

Algal Resistance to Herbivory on a Caribbean Barrier Reef

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Received 20 January 1983; accepted 21 July 1983

Abstract. Field and laboratory research at Carrie Bow Cay, Belize showed that macroalgae, grouped in functional-form units resisted fish and urchin herbivory in the following order (from high to low resistance): Crustose-Group, Jointed Calcareous-Group, Thick Leathery-Group, Coarsely Branched-Group, Filamentous-Group and Sheet-Group; thereby supporting the hypothesis that crustose, calcareous and thick algae have evolved antipredator defenses and should show the greatest resistance to herbivory with a gradation of increasing palatability towards filaments and sheets. Of the 21 species examined, several (e.g., *Dictyota cervicornis* on grids, *Laurencia obtusa* and *Styopodium zonale*) had exceptionally low losses to fish grazing, probably due to chemical defences. The sea urchin, *Diadema antillarum*, was more inclined to feed on algae with known toxic secondary metabolites than were herbivorous fishes; hypothetically related to the differences in mobility and concomitant modes of feeding. Tough leathery forms such as *Sargassum polyceratum* and *Turbinaria turbinata* resisted grazing by bottom feeding parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) but were susceptible when suspended midway in the water column, possibly due to the presence of rudderfishes (Kyphosidae) which readily consume drift Sargassaceae. The overall tendencies support our predicted relationship between grazer-resistance and algal morphology. In conjunction with our previously reported findings concerning primary productivity, toughness and calorimetry for many of the same species, these results lend credence to generalizations relating form with function in marine macroalgae.

Introduction

Temperate shallow water ecosystems are often characterized by moderate to low rates of overall herbivory (see Bakus 1969; Vermeij 1978) except for sea urchins and gastropods in relatively localized patches (e.g., Paine and Vadas 1969; Mann 1977; Slocum 1980). In contrast, tropical reef systems tend to have relatively high grazing by abun-

dant and diverse assemblages of mobile fishes (Stephenson and Searles 1960; Randall 1961, 1965, 1974; Bakus 1964, 1966, 1967; John and Pople 1973; Littler and Doty 1975; Wanders 1977; Borowitzka 1981). Sea urchin grazing (Dart 1972; Ogden et al. 1973; Sammarco et al. 1974; Carpenter 1981), especially by *Diadema antillarum*, also has a significant impact on the localized distribution and abundance of marine macroalgae throughout the world's tropical waters.

Several strategies are potentially available to seaweeds for reducing losses due to the severe grazing pressures on tropical reefs. More than one of these herbivore-resistance mechanisms are often expressed by a given species (Littler and Littler 1980) and include: (1) occupation of refuge habitats that are physically unfavorable or unavailable to herbivores (Ogden et al. 1973; Adey and Vassar 1975; Hay 1981a), (2) unpredictable spatial and temporal distributions (Littler and Littler 1980; Lubchenco and Cubitt 1980), (3) rapid growth involving the replacement of vegetative and reproductive tissues while simultaneously satiating the appetites of grazers (Littler and Littler 1980), (4) close association with unpalatable organisms (Atsatt and O'Dowd 1976), carnivorous predators (Randall 1965; Ogden et al. 1973; Hay 1981c) or highly territorial animals (Hixon and Brostoff 1982) and (5) allocation of materials and energy toward herbivore defences. The last strategy has several non-mutually exclusive components that encompass: (a) toxins, digestion-inhibitors or unpalatable secondary metabolites (Fenical 1975; Norris and Fenical 1982), (b) reduced calorific contents (Paine and Vadas 1969; Littler and Murray 1978), (c) morphological shapes and sizes that minimize accessibility (Hay 1981a; Steneck and Watling 1982), (d) textures that inhibit the physical processes of herbivore manipulation and feeding (Nicotri 1980) and (e) structural materials that decrease palatability or nutritional value (Littler 1976). This study utilizes a morphological-functional approach employing predictive form-groups and addresses aspects of the last four components above (b-e) by means of multifaceted field experiments.

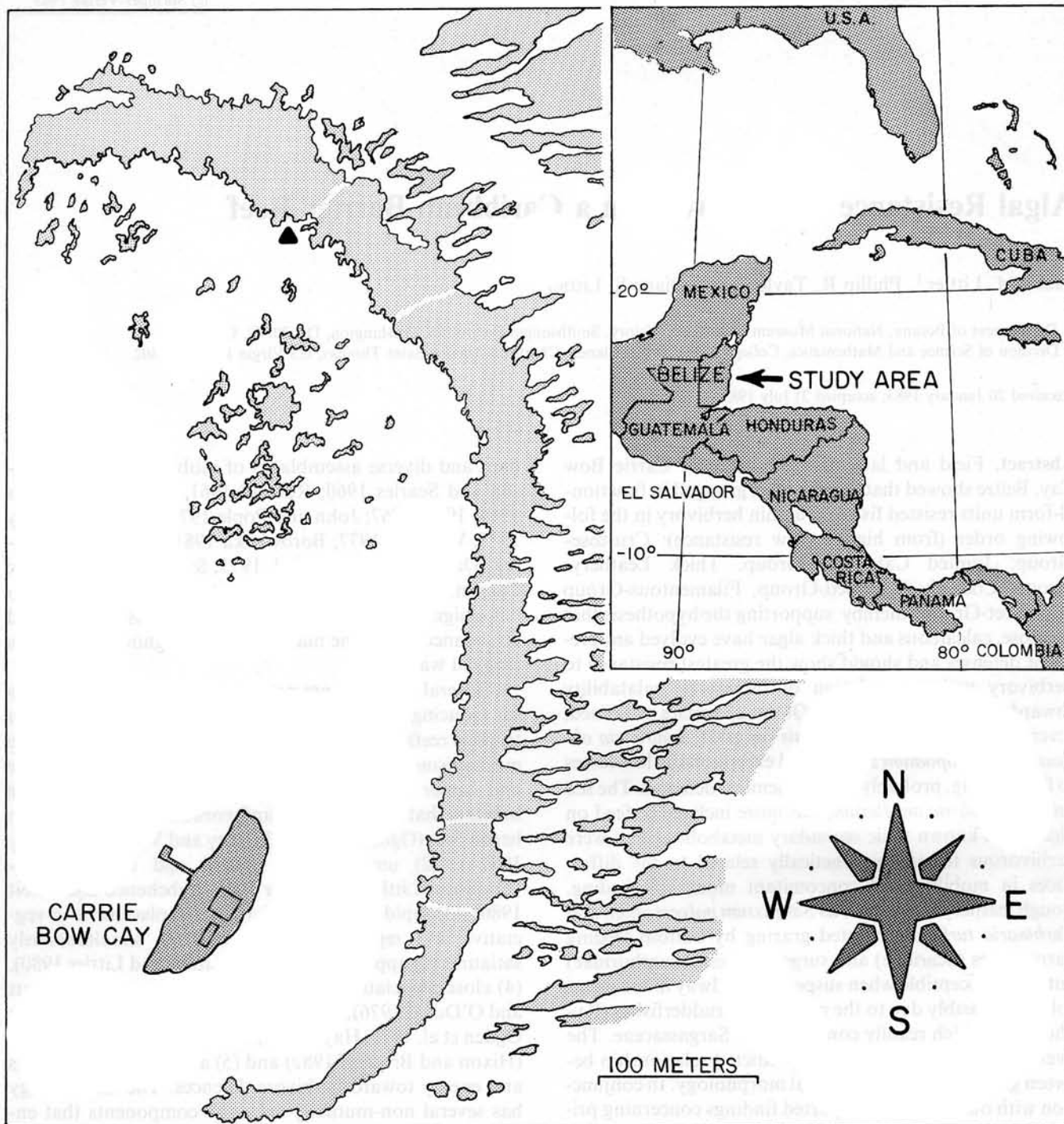


Fig. 1. Location of the study area (dark triangle) on the Belize barrier reef

Study Area

Both field and laboratory research was conducted at Carrie Bow Cay, Belize ($16^{\circ} 48'N$, $88^{\circ} 05'W$, Fig. 1) during April and November 1980 and March 1982. The cay is one of several small islands composed of calcareous debris which has accumulated on the outer margin of the Belizian barrier-reef system remote from the influence of industrial man. The hydrography, geology, natural history and biology are relatively well known (Rützler and Macintyre 1982) as a result of a decade of multidisciplinary investi-

gations. The reef possesses a rich and well-known flora (Norris and Bucher 1982) about which considerable knowledge exists on natural-products chemistry (Norris and Fenical 1982).

Methods and Materials

We have used six functional-form groups of macroalgae (Table 1) ranked on the basis of convergent morphological, anatomical and textural features that are independent of taxonomic and life-history affinities. Details of the anatomical and morphological ranking criteria are given in Steneck and Watling (1982). However, our groupings (Table 1) exclu-

Table 1. Functional-form groups; their characteristics and species examined. As pointed out by Littler et al. (1983), there is little a priori reason for the ordering of the Sheet- and Filamentous-Groups and the two, for equally good reasons, could have been reversed

Functional-form group	External morphology	Internal anatomy	Texture	Species examined
A. Sheet-Group	Thin tubular and sheet like (foliose)	Uncorticated, one-several cells thick	Soft	<i>Anadyomene stellata</i> <i>Dictyota cervicornis</i> <i>Enteromorpha linza</i> <i>Ulva lactuca</i>
B. Filamentous-Group	Delicately branched (filamentous)	Uniseriate, multiseriate or lightly corticated	Soft	<i>Centroceros clavulatum</i> <i>Ceramium nitens</i> <i>Spyridia filamentosa</i>
C. Coarsely Branched-Group	Coarsely branched, upright	Corticated	Fleshy-wiry	<i>Acanthophora spicifera</i> <i>Caulerpa racemosa</i> <i>Laurencia papillosa</i> <i>Laurencia obtusa</i>
D. Thick Leathery-Group	Thick blades and branches	Differentiated, heavily corticated, thick walled	Leathery-rubbery	<i>Gracilaria cf. debilis</i> <i>Sargassum polyceratum</i> <i>Styopodium zonale</i> <i>Turbinaria turbinata</i>
E. Jointed Calcareous-Group	Articulated, calcareous, upright	Calcified genicula, flexible intergenicula	Stony	<i>Amphiroa rigida</i> <i>Halimeda monile</i>
F. Crustose-Group	Epilithic, prostrate, encrusting	Calcified or uncalcified parallel cell rows	Stony or tough	<i>Hydrolithon boergesenii</i> <i>Neogoniolithon strictum</i> <i>Peyssonnelia</i> sp. <i>Porolithon pachydermum</i>

de developmental stages and microscopic algae such as diatoms (Bacillariophyta) and blue-green algae (Cyanophyta) due to the extreme difficulty both taxonomically and logistically in conducting appropriate field experiments on them. We predict, a priori, that if the functional-form groups are ecologically meaningful, then their ranking should correlate with increasing resistance to grazing by generalist herbivores; such resistance should be closely related to fitness (i. e., survival, growth and reproductive output). This ranking does not imply discrete categories but can be best regarded as recognizable portions of a continuum. The saccate cushion-like forms (Littler 1980a) are not well represented at Carrie Bow Cay and were not included in our analyses. Because the studies were conducted on three separate occasions, not all species were present in amounts adequate for all three tests.

Field Experiments

Specimens were collected while submerged and stored in indirect light in polycarbonate trays of seawater. Voucher specimens of all species were preserved in 4.0% buffered Formalin seawater, labelled and deposited in the Algal Collection of the US National Herbarium, Department of Botany, Smithsonian Institution, Washington, DC. All representatives of the six groups (Table 1) that could be obtained in sufficient quantities were examined experimentally with regard to their resistance to fish and urchin predation.

Hypothesis Examined

If members of the Crustose-, Jointed Calcareous- and Thick Leathery-Groups have evolved antipredator defenses (e.g., toughness, structural inhibition, low calorific content or toxicity), then they should show the greatest resistance to herbivory by generalist grazers with a gradation of increasing palatability toward the Coarsely Branched-, Sheet- and Filamentous-Groups.

Natural populations of reef fishes were used to assess the herbivore resistances of 21 species from the 6 algal groups. Experiments were run in the long-shore channel of the reef-flat just shoreward of the reef crest

(Fig. 1) during April and November 1980. This zone is characterized by large schools of numerous species of surgeonfishes (primarily *Acanthurus bahianus*, Acanthuridae) and parrotfishes (mainly *Scarus croicensis* and *Sparisoma chrysopterum*, Scaridae) that move freely along the channel during daylight hours. Fish are the dominant herbivores at Carrie Bow Cay and the experimental zone studied here is the region of greatest herbivory (Hay 1981b). The algae were collected while submerged and returned immediately to the laboratory where they were separated into portions or clumps of equal area (~10 cm², whole thalli or branches). Equal-area clumps were used throughout all experiments to avoid any bias concerning the probability of animals encountering large versus small thalli. For crustose species, thalli were presented on the natural underlying substrata after fragments had been retained for 24 h in running seawater to permit wound healing prior to use. The percentage of thallus area lost to herbivory was the parameter of interest throughout these studies because surface area is usually positively correlated with metabolic activity (Littler 1980a). Measurements of weight consumed would have been the appropriate parameter if palatability to the predator had been our focus. However, it becomes difficult to comparatively interpret palatability data based on absolute biomass (Lawrence 1975) when consumption of a small portion of a heavy alga (e.g., a calcareous form) exceeds a large portion of a delicate, light species (e.g., *Ulva*). When possible, only intact, entire thalli were collected and care was taken to ensure that the algae were not desiccated or unduly injured during handling. Damselfish (Pomacentridae) territories were avoided during all feeding trials to eliminate any bias in the access to individual samples by other herbivorous fishes.

Weighted Grid Method

During April and November 1980, 16 species were placed under elastic bands on four, separate, weighted plastic grids (70 cm × 70 cm) each containing three ~10 cm² clumps per species (4 × 3 = 12 sample replicates per species arranged in mechanically-randomized patterns per experiment). The grids were vigorously dipped in seawater to dislodge any loosely-attached fronds, photographed and then placed on the bottom of

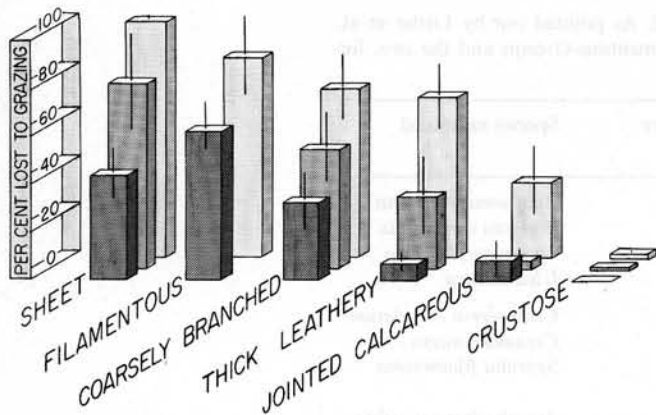


Fig. 2. Mean per cent losses to fish herbivory during weighted grid experiment (dark histograms in front), urchin grazing (medium histograms in middle) and fish herbivory during suspended line study (light, rear) for the six functional-form groups. Lines indicate $\pm 95\%$ confidence limits

the 1.5 m-deep channel for 24 h. Experiments were repeated and the total number of replicates per species was usually in excess of 24. Similar control grids were placed in areas where fish did not graze and no measurable losses or gains occurred when monitored daily over a four-day interval, although wave and current action was relatively vigorous. We observed immediate feeding on the experimental grids by both surgeonfishes and parrotfishes. The experiments were not within range of urchins and all bite marks were attributable to fish. The grids were returned to the laboratory after 24 h and rephotographed; the per cent thallus area (two dimensional) lost to grazing for each specimen was calculated from color transparencies (Kodachrome 64) by the point-intercept method described in Littler (1980b).

Suspended Line Method

Clumps ($\sim 10 \text{ cm}^2$) of 19 algal species were placed between twists of a three-stranded, white nylon line at 0.5-m intervals in a mechanically-randomized pattern that was consistently followed among replicate lines during November 1980 and March 1982. For all trials, four separate lines were used, each containing three clumps per species (12 sample replicates per species). The lines were photographed and then placed midway in the water column with each end tied to coral in the 1.5 m-deep channel for a 6-h daylight period. These were situated near the location of the weighted-grid experiment. Surgeonfishes and parrotfishes were not wary of the lines and began feeding as soon as the divers moved away. Fish fed less furtively on the lines than on the grids, typically moving from clump to clump taking small bites and becoming more persistent as they located a particularly palatable clump. After 6 h, the lines were returned to the laboratory, rephotographed and quantified as described for the weighted grids.

Captive Urchin Method

Medium-sized ($\sim 3\text{-cm}$ mean test diameter) *Diadema antillarum* were collected during November 1980 from the reef flat and 16 were placed in separate 2.0 liter wide-mouth canning jars with the hinged glass lids slightly open ($\sim 4 \text{ cm}$) to prevent the urchins from escaping and to allow gas exchange. The 16 jars were submerged, along with 8 additional control jars without urchins, in large, shaded seawater aquaria within 10 m of the natural habitat. Seawater from the reef flat was added periodically for flushing, aeration and temperature stabilization. To standardize the pre-treatment effects, the sea urchins were fed exclusively on *Ulva lactuca* (which our preliminary experiments showed to be highly preferred) for 2 days, starved for 1 day and then used experimentally. Paired $\sim 10\text{-cm}^2$ clumps of different algae were photographed and presented to individual urchins during each paired-choice feeding trial. On sample of each algal pair was always *U. lactuca* which served as the basis for comparison between species throughout the experiment. No significant ($P > 0.05$) reduction in the consumption of *U. lactuca* occurred over the course of the

experiment. Control pairs were placed in each of the eight bottles without urchins to determine surface area losses due to leaching from wounds, disintegration, etc. Feeding trials were begun consistently between 0800-0900 hours and lasted 10 h, after which time the specimens were recovered, rephotographed and quantified as above. Fecal pellets were flushed from the jars and the urchins were starved until the following morning's experiment. In contrast to other studies (Odgen et al. 1973), no day vs. night differences in *D. antillarum* activity was apparent and relatively large percentages of *U. lactuca* were consistently consumed. We were unable to use delicate filamentous algae in the sea urchin experiment because of fragmentation, i.e. portions of filaments tended to drift and were difficult for the urchins to manipulate, although they consumed filaments quite readily when thalli were trapped near the oral disc. All urchins remained healthy and fed well throughout the two-week experiment and were subsequently returned to the reef.

Data Analysis

The design involved ranking the six functional-form groups on the basis of the three feeding studies. The differences between the means was determined by the Duncan's Multiple Range Test (Steel and Torrie 1960) using arcsine transformed data (% consumed). Because the algal groups represent a continuum, we anticipated that only groups near opposite ends of the spectrum would show significant ($P < 0.05$) differences. Also, all algal species were not expected to linearly fit the predicted pattern since this would imply that the same selective agent is universally operative; obviously, different groups (guilds?) of herbivores could have been involved in the evolution of the various algal forms.

Results

Weighted Grids

The data for per cent thallus lost to fish grazing on the weighted grids over a 24-h period (Fig. 2) tend to support the grazing hypothesis; filaments were statistically ($P < 0.05$) less resistant to grazing than the other groups, while sheets and coarsely-branched forms had significantly greater ($P < 0.05$) losses than the remaining groups. An exception to the predicted pattern was the extremely low value for the thin sheet-like alga *Dictyota cervicornis* (Fig. 3). With *D. cervicornis* omitted from the analysis, the Crustose-, Thick Leathery- and Jointed Calcareous-Groups were significantly ($P < 0.05$) more herbivore resistant than any of the other groups. The most heavily-calci-fied species (crustose corallines and *Amphiroa fragilissima*) were among the least vulnerable to herbivory (Fig. 3) as were the thick leathery species, *Gracilaria cf. debilis*, *Sargassum polyceratum* and *Turbinaria turbinata*. The ranking of the means for each functional-form group (Fig. 2) from high to low percentages consumed were as follows: filaments (62.2% lost per 24 h), sheets (42.0%), coarsely branched (33.2%), jointed calcareous (9.9%), thick leathery (7.3%) and crusts (0.1%), in accordance with our prediction.

Suspended Lines

The suspended-line experiments support the hypothesis as follows (Fig. 2): sheets (99.1% lost per 6 h) were significantly ($P < 0.05$, Duncan's Multiple Range Test) less resistant than filaments (83.3%), coarsely-branched forms (74.5%) and thick leathery forms (67.7%); all of the above groups were significantly ($P < 0.05$) less resistant than the Jointed Calcareous-Group (31.3%). The Crustose-Group

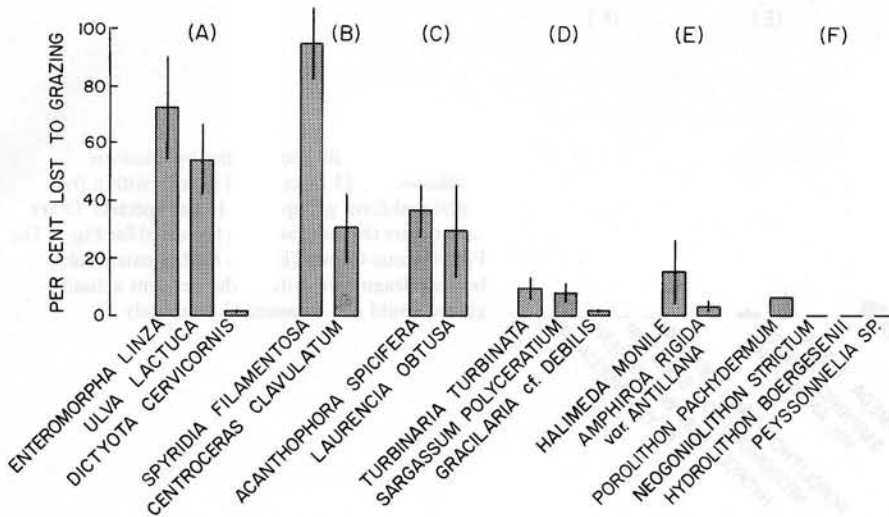


Fig. 3. Susceptibility to fish grazing on weighted grids for 16 macroalgal species within the six functional-form groups. *A* Sheet-Group, *B* Filamentous-Group, *C* Coarsely Branched-Group, *D* Thick Leathery-Group, *E* Jointed Calcareous-Group and *F* Crustose-Group. Lines indicate $\pm 95\%$ confidence limits, $n = \sim 24$ per species

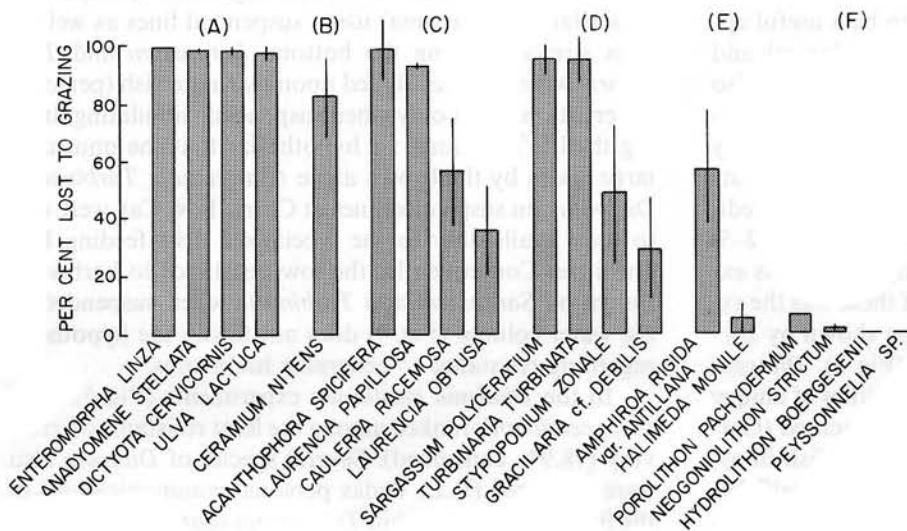


Fig. 4. Susceptibility to fish grazing on suspended lines for 19 macroalgal species within the six functional-form groups ($n = 12$ per species). Other features are the same as those indicated for Fig. 3

(only 1.8% lost) was statistically ($P < 0.05$) more resistant to herbivory than any of the other groups. *Laurencia obtusa* (Fig. 4, 35.6% consumed) was significantly ($P < 0.05$) more herbivore resistant than *L. papillosa* (92.8%). Unlike the findings of the weighted-grid experiment, *Dictyota cervicornis* (99.0% lost), along with all of the other sheet forms (97.9–100%), was almost totally consumed (Fig. 4). Another marked deviation from the weighted-grid experiments was the surprisingly low resistance to herbivory of the thick leathery *Sargassum polyceratum* (96.5% consumed) and *Turbinaria turbinata* (96.1%) when placed midway in the water column on lines. On first interpretation, this last finding appears to partially falsify the hypothesis, but this will be analyzed below.

Urchin Grazing

Captive *Diadema antillarum* consumed the various form groups (Fig. 2) in accordance with the pattern predicted.

The greatest losses to grazing were for sheets (78.9% per 10 h) and coarsely-branched algae (51.9%). These losses were significantly greater ($P < 0.05$) than losses shown by thick leathery species (30.3%), which in turn were significantly greater ($P < 0.05$) than values for either jointed calcareous forms (4.6%) or crustose algae (0.2%). We were unable to obtain accurate data for filaments (due to handling problems), however Carpenter (1981) recorded strong preferences of *D. antillarum* (in the field) for filamentous algae comprising algal turfs. Corroborating the suspended-line results, and in contrast to the weighted-grid experiment, *Dictyota cervicornis* was readily consumed (78.9%) by *D. antillarum* (Fig. 5). Also in agreement with the suspended-line findings, *Laurencia obtusa* (4.8% lost) was far more resistant ($P < 0.05$) to *D. antillarum* than *L. papillosa* (71.2%). Among the three thick leathery forms examined (Fig. 5), *Styopodium zonale* (53.5% consumed) was the least resistant to urchin damage.

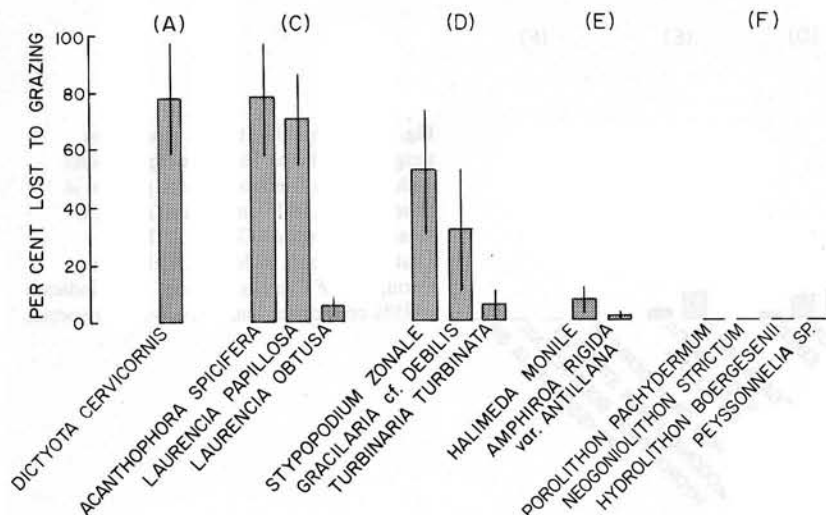


Fig. 5. Susceptibility to grazing by *Diadema antillarum* for 13 macroalgal species within five functional-form groups ($n = 16$ per species). Other features are the same as those indicated for Fig. 3. The Filamentous-Group (B) was readily eaten but, because fragments drifted, the per cent actually grazed could not be assessed accurately

Discussion

The functional-form model has proven to be a useful approach for analyzing morphological, physiological and ecological interrelationships between macroalgae (see also Littler 1980a; Littler and Arnold 1982; Steneck and Watling 1982; Littler et al. 1983) and, as pointed out by Steneck and Watling (1982), may enable marine ecologists to interpret community patterns without having to tediously study the individual species. The data (Figs. 2–5) suggest a trend supportive of the grazing hypothesis except for several specific examples. One of these was the exceptionally high resistance to fish grazing shown by *Dictyota cervicornis* on the weighted grids (Fig. 3). *Dictyota* (and other Dictyotales) contains large quantities of unique secondary metabolites that have been documented (Gerwick 1981; Norris and Fenical 1982) to deter fish in artificial situations. In addition, herbivorous damselfishes have been shown by Montgomery (1980) to avoid *Dictyota* under natural conditions in the Gulf of California. Hay (1981b), using a weighted clothespin technique, transported 10 thalli of *D. cervicornis* from a mangrove to a backreef habitat at Carrie Bow Cay and no individuals were recorded eaten although, curiously, all showed small fish grazing scars.

Anomalously high grazer susceptibilities were found for *Sargassum polyceratum* and *Turbinaria turbinata* (thick leathery) as well as *D. cervicornis* (sheet) when suspended midway in the water column on lines (Fig. 4, cf. Fig. 3). We are reasonably certain, although quantitative data are lacking, that the variance from the weighted-grid data is related to the different modes of feeding (drift feeding versus benthic browsing and grazing) shown by various fish groups. Bermuda chubs (*Kyphosus sectatrix*) were observed within the experimental area on several occasions, and diurnal time-lapse photography (30-s intervals) showed that they readily consumed our samples of Sargassaceae. These fish appeared shy and always fled through the reef crest into deeper waters when they encountered divers. Rudderfishes (e.g., *Kyphosus incisor* and *K. sectatrix*) are among the few documented (Randall 1967) to consume *Sargassum* and *Turbinaria* and they feed primarily on

drifting fucallean algae. During preliminary feeding trials (with which we assisted J. Cubit, August 1979, in the San Blas Islands of Panama) using suspended lines as well as lines stretched along the bottom, *Sargassum* and *Turbinaria* were voraciously fed upon by rudderfish (personal observations), but only when suspended (simulating drifting thalli). Therefore, we hypothesize that the unusually large losses by the brown algae (*Sargassum*, *Turbinaria*, *Dictyota*) on suspended lines at Carrie Bow Cay were due to their availability to the specialized drift feeding Kyphosidae. Consequently, the low resistance to herbivory shown by *Sargassum* and *Turbinaria* when suspended in the water column (Fig. 4) does not falsify the hypothesis regarding resistance to generalist herbivores.

In the *Diadema antillarum* experiments (Fig. 5), *Dictyota cervicornis* ranked among the least resistant to herbivory (78.9% consumed). Several species of *Dictyota* also were preferred (R.L. Vadas personal communication) in the field diet of the urchin *Tripneustes ventricosus*, but this was on the basis of low availability relative to other macroalgae. *Stypopodium zonale*, an alga documented to produce compounds toxic to damselfish at concentrations of 3 $\mu\text{g}/\text{ml}$ and reported as "apparently not eaten" by most herbivores (Norris and Fenical 1982), was the most vulnerable (53.5% consumed) of the Thick Leathery-Group (Fig. 5). It is also the least penetration resistant member of this group tested (Littler et al. 1983). This apparent tolerance of *D. antillarum* to chemicals identified as fish toxins could be evolutionarily related to differences in mobility and feeding strategies. *Diadema antillarum* has a relatively limited feeding range and searching ability and may obtain a considerable portion of its diet by trapping drift algae. The appropriate strategy under such a feeding constraint should be one of extreme generalization in feeding with the concomitant ability to cope with toxic secondary metabolites to a greater degree than the more mobile (and potentially more selective) bottom-feeding herbivorous fishes. This positive response was especially noticeable in the case of the flat algal morphologies, shown by such genera as *Dictyota* and *Stypopodium*, to which urchin tube feet presumably attach relatively easily. In this regard, *T. ventricosus* was shown (Lewis 1958) to prefer broad leafy

forms of algae such as *Dictyota* and *Padina*. However, Lowe (1974, cited in Lawrence 1975) felt that terete plants once captured could be manipulated by urchins to a greater degree than large or flattened forms. Vadas and Ogden (1981) concluded that tropical sea urchin feeding may be governed more by avoidance behavior than by preference. They suggested that tropical algae, as a group, contain a greater array of defensive mechanisms which tend to reduce urchin feeding and therefore diffuse feeding over a greater number of species.

Conversely, *Diadema antillarum* (Fig. 5) and fishes (Fig. 4) showed strong inhibition to feeding on *Laurencia obtusa* (4.8% lost to urchins, 35.6% lost to fishes). *Laurencia obtusa* is not grazed by *D. antillarum* in the field according to Ogden (1976) and is reported (Norris and Fenical 1982) to be avoided by most herbivores. Norris and Fenical (1982) speculated that the toxic compound elatol which constitutes 3% dry weight of *L. obtusa*, if secreted into the surrounding microhabitat, may give this species a selective advantage over other algae by reducing the settlement and development of potential herbivores in its vicinity. This chemical interference if prevalent could also lead to the establishment of recognizable algal defense guilds (Atsatt and O'Dowd 1976), although none were observed. No feeding inhibition was shown for the closely related *L. papillosa* which does not contain high levels of elatol (92.8% lost to fishes, 71.2% lost to urchins). In contrast, the high herbivore resistance of *Gracilaria cf. debilis* throughout all experiments (Figs. 3–5) is hypothetically related to its tough rubbery texture (Littler et al. 1983) or possibly to its cryptic resemblance (mimicry?) to several of the branched corals. The relatively high palatability values (Fig. 2) obtained for the delicate forms *Spyridia filamentosa* and *Acanthophora spicifera*, as well as the low values for the tougher *Sargassum polyceratum* (Littler et al. 1983), are in close agreement with Hay (1981b, cf. Fig. 6). The low values for the Jointed Calcareous- and Crustose-Groups support the contentions of Larkum et al. (1967), Paine and Vadas (1969), Littler (1976) and Littler and Littler (1980) that calcification (and low caloric values) decreases the digestibility and energetic return to herbivores and, therefore, is important for persistence under exposure to high grazing pressures.

Field observations and laboratory experiments have provided inferences (Paul and Fenical 1983) that the substance halimedatrial (diterpenoid trialdehyde) is a potential chemical defense compound in the calcareous genus *Halimeda*. *Halimeda* was consistently the alga least preferred by *Lytechinus variegatus* (Lawrence 1975); although this tropical urchin feeds mainly on detrital leaves of the turtle grass *Thalassia testudinum* (Lowe and Lawrence 1976; Vadas et al. 1982). The last authors also point out the low overall feeding by *L. variegatus* on calcareous Chlorophyta. The tropical urchin *Tripneustes ventricosus* was suggested (Lewis 1958) to refuse *Halimeda* because of the alga's calcium carbonate. However, Paul and Fenical (1983) felt this rejection might also be attributable to the chemical halimedatrial. Therefore, the high resistance of *Halimeda* to both fish and urchin grazing (Figs. 3–5) is

likely to be the result of a synergistic spectrum of structural and chemical defensive adaptations.

Our data reveal important contrasting costs and benefits of adopting structural vs. chemical defenses. Forms that rely primarily on chemical defenses (e.g., *Dictyota cervicornis*, *Laurencia obtusa*, *Styopodium zonale*) are able to maintain high photosynthetic rates (each had the highest productivity of its respective group: Littler et al. 1983), but remain susceptible to physical forces such as wave shear and sand scour.

Contrastingly, the coarser and tougher species such as thick forms, calcareous and encrusting species resist both grazing and physical forces by means of relatively high proportions of structural materials (Littler et al. 1983), but at the cost of markedly lower photosynthetic and growth rates.

Macrophytes in the Sheet- and Filamentous-Groups (such as *Ulva lactuca*) appear to be relatively vulnerable to herbivorous fishes compared with the tougher forms. This finding agrees with statements by Lubchenco (1978) concerning the generalist snail *Littorina littorea* and the data of Littler and Littler (1980) for the generalist urchin *Strongylocentrotus purpuratus*. Some of our numbers for the Belizean tropical system, in which chemical defenses are thought (Norris and Fenical 1982) to be high, do not precisely fit temperate paradigms where the evolution of chemical defenses is reportedly low (Fenical 1980). For example, exceptions such as *Dictyota cervicornis*, *Styopodium zonale* and *Laurencia obtusa* are likely to be specialized algae that have evolved chemical defenses against herbivores (see Norris and Fenical 1982). There is no reason to predict that all species would fit the model in a linear fashion since that would imply the unlikely possibility that the same factors have controlled the evolution of all algae, or that there is only one solution to each evolutionary problem. However, the overall trends predicted here (see also Steneck and Watling 1982) consistently correlate with reported findings concerning primary productivity (Littler 1980a; Littler and Arnold 1982), toughness and calorimetry (Littler et al. 1983) and lend credence to the generality of the functional-form model.

Acknowledgements. We are grateful for the sponsorship we received from the Smithsonian Institution's Investigations of Marine Shallow Water Ecosystems Program ably directed by Klaus Rützler. Thanks are due to James N. Norris for helping identify our taxonomic vouchers, and also to he, Mark E. Hay and Robert L. Vadas for constructive comments on the manuscript. Our appreciation is sincerely extended to Kjell B. Sandved for conducting the time-lapse photography used in this study. Contribution no. 126 of Smithsonian Institution's Reef and Mangrove Study, Belize, partly supported by the Exxon Corporation.

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 (1964) The effects of fish-grazing on invertebrate evolution in shallow tropical waters. Allan Hancock Foundation Publications Occasional Papers 27:1–29
- Bakus GJ (1966) Some relationships of fishes to benthic organisms on coral reefs. *Nature (London)* 210:280–284

- Bakus GJ (1967) The feeding habits of fishes and primary production at Eniwetok, Marshall Islands. *Micronesica* 3:135-149
- Bakus GJ (1969) Energetics and feeding in shallow marine waters. *Int Rev Gen Exp Zool* 4:275-369
- Borowitzka MA (1981) Algae and grazing in coral reef ecosystems. *Endeavour* 5:99-106
- Carpenter RC (1981) Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *J Mar Res* 39:749-765
- Dart JKG (1972) Echinoids, algal lawn and coral recolonization. *Nature (London)* 239:50-51
- Fenical WH (1975) Halogenation in the Rhodophyta: a review. *J Phycol* 11:245-259
- 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, pp 144-151
- Gerwick WH (1981) The natural products chemistry of the Dictyotaceae. PhD dissertation, University of California, San Diego, Cal
- Hay ME (1981 a) The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 62:739-750
- Hay ME (1981 b) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat Bot* 11:97-109
- Hay ME (1981 c) Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *Am Nat* 118:520-540
- 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*. Proc 3rd Pacific Workshop, University of Washington Sea Grant Program
- John DM, Pople W (1973) The fish grazing of rocky shore algae in the Gulf of Guinea. *J Exp Mar Biol Ecol* 11:81-90
- Larkum AWD, Drew EA, Crossett RN (1967) The vertical distribution of attached marine algae in Malta. *J Ecol* 55:361-371
- Lawrence JM (1975) On the relationships between marine plants and sea urchins. In: Barnes H (ed) *Oceanography and marine biology*, annual review, vol 13. Allen and Unwin, London
- Lewis JB (1958) The biology of the tropical sea urchin *Tripneustes esculentus* Leske in Barbados, British West Indies. *Can J Zool* 36:607-621
- Littler MM (1976) Calcification and its role among the macroalgae. *Micronesica* 12:27-41
- Littler MM (1980 a) Morphological form and photosynthetic performances of marine macroalgae: tests of a functional/form hypothesis. *Bot Mar* 22:161-165
- Littler MM (1980 b) Southern California rocky intertidal ecosystems: methods, community structure and variability. In: Price JH, Irvine DEG, Farnham WF (eds) *The shore environment*, vol 2: *Ecosystems*. Academic Press, London (Systematics Association Special Volume 17b)
- Littler MM, Arnold KE (1982) Primary productivity of marine macroalgal functional-form groups from southwestern North America. *J Phycol* 18:207-311
- Littler MM, Doty MS (1975) Ecological components structuring the seaward edges of tropical Pacific reefs: the distribution, communities and productivity of *Porolithon*. *J Ecol* 63:117-129
- 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, Taylor PR (1983) Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J Phycol* 19:229-237
- Littler MM, Murray SN (1978) Influence of domestic wastes on energetic pathways in rocky intertidal communities. *J Appl Ecol* 15:583-595
- Lowe EF, Lawrence JM (1976) Absorption efficiencies of *Lytechinus variegatus* (Lamarck) (Echinodermata: Echinoidea) for selected marine plants. *J Exp Mar Biol Ecol* 21:223-234
- Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am Nat* 112:23-39
- Lubchenco J, Cubit J (1980) Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* 61:676-687
- Mann KH (1977) Destruction of kelp-beds by sea-urchins: a cyclical phenomenon or irreversible degradation? *Helgol Wiss Meeresunters* 30:455-467
- Montgomery WL (1980) The impact of non-selective grazing by the giant blue damselfish, *Microspathodon dorsalis*, on algal communities in the Gulf of California, Mexico. *Bull Mar Sci* 30:290-303
- Nicotri ME (1980) Factors involved in herbivore food preference. *J Exp Mar Biol Ecol* 42:13-26
- Norris JN, Bucher KE (1982) Marine algae and seagrasses from Carrie Bow Cay, Belize. In: Rützler K, Macintyre IG (eds) *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. I. Structure and communities*. Smithsonian Contributions to the Marine Sciences 12. Smithsonian Institution Press, Washington, DC, pp 167-223
- 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 Contributions to the Marine Sciences 12. Smithsonian Institution Press, Washington, DC, pp 417-431
- Ogden JC (1976) Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquat Bot* 2:103-116
- 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
- Paine RT, Vadas RL (1969) Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. *Mar Biol* 4:79-86
- Paul VJ, Fenical W (1983) Isolation of halimeda: chemical defense adaptation in the calcareous reef-building alga *Halimeda*. *Science* 221:747-749
- 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* 5:655-697
- Randall JE (1974) The effect of fishes on coral reefs. *Proc 2nd Int Coral Reef Symp*, Brisbane
- Rützler R, Macintyre IG, eds (1982) *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. I. Structure and communities*. Smithsonian Contributions to the Marine Sciences 12. Smithsonian Institution Press, Washington, DC
- 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
- Slocum CJ (1980) Differential susceptibility to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. *J Exp Mar Biol Ecol* 46:99-110
- Steel RGD, Torrie JH (1960) *Principles and procedures in statistics*. McGraw-Hill, New York
- Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar Biol* 62:299-319
- Stephenson W, Searles RB (1960) Experimental studies on the ecology of intertidal environments at Herron Island. *Aust J Mar Freshwater Res* 11:241-267
- Vadas RL, Fenchel T, Ogden JC (1982) Ecological studies on the sea urchin, *Lytechinus variegatus*, and the algal-seagrass communities of the Miskito Cays, Nicaragua. *Aquat Bot* 14:109-125
- Vadas RL, Ogden JC (1981) Comparative aspects of algal-sea urchin interactions in boreal and tropical waters. *Int Echinoderms Conf*, Tampa, Florida (abstr)
- Vermeij GJ (1978) *Biogeography and adaptation*. Harvard University Press, Cambridge, Massachusetts
- Wanders JBW (1977) The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). III. The significance of grazing. *Aquat Bot* 3:357-390