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## EVOLUTIONARY STRATEGIES IN A TROPICAL BARRIER REEF SYSTEM: FUNCTIONAL-FORM GROUPS OF MARINE MACROALGAE<sup>1</sup>

Mark M. Littler, Diane S. Littler

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560

and

Phillip R. Taylor

Division of Science and Mathematics, College of the Virgin Islands, Charlotte Amalie, Saint Thomas, U.S. Virgin Islands 00801

### ABSTRACT

Predictions of an evolutionary model were examined for 43 tropical macroalgae using a functional-form group approach. The ranking from high to low primary producers (Sheet- and Filamentous-Groups > Coarsely Branched- and Thick Leathery-Groups > Jointed Calcareous- and Crustose-Groups), and data from the literature, support the hypothesis that persistent forms which allocate resources for environmental resistance, interference competition or antiherbivory defenses do so at the cost of lower primary production rates. The results for percent thallus lost to fish grazing over a 24 h period support the hypothesis that members of the Thick Leathery-, Jointed Calcareous- and Crustose-Groups have evolved antipredator defenses, with a tendency for decreasing herbivore resistance toward the Sheet- and Filamentous-Groups. The most heavily-calcified species (e.g. crustose corallines)

ranked among the most grazer resistant as did the thick rubbery or leathery species. The ranking of functional-form group means for resistance to predation was as follows: Filamentous-Group (62% lost·24 h<sup>-1</sup>), Sheet-Group (42%), Coarsely Branched-Group (33%), Jointed Calcareous-Group (10%), Thick Leathery-Group (7%) and Crustose-Group (0%), in accordance with the hypothesis. The algal groups generally showed an increase in mean penetration toughness from filaments (<200 g·cm<sup>-2</sup> to shear thallus) to sheets (216 g·cm<sup>-2</sup>), coarsely branched forms (328 g·cm<sup>-2</sup>) and thick leathery species (1800 g·cm<sup>-2</sup>) in agreement with the predictions of the model. Contrary to earlier findings, there was no consistent gradation between the first four groups (i.e. fleshy algae) based on calorific values. However, in partial support of the functional-form model, a seven-fold difference was noted when the mean for these groups (1.7 kcal·g<sup>-1</sup>) was compared with that of the Jointed Calcareous- and Crustose-Groups (0.2 kcal·g<sup>-1</sup>). The functional-form group approach appears to have pow-

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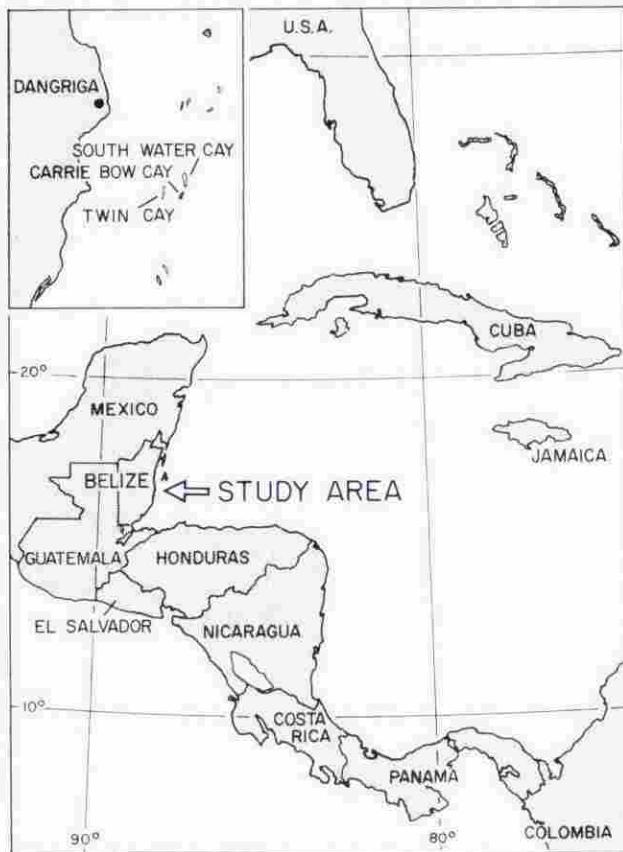


FIG. 1. Location of the study site on the Belize barrier reef.

erful capabilities in that it can indicate important morphological-metabolic-ecological interactions in a given community, where the macroalgae are known, without the need to examine each population in detail and without being constrained to a specific habitat or geographical region.

**Key index words:** tropical macroalgae; functional-form groups; productivity; herbivory; toughness; calorific values

Marine macroalgae have evolved an astounding variety of external morphologies, sizes, life histories, internal anatomical features, metabolic activities and phenotypic plasticities. However, even among widely differing phylogenetic lines (Divisions), certain forms are repeated consistently, illustrating convergent adaptations to factors that regulate survival and reproduction (i.e. fitness). Therefore, ecological analyses of factors affecting survival and reproduction in convergent form-groups have the potential to assess selective processes that regulate morphological form.

Recently, an interest has been shown in dealing with marine macroalgae from a functional-form perspective. Morphological and functional adaptations of an organism to its environment play a critical role in the fitness of individuals. For example, the turf growth forms of certain intertidal algae have been

shown (Hay 1981a) to confer tolerance to herbivory and desiccation. Also, crustose alternates in the life histories of frondose algae such as *Gigartina* are thought (Littler and Littler 1980, Lubchenco and Cubitt 1980, Slocum 1980, Dethier 1981) to allow persistence under conditions of high herbivory, and possibly severe wave shock or sand scouring (Littler and Littler unpublished). Specialized internal cytological structures to withstand current shearing (Neushul 1972, Koehl and Wainwright 1977) or to deal with various light regimes (Ramus 1978) have been identified.

Of particular value are those approaches (Littler and Littler 1980) that synthesize the adaptive significance of morphology, physiology and ecology. Several workers (Lieberman et al. 1979, Littler 1980a, Montgomery 1980a, Steneck and Watling 1982) have attempted to categorize, with varying degrees of success, marine algae into ecologically-meaningful (i.e. functional) groups. The functional-group departure provides a more utilitarian scheme than the classical "life-form" classifications of Funk (1927), Feldmann (1938, 1951, 1966) and Chapman and Chapman (1976). The primary shortcoming of these largely ignored life-form systems is that they are restricted to phylogenetic, life history and habitat attributes. We believe that a system of functional-form groups (including convergent anatomical, physiological and ecological features) that transcend phylogenetic lines represents a considerable improvement in realistically interpreting the evolutionary interactions that have resulted in such a broad array of morphological forms in marine macroalgae. Given sufficient understanding of form/function groupings, ecologists may be able to use them to interpret patterns as well as environmental or biotic relationships within a given community without having to laboriously study each component species.

The hypothetical morphological adaptations of opportunistic vs. persistent macroalgae have been postulated and contrasted by Littler and Littler (1980, see their tables 1, 2) in view of concomitant physiological and ecological trade-offs. This functional-form paradigm bears superficial resemblance to r- and K-selection concepts developed in the past decade (Pianka 1970) and to R-C-S strategies suggested (Grime 1977) for terrestrial plants. The opportunistic end of the functional-form group spectrum can be related to these concepts (high intrinsic growth rates, ruderals = early colonizers, also comparable to the ephemeral functional-group proposed by Dayton 1975). However, the inclusion of (1) physically-resistant forms and (2) predation-tolerant forms as well as (3) physiologically-resistant and (4) competitive strategists (S- and C-strategists, respectively, sensu Grime 1977) at the opposite end of the spectrum lends improved robustness to the functional-form model. It will become apparent upon examination of the form-groups proposed in this paper, that carrying capacity (the "K" in K-selection

TABLE 1. Functional-form groups for macroalgae, their characteristics and genera examined.

Functional-form group	External morphology	Internal anatomy	Texture	Genera examined
Sheet-Group	thin tubular and sheet-like (foliose)	uncorticated, one-several cells thick	soft	<i>Ulva</i> , <i>Enteromorpha</i> , <i>Dictyota</i>
Filamentous-Group	delicately branched (filamentous)	uniseriate, multiseriate or lightly corticated	soft	<i>Centroceros</i> , <i>Caulerpa</i> , <i>Spyridia</i> , <i>Chaetomorpha</i> , <i>Ceramium</i> , <i>Centroceros</i>
Coarsely Branched-Group	coarsely branched, upright	corticated	fleshy-wiry	<i>Acanthophora</i> , <i>Laurencia</i> , <i>Rhipocephalus</i> , <i>Liagora</i> , <i>Udotea</i> , <i>Caulerpa</i> , <i>Penicillus</i> , <i>Neomeris</i>
Thick Leathery-Group	thick blades and branches	differentiated, heavily corticated, thick walled	leathery-rubbery	<i>Sargassum</i> , <i>Lobophora</i> , <i>Gracilaria</i> , <i>Turbinaria</i> , <i>Padina</i> , <i>Stypopodium</i> , <i>Udotea</i>
Jointed Calcareous-Group	articulated, calcareous, upright	calcified genicula, flexible intergenicula with parallel cell rows	stony	<i>Halimeda</i> , <i>Galaxaura</i> , <i>Jania</i> , <i>Amphiroa</i>
Crustose-Group	epilithic, prostrate, encrusting	calcified or uncalcified parallel rows of cells	stony or tough	<i>Porolithon</i> , <i>Hydrolithon</i> , <i>Neogoniolithon</i> , <i>Peyssonnelia</i>

sensu Pianka 1970) is not a consideration here (e.g. long-lived algal crusts are small and very low in organic biomass per unit area). In their first tests of the model, Littler and Littler (1980) found that patterns of form and function correlated well with successional status and also degree of temporal constancy (Littler and Littler 1981). The implication is that macroalgae have evolved distinct and predictable patterns of adaptation in response to environmental stresses and disturbances; however, these predictions have been examined only for a limited number of species from a temperate system.

Western continental temperate coasts in general, and southern California in particular, are often characterized by relatively less overall herbivory than is the case for most tropical systems (Bakus 1969, Vermeij 1978, Wheeler 1980, Norris and Fenical 1982), except for urchins and gastropods in localized patches (Paine and Vadas 1969, Slocum 1980), as well as high nutrient enrichment due to sporadic upwelling (Reid et al. 1958, Bakus 1969, Jones 1971, Kimura 1974). Therefore, the robustness and generality of the functional-form model (tables 1 and 2 in Littler and Littler 1980) could be examined by parallel research in a tropical reef system, where nutrients are typically low (Bakus 1969, Vermeij 1978) and herbivory, due to urchins in patches (Ogden and Lobel 1978, Vadas 1982) and abundant and diverse fishes (Brawley and Adey 1977, Wanders 1977, Montgomery 1980a, Hay 1981b), is high. We examined aspects of the model using the functional group approach of Littler (1980a, Littler and Arnold 1982, Steneck and Watling 1982), and pre-

dicted distinct patterns linking metabolic and ecological processes with algal morphology.

#### METHODS AND MATERIALS

*Study area.* The field portion of the research was conducted at Carrie Bow Cay, Belize (16°48' N, 88°05' W, Fig. 1) during April and November 1980. 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. Carrie Bow Cay and its environs represent a well-developed biotic reef removed from the influence of industrial man. It possesses a rich and well known flora (Norris and Bucher 1982) with a detailed chemical inventory of algal natural products (Norris and Fenical 1982).

*Functional-form groups.* Herein, we have derived six functional-form groups of macroalgae (Table 1) based on convergent features that transcend taxonomic and life-history affinities. The groups are ranked according to external morphology, internal anatomy, texture and their hypothetical abilities to persist in undisturbed "mature" communities. These groupings exclude developmental stages and microscopic filamentous algae, diatoms (Bacillariophyta) and blue-green algae (Cyanophyta) due to the extreme difficulty both taxonomically and logistically in conducting appropriate experiments on them. We predicted, a priori, that if these functional-form groups are ecologically meaningful, the ranking would correlate with parameters indicative of survival strategies such as productivity, resistance to generalist herbivores, toughness and calorific values. This ranking does not imply discrete entities but is best regarded as recognizable points along a continuum. The saccate cushion-like forms (Littler 1980a) are not well represented at Carrie Bow Cay and have been eliminated from our analyses.

The functional-form group ranking (Table 1) progresses from the thin sheet and tubular (often collapsed) foliose forms (Sheet-Group) that are from one to several cells thick toward the Filamentous-Group with uniseriate or lightly-corticated filaments which usually are delicately branched. Because many members of the Filamentous-Group are somewhat corticated, they have

slightly greater surface to volume ratios than the Sheet-Group, although the order of these two groups could with equally good justification have been reversed. For this reason we do not predict a consistent ordering of comparative data between these sheets and filaments. The third functional group (Coarsely Branched-Group) is the most varied but includes coarsely-branched, upright extensively-corticated forms that range from wiry to fleshy in texture and often act to increase the spatial heterogeneity of a community. The thick bladed and branched forms (Thick Leathery-Group) tend to be thicker-walled and rubbery or leathery giving them sufficient strength to become relatively large. The upright, articulated calcified forms (Jointed Calcareous-Group) are roughly the size and shape of members of the Coarsely Branched-Group, but since they contain calcium carbonate within and on the surfaces of their cell walls, they have an extremely tough and stony texture. Because members of the Jointed Calcareous-Group are uniquely constructed of calcified segments joined by flexible intergenicula, they flex and bend in response to physical forces that would otherwise shear them. The last group (Crustose-Group) includes the prostrate, epilithic encrusting forms that characteristically have a stony (i.e. crustose Corallinaceae) or extremely tough (e.g. Peyssoneliaceae, Ralfsiaceae) texture and a relatively low surface area to volume ratio.

*Field experiments.* Specimens were collected while submerged and stored in polycarbonate trays of seawater until experimental examination. Voucher specimens of all species were preserved in 4.0% buffered formalin, labelled and deposited with the U.S. National Herbarium, Smithsonian Institution for corroboration of identifications. We concentrated on the dominant macroalgal species [see Taylor (1960) for authors of species mentioned in this paper] of Carrie Bow Cay and its environs; however, not all of the 43 species used could be obtained in amounts adequate for the large number of replicates required by our four tests. Consequently, only 13 taxa appear in all tests, but, as discussed below, they gave parallel results to those for all 43.

All representatives of the six groups (Table 1) that could be obtained in sufficient quantities were examined experimentally in terms of their productivity, predation resistance, toughness and calorific values in accordance with the predictions of the functional-form model as follows. The assumption is that for a given feature to be selected, the benefits from the investment of materials or energy from a finite pool of resources must be greater than the alternative investments within the organism's genetic limitations.

1. *Productivity Hypothesis.* Sheets and filaments should tend to show higher net primary production rates than other groups with a decline (Table 1) toward crusts, due to the increasing allocation of resources (e.g. for environmental resistance, interference competition or antiherbivory defenses) at the expense of photosynthetic tissue.

Measurements of net photosynthesis were made for 39 representatives of the six functional-form groups (four replicates each) 0.5 m deep on the shallow reef flat in a long-shore current channel. Incubation occurred between 0900 and 1500 h during April 1980 at 29° C under skies that averaged about 1500  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  Ph.A.R. (range of 500 to 2100  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Net productivity was calculated as milligrams of carbon fixed per gram dry algal weight per hour; the dry weight values for calcareous macroalgae were converted to ash free numbers following combustion at 500° C for 24 h. All algae used were from shallow habitats in full sunlight. The methods concerning the handling of algae, incubation and oxygen analysis were similar to those recommended by Littler (1979) and Littler and Arnold (1980).

2. *Predation Hypothesis.* If members of the Thick Leathery-, Jointed Calcareous- and Crustose-Groups have evolved antipredator defenses (e.g. toughness, low calorific content or toxicity), then they should show the greatest resistance to herbivory by generalist grazers with a gradation of increasing palatability toward sheets and filaments.

Natural populations of reef fishes were used to assess the pal-

atability of 16 representatives of all six algal groups. Experiments were run in the long-shore channel of the reef-flat just shoreward of the reef crest during April and November 1980. This zone is characterized by large schools of numerous surgeonfishes (Acanthuridae) and parrotfishes (Scaridae) that move freely along the channel during daylight hours. Hay (1981b) indicated that fish were the dominant grazers at Carrie Bow Cay and the zone studied here was the region of greatest herbivory. The algae were collected while submerged and returned immediately to the laboratory where they were separated into portions or clumps of equal area ( $\sim 2.5\text{ cm}^2$ ). Care was taken to ensure that the algae were not desiccated or mechanically injured during handling. 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. The algae were placed under elastic bands on four separate weighted plastic grids (70 cm  $\times$  70 cm) each containing three clumps per species arranged in mechanically-randomized patterns, vigorously dipped in seawater to dislodge any poorly attached fronds, photographed and then placed in the 1.5 m deep channel for 24 h. The entire experiment was repeated so that replication never fell below 24 per species. Similar control grids were placed in areas where fish did not graze and no measurable losses, monitored daily, occurred over a 4-day interval, although wave and current action were relatively vigorous. We usually observed immediate feeding on the experimental grids both by surgeonfishes and parrotfishes. The grids were returned to the laboratory after 24 h and re-photographed; the percent thallus area lost to grazing for each  $\sim 2.5\text{ cm}^2$  specimen was calculated from color transparencies (Kodachrome 64) by the point intercept method described in Littler (1980b).

3. *Toughness Hypothesis.* If selection for persistence has occurred in the more highly structured groups, then the groups should show an increase in toughness (resistance to penetration) from sheets and filaments toward the Crustose-Group.

A penetrometer was used to ascertain the frond toughness throughout the first four functional-form groups (10 species). Frond portions most often grazed by fishes were gently clamped between two acrylic plates across 6.5 mm diameter holes that were precisely aligned on both plates. Several fronds, tightly juxtaposed, were used for thalli with a cross section that was less than 6.5 mm. For crustose species, thalli were carefully chipped from the underlying substrate and retained for 24 h in running seawater to permit wound healing prior to use. A cylindrical steel plunger, 6.3 mm in diameter with blunted edges, attached below a 1.0 liter plastic cup, was carefully placed vertically through the hole in the upper plate so that it rested on the algal thallus. Sand was then gently titrated into the cup until the plunger sheared the thallus, simulating a penetrating fish bite, at which time the total weight of sand, cup and plunger was recorded. Calcareous species were so stony and tough that penetration did not occur within the capacity (8 kg) of this device and, consequently, no data are given for the Jointed Calcareous- or Crustose-Groups. Different individuals were used for each determination and 25 replicates were run for every species.

4. *Calorific Hypothesis.* Calorific values should decline from sheets and filaments toward crusts if selection has acted to increase structure at the cost of lipids and protoplasm in the relatively structured groups.

Samples of 19 representatives of all six groups were partially air dried on black polyethylene sheets. Upon their return to the laboratory at the University of California, Irvine, they were cleaned, briefly rinsed in distilled water and dried to constant weight at 80° C. The algae were then ground to a fine powder, pelletized and three replicates ignited in a Parr Model 1411 semi-micro oxygen bomb calorimeter. An endothermy correction was applied to our samples containing  $\text{CaCO}_3$ . The data were expressed as  $\text{kcal}\cdot\text{g}^{-1}$  dry wt. determined on replicate aliquots of the homogeneous milled samples.

*Data analysis.* The experimental design involved ranking the

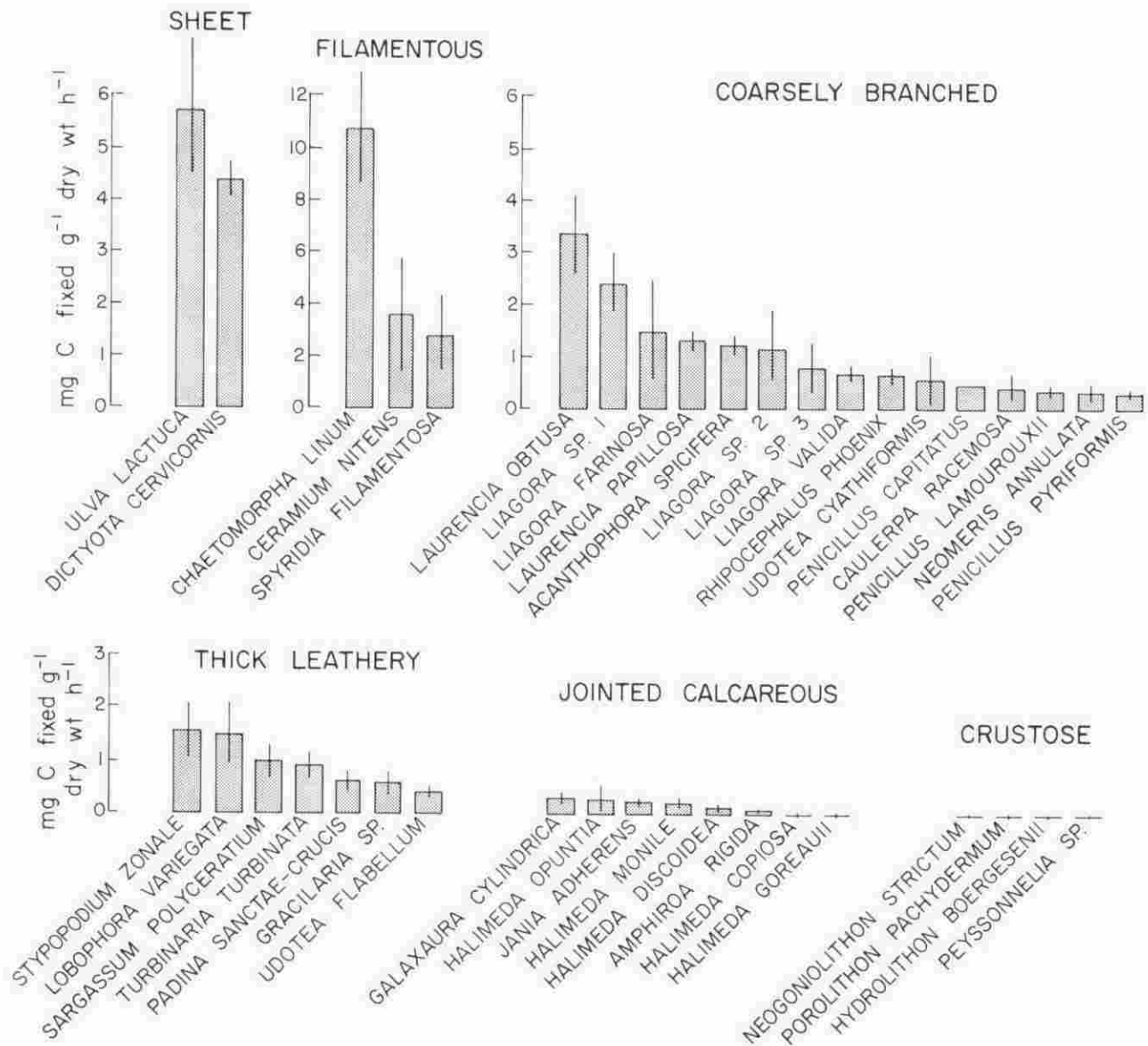


FIG. 2. Net primary productivity of macroalgal species within the six functional-form groups. Lines indicate  $\pm 95\%$  confidence limits. Note the greatly compressed scale for the Filamentous-Group.

six functional-form groups on the basis of the four empirical parameters mentioned above. 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 were primarily responsible for the evolution of all algae. The differences between the means ( $P = 0.05$ ) was assessed by both analysis of variance (Sokal and Rohlf 1969) and the Duncan's multiple range test (Steel and Torrie 1960). Because the algal groups represent a continuum, we did not expect each group to be statistically different from all others. However, groups near opposite ends of the spectrum should show statistically significant differences.

#### RESULTS

**Productivity studies.** Figure 2 shows a clear separation between the extremely low production rates of crusts and jointed calcareous species and those of all other groups. *Penicillus* spp. and *Neomeris annu-*

*lata* not unexpectedly ranked the lowest of the Coarsely Branched-Group; because of their somewhat calcareous nature they would be predicted to yield production numbers similar to those for the Jointed Calcareous- and Crustose-Groups. This same phenomenon occurred in the Thick Leathery-Group in the cases of *Padina sanctae-crucis* and *Udotea flabellum*. Also, as might be expected, the most delicate forms of each group tended to show the highest rates for their respective categories. The ranking of the means for each functional-form group (Fig. 3) from high to low producers strongly supported the productivity hypothesis with the Sheet- and Filamentous-Groups by far the highest (5.06 and 5.65 mg C  $\cdot$  g<sup>-1</sup>  $\cdot$  h<sup>-1</sup>, respectively; significantly different at  $P < 0.001$  from all other groups) followed by the Coarse-

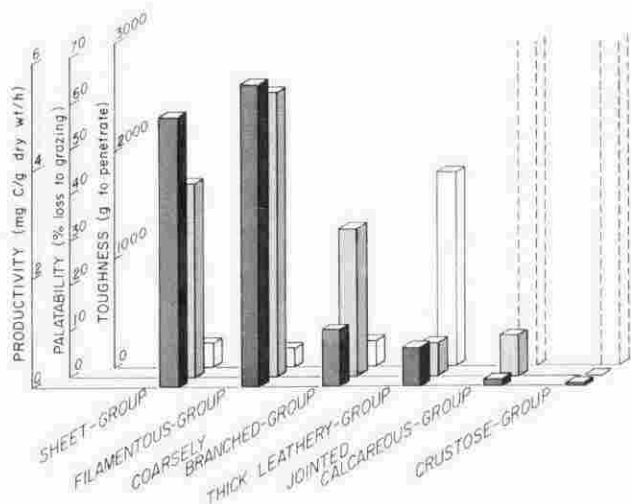


FIG. 3. Mean net primary productivity (histograms in front), palatability (middle) and toughness (rear) for the six functional-form groups. Dashed histograms indicate  $> 8$  kg (offscale) values for stony taxa.

ly Branched- and Thick Leathery-Groups (1.09 and 0.88, respectively), the Jointed Calcareous-Group (0.18) and, lastly, the Crustose-Group (0.02). The 13 species, abundant enough to be included in all four tests, showed identical productivity trends to the above.

**Predation studies.** The data for percent thallus loss to fish grazing over a 24 h period (Fig. 4) tend to support the predation hypothesis, with filaments being statistically ( $P < 0.003$ ) less resistant to herbivores than the other groups. An exception to the predicted pattern was the unexpectedly high resistance for the thin sheet form *Dictyota cervicornis*. With *D. cervicornis* omitted from the analysis, the Crustose-, Thick Leathery- and Jointed Calcareous-Groups were significantly ( $P < 0.001$ ) more resistant than any of the other groups. The same result was obtained when the 13 taxa used in all four tests were considered. The most heavily-calcified species (crustose corallines and *Amphiroa rigida*) were among the most grazer resistant (Fig. 4) as were the thick leathery species, *Gracilaria* sp., *Sargassum polyceratum* and *Turbinaria turbinata*. The ranking of the means for each functional-form group (Fig. 3) from low to high resistance was as follows: filaments (62.2% lost per 24 h), sheets (42.0%), Coarsely Branched-Group (33.2%), Jointed Calcareous-Group (9.9%), Thick Leathery-Group (7.3%) and crusts (0.0%), in accordance with the prediction.

**Toughness studies.** *Spyridia filamentosa* ( $< 200$  g·cm<sup>-2</sup> to penetrate thallus), *Dictyota cervicornis* ( $< 200$  g·cm<sup>-2</sup>) and *Ulva* sp. (231 g·cm<sup>-2</sup>), of the Filamentous- and Sheet-Groups, were the least tough (Fig. 5) even when compared to *Acanthophora spicifera* (309 g·cm<sup>-2</sup>) and *Sargassum polyceratum* (909 g·cm<sup>-2</sup>), the weakest members of the Coarsely Branched- and Thick Leathery-Groups, respectively. The heavily-calcified species characteristic of the Jointed Cal-

careous- and Crustose-Groups were carefully chipped from the substrate but could not be assessed accurately by our method (e.g.  $> 8$  kg·cm<sup>-2</sup> to penetrate thallus for three crustose corallines) because of their stony texture. However, they would obviously be the most physically resistant to the feeding apparatuses of virtually all herbivores. Consequently, we interpret these data as tending to support the toughness hypothesis, with the Thick Leathery-Group being statistically ( $P < 0.001$ ) tougher than the other groups examined. The identical trend was shown for the 13 taxa available in sufficient quantities for all four tests. This penetration toughness no doubt influences the low palatability (Fig. 4) recorded for the Thick Leathery-Group. Based on the mean numbers for all species examined (Fig. 3), the groups ranged from lowest to highest as follows: filaments ( $< 200$  g·cm<sup>-2</sup> to penetrate thallus), sheets (216 g·cm<sup>-2</sup>), coarsely branched forms (328 g·cm<sup>-2</sup>) and thick leathery species (1800 g·cm<sup>-2</sup>) in accordance with the prediction.

**Calorific studies.** There was no consistent gradation between the first four groups based on calorific data, contrary to earlier findings (Littler and Murray 1978, Littler and Littler 1980) for fleshy cold-temperate algae. However, a conspicuous difference existed when the mean for these groups (1.7 kcal·g<sup>-1</sup>, A–D in Fig. 6) was compared with that of species from the Jointed Calcareous- and Crustose-Groups (0.3 kcal·g<sup>-1</sup>), which was statistically ( $P < 0.002$ ) lower. This last point, at least partially, is consistent with the calorific hypothesis. Therefore the range of calorific values among the algae, with the exception of the Corallinaceae and a few ephemeral forms, does not seem great enough for selection to have acted upon it to the extent that Paine and Vadas (1969) and Littler and Littler (1980) proposed.

## DISCUSSION

The productivity data (Figs. 2, 3) clearly indicate a tendency for selection to have linked high net

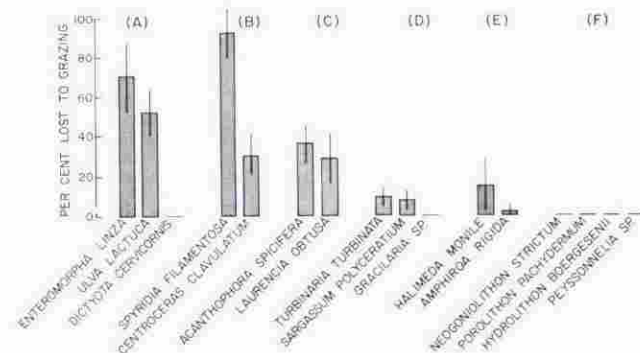


FIG. 4. Grazer susceptibility of macroalgal species within the six functional-form groups. (A) Sheet-Group, (B) Filamentous-Group, (C) Coarsely Branched-Group, (D) Thick Leathery-Group, (E) Jointed Calcareous-Group and (F) Crustose-Group. Lines indicate  $\pm 95\%$  confidence limits.

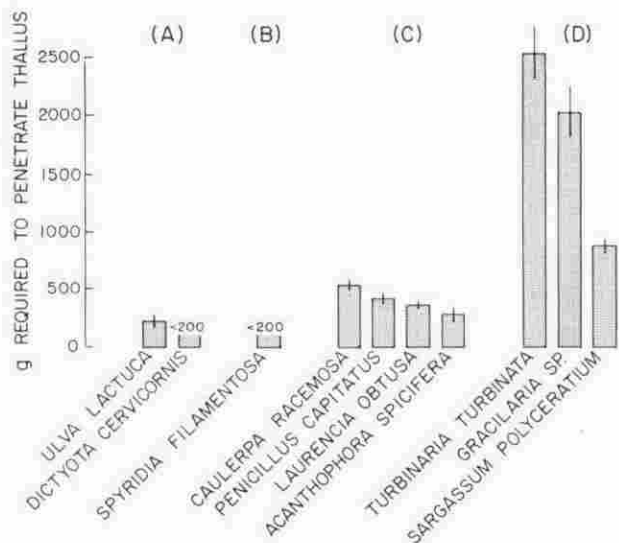


FIG. 5. Toughness of macroalgal species within the six functional-form groups. Other features are as indicated for Fig. 4. Values for stony forms were offscale.

primary productivity with morphology in the Sheet and Filamentous-Groups, while the thicker and calcareous species conspicuous in temporally constant habitats (Littler and Littler 1981), are able to persist at the cost of lower photosynthetic rates (and presumably slower potential growth rates). This is due to a differential allocation of resources and energy to photosynthetic as opposed to structural tissues. The literature in support of the productivity hypothesis is compelling. For example, Littler (1980a) noted that 45 species of macroalgae ranked as follows from highest to lowest producer: sheets > filaments > coarsely-branched forms > jointed species > thick leathery forms > crusts. The same pattern was found (Littler and Arnold 1982) for 62 different species, except that thick leathery forms exceeded jointed and crustose species. Also in agreement are the data of Odum et al. (1958), Kanwisher (1966), Littler and Murray (1974) and King and Schramm (1976), all of whom recorded that finely-branched algae with high surface to volume ratios showed greater productivities than forms with relatively low ratios, such as coarsely-branched species. As indicated by Littler (1980c), one exception to this trend involves algal turfs. It is likely that selection for resistance to heating, desiccation or grazing, by cropping exposed branch tips, has led to the tightly clumped habits of certain filamentous algae (Hay 1981a) which greatly lowers their photosynthetic capacity (Dawes et al. 1978, Littler and Arnold 1980) even though they retain high surface to volume ratios (probably negated by self-shading and overlapping diffusion gradients in the turf unit).

The higher producers have a thallus form that is better adapted to obtaining nutrients and utilizing light energy. For example, the sheet form, *Ulva*, was shown (Ramus 1978) to have an anatomy well suited

to high light conditions. Also,  $^{32}\text{PO}_4^{3-}$  uptake is more rapid (Odum et al. 1958) in algae with high surface to volume ratios. *Chaetomorpha*, *Ulva* and *Dictyota* had considerably higher apparent photosynthetic rates than any other species measured. Internal self-shading is minimized by their thin construction in accord with the interpretation of Littler (1980a) for *Ulva californica* and *Enteromorpha* sp. Because the thallus form-productivity relationship now has been documented (King and Schramm 1976, Littler 1980a, Littler and Littler 1981, Littler and Arnold 1982, this paper) over a broad latitudinal range of diverse habitats, it would appear that selection pressures for delicate thalli with rapid growth (and assumed high reproductive output), as well as selection for tougher morphologies (Figs. 3, 5) with slower growth (due to considerable structural tissues), are widespread, divergent evolutionary forces among the seaweeds.

The predation-resistance data (Figs. 3, 4) suggest a trend supportive of the predation hypothesis except for the exceptionally low preference values for *Dictyota cervicornis*. *Dictyota* (and other Dictyotales) has been shown (Gerwick 1981, Norris and Fenical 1982) to contain high quantities of unique secondary metabolites that have been experimentally documented to act as deterrents to fish in artificial systems. In this regard, two herbivorous damselfish have been shown (Montgomery 1980b) to virtually avoid *Dictyota* under natural conditions in the Gulf of California. Also, Hay (1981b) transplanted 10 thalli of *D. cervicornis* from a mangrove to a back-reef habitat at Carrie Bow Cay and recorded no individuals were eaten even though all showed small fish grazing scars. On the other hand, the low palatability of *Gracilaria* sp. (*cf. debilis*) is hypothetically related to its tough rubbery texture (or possibly to its cryptic resemblance to several of the branched corals). Concerning the species we examined in common with those of Hay (1981b), the relatively low herbivore resistance values (Fig. 4) obtained for the delicate forms (Fig. 5) *Spyridia filamentosa* and *Acanthophora spicifera*, as well as the high values for the tougher *Sargassum polyceratum*, are in close agreement (cf. table

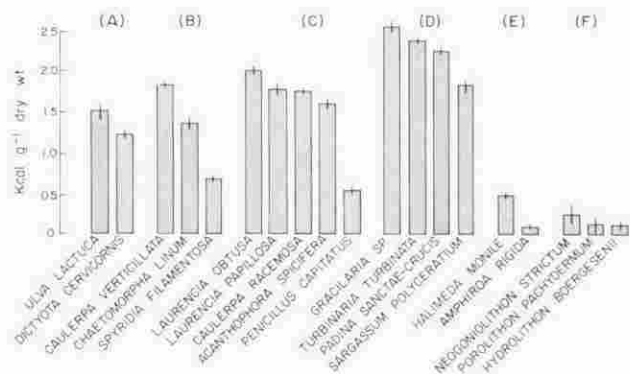


FIG. 6. Calorific values of macroalgal species within the six functional-form groups. Other features are as indicated for Fig. 4.

II in Hay 1981b). The high 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 calorific values decrease the digestibility and energetic return to herbivores and, therefore, are important for persistence under exposure to high grazing pressures. Macrophytes in the Sheet- and Filamentous-Groups (such as *Ulva*) appear to be relatively vulnerable to the spectrum of herbivorous fishes compared with the tougher forms, which agrees with statements by Lubchenco (1978) concerning the generalist snail *Littorina littorea* and the data of Littler and Littler (1980) on the generalist urchin *Strongylocentrotus purpuratus*. It should be acknowledged that different groups (guilds?) of herbivores may have been involved in the evolution of various algal forms. Because most of the published palatability data are for temperate macroalgae where the evolution of toxic chemical defenses is thought to be low (Fenical 1980), our numbers for a tropical system where chemical defenses are implicated (Norris and Fenical 1982) to be high, do not precisely fit temperate models. For example, exceptions to the functional-form model such as *Dictyota* are likely to be species that employ chemical defenses against herbivory (Gerwick 1981).

The ranking of penetrometry data (Figs. 3, 5), strongly supports the toughness hypothesis. It would seem that algae in the more highly structured groups have gained persistence in time at the cost of decreased primary productivity by diverting substantial resources away from photosynthetic components. Tough algae, in addition to being more resistant to the feeding mechanisms of most grazers, have the ability to withstand abrasion and wave-shearing forces, as well as being able to interfere with more delicate competitors for light and space by a whiplash effect (Dayton 1975).

Our calorific data, while not showing as consistent a pattern as that predicted, did agree with the findings of Littler and Murray (1978), Paine and Vadas (1969) and Littler and Littler (1980), in that heavily-calcified algae had markedly lower values (seven times lower, Fig. 6, same trend for the 13 species common to all tests). This observation verifies the suggestion (Paine and Vadas 1969, Littler 1976) that crustose calcareous forms may have reduced their appeal to predators through evolution of thalli which are tough and low in nutritive content. The low calorific numbers for jointed calcareous algae (Fig. 6) are in accord with the data of Littler and Murray (1978) for other members of that group (*Corallina*, *Haliptylon* and *Lithothrix*) from a temperate system. In view of these probable defenses, it is not surprising that concomitant secondary metabolites, abundant enough to be of possible anti-herbivore significance, have not been found (Fenical, personal communication) in any of the dozens of temperate or tropical Corallinaceae examined.

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