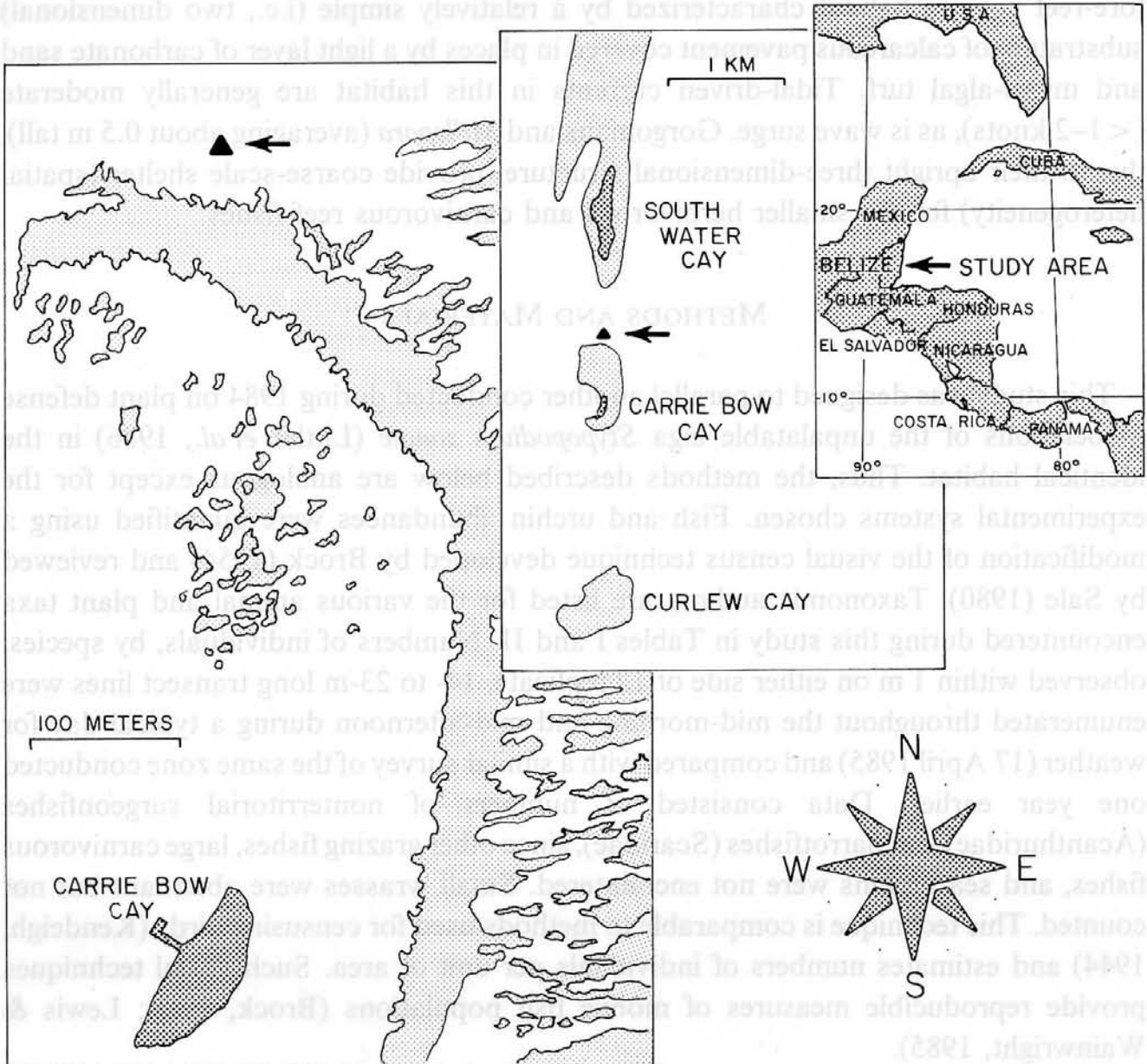

Fig. 1. Location of the study site (dark triangle) on the Belize barrier fore-reef.

variation (Burke, 1982), is representative of the entire reef platform (Ruetzler & Macintyre, 1982) and is similar in biological–geological zonation to the barrier reefs of the north coast of Jamaica (Goreau, 1959; Goreau & Land, 1974). The Carrie Bow Cay reef system possesses a rich and well-known biota (Ruetzler & Macintyre, 1982) well removed from human influences.

We have been conducting research on reefs near Carrie Bow Cay since 1980, and the available evidence (Hay, 1981a; Littler et al., 1983a, 1983b, 1986; Lewis & Wainwright, 1985), in all habitats accessible to grazing fishes, including the site studied here, has implicated herbivory by fishes (primarily Acanthuridae and Scaridae) as a major factor

controlling macroalgal distribution and abundance patterns. This condition prevailed even before the mass mortality of *Diadema antillarum* throughout the Caribbean (Lessios *et al.*, 1984).

This study was done over a depth range of 4–6 m in a 1-ha portion of the upper fore-reef zone, a habitat characterized by a relatively simple (i.e., two dimensional) substratum of calcareous pavement covered in places by a light layer of carbonate sand and micro-algal turf. Tidal-driven currents in this habitat are generally moderate (< 1–2 knots), as is wave surge. Gorgonians and *Millepora* (averaging about 0.5 m tall), due to their upright three-dimensional structure, provide coarse-scale shelter (spatial heterogeneity) for the smaller herbivorous and carnivorous reef fishes.

METHODS AND MATERIALS

This study was designed to parallel another conducted during 1984 on plant defense associations of the unpalatable alga *Stypopodium zonale* (Littler *et al.*, 1986) in the identical habitat. Thus, the methods described below are analogous except for the experimental systems chosen. Fish and urchin abundances were quantified using a modification of the visual census technique developed by Brock (1954) and reviewed by Sale (1980). Taxonomic authors are listed for the various animal and plant taxa encountered during this study in Tables I and II. Numbers of individuals, by species, observed within 1 m on either side of 12 replicate, 14- to 23-m long transect lines were enumerated throughout the mid-morning and mid-afternoon during a typical day for weather (17 April 1985) and compared with a similar survey of the same zone conducted one year earlier. Data consisted of numbers of nonterritorial surgeonfishes (Acanthuridae) and parrotfishes (Scaridae), since other grazing fishes, large carnivorous fishes, and sea urchins were not encountered. Small wrasses were abundant but not counted. This technique is comparable to methods used for censusing birds (Kendeigh, 1944) and estimates numbers of individuals per unit of area. Such visual techniques provide reproducible measures of mobile fish populations (Brock, 1982; Lewis & Wainwright, 1985).

To assess whether or not macroalgae were positively associated with *Gorgonia ventalina* Linnaeus or *Millepora alcicornis* Lamarck, we chose 30 individual colonies (about 0.5 m tall) of each animal nearest the 30 randomly chosen meter marks along a 50-m long transect. The *M. alcicornis* we studied were entirely encrusting dead *Pseudopterogorgia*. For each specimen, we recorded all macroalgae within a 10-cm radius from the base of the colony and measured the distance to the nearest individual of each associated species. We repeated this same process from 30 randomly selected locations that were at least 30 cm in distance from any individual of *Gorgonia ventalina* or *Millepora alcicornis* along the same transect. To examine whether the dominant algae were distributed independently of either animal species, we performed a contingency-table analysis on the number of sample points in which a particular species was within a given distance of the sample point.

There are several hypotheses that could explain increased survivorship of macroalgae associated with these large sessile animals.

(1) There might be some physical/chemical microhabitat factor that is produced by the animals and required by certain algae.

(2) There may be enhanced numbers of carnivorous predators associated with the large sessile animals, thereby reducing exposure of macroalgae to herbivores.

(3) Macroalgal herbivores may require large monospecific stands of their plant prey in order to locate and exploit them efficiently, and the presence of sessile animals may dilute the concentration of prey.

(4) The presence of chemical or physical predator defenses in the animals could result in omnivore/herbivore avoidance or a physical feeding barrier, thereby providing a refuge for macroalgae.

To test whether *Gorgonia ventalina* or *Millepora alcicornis* afford neighboring macroalgae protection from fish grazing, we haphazardly selected 30 additional individuals of each. All colonies were identified by tying a numbered tag to a branch of the animal. Close-up photographs of marked plots adjacent to each *Gorgonia ventalina* or *Millepora alcicornis* were taken using an extension tube with fixed framer on a 35-mm Nikonos camera equipped with an electronic flash and Kodachrome 25 transparency film. This yielded 108-cm² quadrats (9×12 cm) that were used to document the species and amount of cover present. A sub-group of 15 individual colonies of each animal was assigned randomly to a removal treatment, while the remaining 15 served as controls. In the former, *Gorgonia ventalina* and *Millepora alcicornis* were carefully dislodged from the substratum with minimal disturbance to the surrounding biota. Care was taken to avoid the loss of macroalgae and to minimize contact with the substratum, which could attract the attention of herbivorous fishes (or wrasses) that might have further disturbed the surrounding seaweeds. The removal quadrats were again photographed. The second set of 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 various intervals throughout the experiment and confirmed that fishes were the only agents removing algal cover. After 66 h, all removal and control quadrats were re-photographed.

The photosamples were assessed in the laboratory to determine the percent cover of each alga in the 108-cm² quadrats. Scoring was accomplished by projecting the transparencies onto a sheet of white Bristol paper containing a pattern of randomly spaced dots (average 2 dots per cm²). The scoring was repeated for each photograph following blind movement of the dot grid, and ≈ 1000 dots were scored per quadrat. Reproducibility was high with this method, seldom varying more than ± 5% of the previous value for each of the dominant algae. The relative percent cover loss (total and by taxa) was calculated from the differences before and after 66 h.

A one-tailed *t*-test (Sokal & Rohlf, 1969) of the initial percent cover of macroalgae in the removal and control quadrats was performed to test the hypothesis that the removal would result in significant losses of associated algae. Tests of treatment effects

on the predicted loss of algal cover (percent change) following the removal of *Gorgonia ventalina* and *Millepora alcicornis* (before and after 66 h) also were conducted using the one-tailed *t*-test (since there was an a priori expectation in the direction of deviations) on species and total algal cover. In both analyses, assumptions of normality and homoscedasticity were tested and met without transforming the percent cover data.

As a further measure of the effectiveness of *Gorgonia ventalina* and *Millepora alcicornis* in deterring herbivory, *Acanthophora spicifera*, an alga that has been shown to be highly palatable to a variety of reef fishes (Littler *et al.*, 1983b; Hay, 1984; Lewis, 1985; Lewis & Wainwright, 1985), was used in a bioassay experiment. At the start of each of two separate periods, 7-cm long basal segments of unbranched *A. spicifera* were attached by rubber bands to ≈ 10-cm long fragments of coral rubble that were placed ≈ 5 cm from the base of 35 living *Gorgonia ventalina* or *Millepora alcicornis*. Thirty-five replicate *Acanthophora spicifera* segments were also placed at distances of 30 cm from each animal colony under examination. 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 various intervals, and losses were determined after 20.5 h on 21 April 1985 and 1.5 h on 22 April 1985 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 artifactual breakage or fragmentation was detected. Differences in the loss of segment length were analyzed using ANOVA (Sokal & Rohlf, 1969).

RESULTS

A total of two surgeonfish and seven parrotfish species were enumerated (Table I) during the fish surveys. The surgeonfish *Acanthurus bahianus* was the numerical dominant ($0.155 \cdot m^{-2}$ of substratum), whereas three parrotfishes (*Sparisoma aurofrenatum* ($0.077 \cdot m^{-2}$), *S. rubripinne* ($0.052 \cdot m^{-2}$), *Scarus croicensis* ($0.032 \cdot m^{-2}$)) ranked next in abundance. Damselfishes were too low in numbers of individuals and species in this habitat to occur in our counts, possibly due to the lack of crevices or holes in the carbonate substratum. Sea urchins were not observed.

The contingency-table analysis revealed an association of macrophyte taxa directly related to the presence of either *Gorgonia ventalina* or *Millepora alcicornis*. On a species by species basis (Table II), this association with *Gorgonia ventalina* was confirmed ($P < 0.05$ with Yate's correction; Sokal & Rohlf, 1969) within the 2-cm interval for *Galaxaura cylindrica*, *Dictyota* spp., *Laurencia poitei*, *Lobophora variegata*, *Chondria* sp., and *Amphiroa rigida*. Species positively associated with *Millepora alcicornis* (within 2.0 cm) were *Galaxaura cylindrica*, *Dictyota* spp., *Laurencia poitei*, and *Amphiroa fragilissima*. Only the diminutive turf-form of *Digenia simplex* was negatively associated with the sessile animals within the 5-cm zones ($P < 0.01$, Yate's correction). However, we observed that the upright frondose form of this alga was usually restricted to within

6.0 cm of *Gorgonia ventalina* or *Millepora alcicornis*. Almost twice as many taxa occurred within 9 cm of *Gorgonia ventalina* and *Millepora alcicornis* as within 9 cm of an equal number of random, *Gorgonia ventalina-* and *Millepora alcicornis*-free points (Table II), and seven were only found in samples within 10 cm of the two invertebrates.

TABLE I

Fish abundances (number · m^{-2} of substratum, ± 1 SE) within the study site: transects were 14–23 m long by 2 m wide.

Fish species	17 April 1985 ($n = 12$)	10 April 1984 ($n = 8$)
Surgeonfishes		
Acanthurus bahianus Castelnau	0.155 ± 0.021	0.169 ± 0.024
Acanthurus coeruleus Bloch & Schneider	0.029 ± 0.008	0.024 ± 0.018
Acanthurus chirugus Bloch	–	0.005 ± 0.005
Total	0.184 ± 0.023	0.198 ± 0.038
Parrotfishes		
Sparisoma aurofrenatum Valenciennes	0.077 ± 0.014	0.077 ± 0.014
Sparisoma rubripinne (Cuvier & Valenciennes)	0.052 ± 0.005	–
Scarus croicensis Bloch	0.032 ± 0.015	0.030 ± 0.025
Scarus taeniopterus Desmarest	0.026 ± 0.018	0.090 ± 0.055
Sparisoma viride Bonnaterre	0.024 ± 0.011	0.050 ± 0.022
Sparisoma chrysopterum Bloch & Schneider	0.015 ± 0.006	0.019 ± 0.014
Scarus vetula (Bloch & Schneider)	0.005 ± 0.003	–
Total	0.206 ± 0.043	0.266 ± 0.088

The association of several macroalgae with either *Gorgonia ventalina* or *Millepora alcicornis* resulted in considerably greater survivorship during the 66-h monitoring period despite the presence of herbivorous fishes. In the experiments involving the assessment of macrophyte losses to herbivory following the removal of either *Gorgonia ventalina* or *Millepora alcicornis* (Table III), comparisons (one-tailed *t*-test) of the total absolute macroalgal cover indicated no initial (pre-manipulation) differences ($P = 0.44$) between *Gorgonia ventalina* removal (27.9 ± 3.8, $\bar{x} \pm$ SE) and control (28.7 ± 3.7) treatments. Similarly, algal cover associated with *Millepora alcicornis* indicated no difference ($P = 0.45$) between removal (42.3 ± 9.0) and control (43.7 ± 9.1) treatments.

Following the 66-h experimental period, the removal treatment for both *Gorgonia ventalina* and *Millepora alcicornis* exhibited significantly greater ($P < 0.001$, one-tailed *t*-test) loss of total macroalgal cover ($35.0 \pm 4.1\%$, $34.1 \pm 4.9\%$, respectively, relative to initial values) than did the control groups in which *Gorgonia ventalina* and *Millepora alcicornis* had been left intact ($3.0 \pm 1.9\%$ and $0.2 \pm 1.8\%$ loss of relative cover, respectively). Dramatic losses appeared in 11 species (Table III). The presence of *Gorgonia ventalina* significantly reduced losses to herbivores in seven species: *Chondria* sp., *Laurencia poitei*, *Amphiroa rigida* ($P < 0.05$); *Stypopodium zonale* ($P < 0.01$); *Gal-*

axaura cylindrica, Dictyota dichotoma, D. bartayresii ($P < 0.005$). *Millepora alcicornis* significantly ameliorated herbivore losses during the 66-h test period in the following five species: *Galaxaura cylindrica, Dictyota dichotoma, D. bartayresii, Jania* sp. ($P < 0.05$), and *Digenia simplex* ($P < 0.01$).

The *Acanthophora spicifera* bioassay yielded consistent results even though the replicated experimental intervals varied from 1.5 to 20.5 h (Fig. 2). In general, only half as much *A. spicifera* was eaten (significant at $P < 0.05$, ANOVA) when within 5 cm of either *Gorgonia ventalina* or *Millepora alcicornis* than when located 30 cm away. About half of the losses occurred within the first 1.5 h and were entirely due to herbivorous fishes, as evidenced by direct observations and grazing scars.

TABLE II

Mean distance (cm, ± 1 SE) within a 10-cm radius from randomly selected *Gorgonia ventalina* and *Millepora alcicornis* individuals or randomly selected *Gorgonia/Millepora*-free point locations ($n = 30$): asterisks indicate a positive association at 2.0 cm: *, $P < 0.05$; **, $P < 0.01$; ⧣ indicates a negative association at $P < 0.01$ (contingency-table analysis with Yates correction).

Species	Gorgonia	Millepora	Random locations
Galaxaura cylindrica (Ell. & Sol.) Lamour.	2.5 ± 0.6**	4.8 ± 0.8**	absent
Dictyota spp.	2.8 ± 0.5**	4.8 ± 0.7*	7.3 ± 0.5
Laurencia poitei (Lamour.) Howe	3.7 ± 0.7**	5.8 ± 0.8**	9.2 ± 0.3
Jania adherens Lamour.	4.6 ± 0.6	4.6 ± 0.7	6.9 ± 0.8
Dictyota bartayresii Lamour.	4.8 ± 0.7	7.0 ± 0.6	8.4 ± 0.6
Digenia simplex (Wulf.) C. Ag.	5.4 ± 0.6⧣	5.9 ± 0.6⧣	0.5 ± 0.2
Lobophora variegata (Lamour.) Womersley	6.0 ± 0.7**	7.6 ± 0.7	9.7 ± 0.2
Chondria sp.	6.4 ± 0.8**	8.6 ± 0.5	9.5 ± 0.3
Hydrolithon boergesenii (Foslie) Foslie	6.5 ± 0.7	6.6 ± 0.6	8.1 ± 0.6
Amphiroa rigida Lamour.	6.5 ± 0.7*	8.2 ± 0.6	absent
Stypopodium zonale (Lamour.) Papenf.	6.5 ± 0.6	8.6 ± 0.6	9.8 ± 0.2
Amphiroa fragilissima (L.) Lamour.	7.2 ± 0.6	5.6 ± 0.7**	absent
Halimeda incrassata (Ellis) Lamour.	8.6 ± 0.5	7.2 ± 0.6	9.9 ± 0.1
Amphiroa tribulus (Ell. & Sol.) Lamour.	8.6 ± 0.6	9.4 ± 0.3	absent
Peyssonnelia sp.	9.0 ± 0.4	9.3 ± 0.3	9.9 ± 0.1
Dictyosphaeria cavernosa (Forssk.) Børg.	9.3 ± 0.3	7.3 ± 0.7	8.0 ± 0.6
Gelidiella acerosa (Forssk.) Feldm. & Hamel	9.3 ± 0.4	7.9 ± 0.6	absent
Halimeda opuntia (L.) Lamour.	9.7 ± 0.2	9.6 ± 0.3	absent
Liagora sp.	9.0 ± 0.2	absent	absent

TABLE III

Percent cover (mean ± SE, n where present) initially present and losses (or increases when denoted with a +) relative to initial cover 66 h after the experimental removal of 15 *Gorgonia ventalina* and 15 *Millepora alcicornis* compared with controls retaining these animals: *, indicates significant reduction (one-tailed t-test) in removal treatment at P < 0.05; ** at P < 0.01; *** at P < 0.005, as compared with controls; quadrats in which a species was absent are excluded for that species; [a] eight additional taxa were encountered which did not occur in sufficient instances to allow statistical comparisons; these were *Amphiroa fragilissima, A. tribulus, Cladophora* sp., *Galaxaura subverticillata* Kjellman, *Gelidiella acerosa, Hydrolithon boergesenii, Liagora* sp., and *Peyssonnelia* sp.

|	Mean relative cover changes (± SE, n)			
Species	Gorgonia removed	Gorgonia present	Millepora removed	Millepora present
Chondria sp.	55.9 (17.3, 4)	0.0 (0.0, 3)*	–	–
Galaxaura cylindrica	50.2 (18.1, 7)	2.5 (1.1, 9)***	47.9 (21.1, 6)	0.3 (0.3, 3)*
Digenia simplex	–	–	49.0 (14.2, 4)	0.8 (3.7, 4)**
Laurencia poitei	48.4 (15.9, 8)	8.0 (12.1, 9)*	41.3 (20.8, 5)	9.5 (7.0, 5)
Dictyota dichotoma	37.3 (9.1, 11)	2.6 (1.3, 10)***	35.3 (16.9, 8)	+ 5.6 (6.7, 8)*
Stypopodium zonale	30.7 (6.9, 8)	1.4 (1.0, 4)**	–	–
Dictyota bartayresii	27.8 (9.6, 7)	1.9 (1.1, 9)***	35.7 (14.4, 4)	+ 10.0 (10.2, 5)*
Amphiroa rigida	24.1 (8.2, 5)	0.0 (0.0, 2)*	0.0 (0.0, 2)	1.2 (1.2, 3)
Dictyosphaeria cavernosa	21.9 (12.9, 4)	+ 8.1 (4.8, 3)	10.0 (10.0, 2)	1.8 (5.1, 4)
Jania sp.	5.2 (5.1, 2)	0.0 (0.0, 2)	27.7 (15.2, 2)	0.9 (1.0, 5)*
Halimeda incrassata	–	–	22.5 (7.7, 4)	1.1 (1.3, 6)
Lobophora variegata	0.2 (0.2, 3)	+ 0.8 (2.7, 5)	–	–
All algal taxa[a]	35.0 (4.1, 15)	3.0 (1.9, 15)**	33.3 (4.9, 15)	0.2 (1.8, 15)**
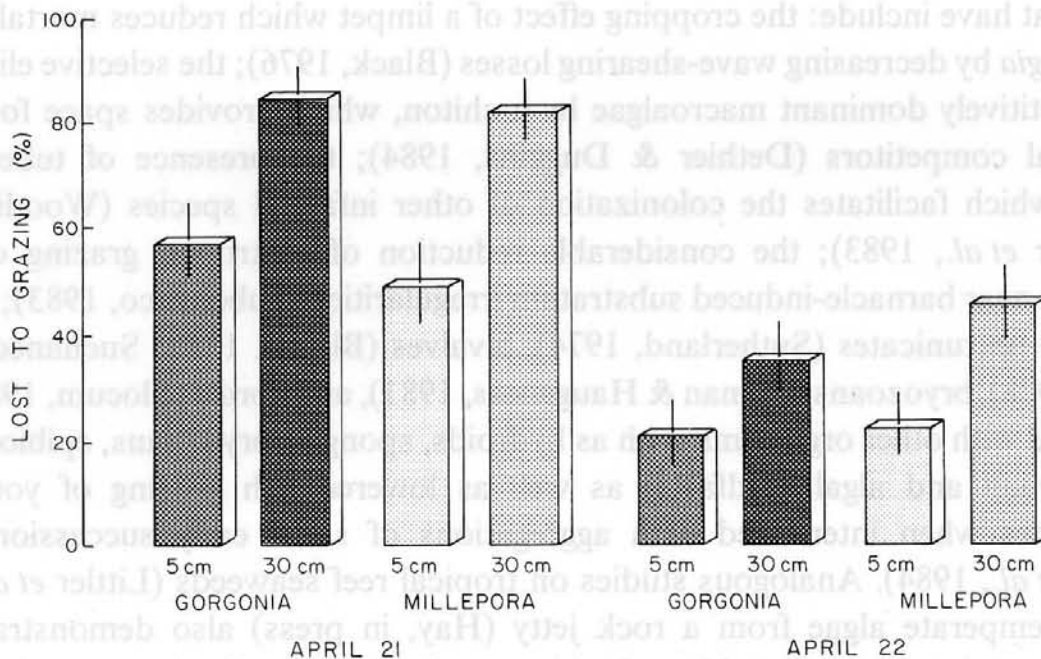
Fig. 2. Percent losses (% thallus length with ± 1 SE bars) of the palatable alga *Acanthophora spicifera* as a function of distance from *Gorgonia ventalina* and *Millepora alcicornis* following 20.5 h on 21 April and 1.5 h on 22 April of exposure to grazing: losses at the 5-cm distance are significantly lower (P < 0.05, ANOVA) than losses at the 30-cm distance in all cases.

DISCUSSION

This study measured the relative susceptibility of algae to removal by natural assemblages of grazing fishes and was not designed to differentiate among fish species or to determine specific preferences for any given species. Fish surveys made 1 yr earlier (10 April 1984, Littler et al., 1986) are consistent with the present findings of domination by herbivorous surgeonfishes and parrotfishes, with no observations of large carnivorous fishes or sea urchins during the quantitative counts. In the present study, *Acanthurus bahianus* and *A. coeruleus* were the predominant acanthurids at similar abundances to those recorded one year earlier by Littler et al. (1986). Of the parrotfishes, the 1985 dominant *Sparisoma aurofrenatum*, as well as *Scarus croicensis* and *Sparisoma chrysopterum*, occurred in the same abundances during 1984. Assays of herbivore pressure conducted throughout the Carrie Bow Cay environs using the relatively palatable seagrass *Thalassia testudinum* (Hay, 1981a), as well as the delicate rhodophyte *Acanthophora spicifera* (Lewis & Wainwright, 1985), have characterized the zone we studied as among the highest in terms of fish grazing intensity (mainly attributed to Acanthuridae and Scaridae). The herbivores studied at this location (Table I, Littler et al., 1983b, 1986), as a guild, represent generalist feeders that together are capable of consuming a broad spectrum of algal species (Randall, 1967). Some parrotfishes (e.g., *Sparisoma viride*) readily "graze" calcareous corals (pers. obs.) and could represent a potential threat to gorgonians and fire corals, if not repelled.

In contrast to terrestrial systems (e.g., Simberloff et al., 1978; Inouye, 1982), "positive" biotic associations (e.g., direct and indirect mutualism, commensalism) within or between trophic levels have not been widely explored in marine environments. Those that have include: the cropping effect of a limpet which reduces mortality of the kelp *Egregia* by decreasing wave-shearing losses (Black, 1976); the selective elimination of competitively dominant macroalgae by a chiton, which provides space for inferior microalgal competitors (Dethier & Duggins, 1984); the presence of tube-building infauna which facilitates the colonization of other infaunal species (Woodin, 1978; Gallagher et al., 1983); the considerable reduction of gastropod grazing on *Fucus* germlings near barnacle-induced substratum irregularities (Lubchenco, 1983); lessened predation on tunicates (Sutherland, 1974), bivalves (Bloom, 1975; Suchaneck, 1978; Vance, 1978), bryozoans (Osman & Haugsness, 1981), and corals (Slocum, 1985) when associated with other organisms such as hydroids, sponges, bryozoans, epibiotic algae, or gorgonian and algal holdfasts; as well as lowered fish grazing of young kelp sporophytes when intermixed with aggregations of small early successional algae (Harris et al., 1984). Analogous studies on tropical reef seaweeds (Littler et al., 1986) and on temperate algae from a rock jetty (Hay, in press) also demonstrated that palatable species are protected from herbivores when growing in close association with relatively unpalatable plants. A similar effect has been shown (Hixon & Brostoff, 1983) where algal diversity is increased by a damselfish that decreases the intensity of herbivory within its territories.

The study of chemical defense in the marine environment is still in its infancy, making it at present impossible to document the mechanisms by which *Gorgonia ventalina* and *Millepora alcicornis* reach such large standing stocks in a reef habitat containing abundant populations of benthic feeding fishes. Fenical (unpubl. data) has recorded a marked reduction in palatability when fish pellets were presented to predatory reef fish (wrasses) after being coated with extracts from *Gorgonia ventalina*. Studies by a gorgonian specialist (Muzik, 1982) at Carrie Bow Cay resulted in no observations of fish predation on *G. ventalina*, and that author speculated that noxious chemistry may play an important anti-predator role. In the case of the fire coral *Millepora alcicornis*, the avoidance by common reef fishes is probably due to the strong stinging reactions. Both sessile animals, however, have small predators that apparently have evolved solutions to these coelenterates' defense mechanisms; i.e., the carnivorous polychaete *Hermodice* in the case of *Millepora*, and the gastropod *Cyphoma* which preys on *Gorgonia*.

Whether the two colonial invertebrates are palatable or not does not rule out the possibility that the protective effect for macrophytes may result from a physical barrier to effective location and feeding by herbivorous fishes. Littler *et al.* (1986) examined this possibility for the toxic alga *Stypopodium zonale* by contrasting living thalli with plastic models. The physical presence of the artificial models significantly reduced herbivory ($P < 0.05$); however, the proximity of living *S. zonale* afforded significantly greater protection against grazing fishes than did the models.

If unpalatable large sessile animals decrease predation on smaller palatable macro-algae primarily by facultatively providing cryptic microhabitats or refuges against large mobile fishes that use them as macrohabitat shelter, then the type of association described here could be quite widespread since it does not require a long history of selection and coevolution as is presumably (Vermeij, 1983) essential for the development of more tightly coupled mutualisms. A temporary symbiosis (mutualism) has been noted (Slocum, 1985) between juveniles of gorgonians and algae, where algae appear to benefit from the spatial refuge provided near the coral base. Whether or not macrophytes decrease mortality due to grazing by actively colonizing regions near the bases of such defended, sessile animals still needs to be resolved. Alternatively, the presence of macrophytes adjacent to well-defended, conspicuous animals may be due only to chance settlement and subsequent post-settlement survival and development in those areas where macroalgae are not continually removed by grazing. However, these associations, whether actively or passively derived, still result in increased algal fitness and community complexity.

The removal experiment (Table III) coupled with direct observations of grazing by fishes, as well as the algal bioassay (Fig. 2), argue strongly against the hypothesis that some physical/chemical microhabitat factor produced by the animals is required by the algae. Many of the species associated with *Gorgonia* or *Millepora* (e.g., *Dictyota*, *Galaxaura*, *Lobophora*, *Chondria*, *Laurencia*) are common elsewhere away from either abiotic or biotic structure where grazing intensity is lower. We have made no obser-

vations that would support the hypothesis that sessile animals enhance the numbers of carnivorous predators (thereby reducing the exposure of macroalgae to herbivores) despite many personal hours of diver observations over a 5-yr period in this habitat. For example, no barracuda (Sphyraenidae), groupers (Serranidae), jacks (Carangidae), snappers (Lutjanidae), moray eels (Muraenidae), or other predators capable of taking herbivorous fishes, have been observed in sufficient abundance within the gorgonian/fire coral-dominated community to be of significance to this hypothesis. Additionally, the effect of such predators would have to be restricted to an unreasonably small microscale (i.e., associated only with the basal portions of the sessile animals).

The hypothesis that herbivores may require large monospecific populations of their prey in order to locate and exploit them has been largely supported for stands of terrestrial crop plants where successful location and colonization of prey have been shown (Kareiva, 1982) to be of paramount importance for the completion of the life histories for many specialized insects. However, herbivorous reef fishes, because of their relatively large sizes, great mobility, high metabolic rates, range of sophisticated sensory cues, and orientation behavior, have little trouble in locating palatable algae that are accessible to them. Such fishes readily find individual *Acanthophora* and *Thalassia* thalli scattered widely (i.e., transplanted) in reef environments (Fig. 2; Hay, 1981a; Hay & Taylor, 1985; Lewis & Wainwright, 1985). As pointed out by Littler *et al.* (1986), a diversity of variable-quality plant types is maintained on reefs through a broad spectrum of morphological, chemical, nutritional, temporal, and spatial mechanisms. Such availability of diverse prey could, hypothetically (Steneck, 1982), explain the relative lack of highly specialized fish–plant relationships (Randall, 1967; Ogden & Lobel, 1978) on tropical reef systems.

This study (see also Littler *et al.*, 1986) provides considerable support for the hypothesis that the presence of the large conspicuous colonies of *Millepora alcicornis* and *Gorgonia ventalina* results in microscale avoidance by herbivores, thereby providing a refuge for macroalgae. The system studied here, where abundant and apparently well-defended sessile animals (Muzik, 1982; Fenical, unpubl. data) provide an important refuge for 11 macroalgae, not only facilitates the survival of some taxa not generally found in the surrounding area, but more importantly enhances within-microhabitat population abundances throughout the reef. Few examples have been found (Connell & Slatyer, 1977) for facilitation in community development. Although we can only draw tentative inferences, this mechanism may be more common on tropical reefs than suspected (see also Littler *et al.*, 1986; Hay, in press). The competitive costs (lowered growth rates) to palatable algae of being associated with another plant were found (Hay, in press) to be much less than the costs of increased herbivory in the absence of that plant. Such results suggest an interaction counter to the process of competitive exclusion, as do our findings where two conspicuously abundant organisms, utilizing the same resource, have a positive rather than negative overall effect on the abundances of other species.

In summary, the association documented here can probably best be interpreted as

facultative and not obligate or coevolved (see Vermeij, 1983). The defensive nature of this association is a result of algal susceptibility to herbivory that depends not only on the inherent properties of the alga, but on the morphological, chemical, distributional, and abundance features of other sessile organisms. The inhibition of a coevolutionary relationship between a potential prey plant and grazer may well be influenced by the presence of defensive associations (Littler *et al.*, 1986). We emphasize that this group attribute could not be inferred from a study of the relationships between a single macrophyte species and its grazers alone. Positive interactions such as documented here should be quite widespread, particularly on tropical reefs. The study of plant and animal defense associations and their role in community development, as well as in other aspects of tropical reef ecology, is a promising topic for further research.

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