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RELATIONSHIPS BETWEEN MACROALGAL FUNCTIONAL FORM GROUPS AND SUBSTRATA STABILITY IN A SUBTROPICAL ROCKY-INTERTIDAL SYSTEM

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Abstract: The general hypothesis that morphological, physiological, and ecological adaptations of macroalgal functional-form groups can be related to the level of disturbance encountered in a natural environment was examined. Two articulated calcareous coralline algae (*Amphiroa van-bosseae* Lemoine, 24% cover and *Corallina frondescens* Post. & Rupr. 20%) and one non-articulated coralline alga (*Lithophyllum* sp., 16%), all late-successional predation-tolerant strategists, comprise most of the community cover on stable bedrock substrata at Punta Las Cuevitas, Sonora, Mexico. Conversely, *Ulva rigida* C. ag. (26% cover) and a ralfsioid crust (23%), shows to be early-successional opportunistic strategists, cover more of the disturbed boulder habitat. *Porolithon sonorense* Daws., a stress-tolerant strategist, is uniquely abundant on both substratum types (13% cover on boulders, 10% on bedrock). The sheet-like and filamentous algae, prevalent in the temporally unstable habitat, generally show greater productivity ($> 2 \times$) than the thicker and calcareous forms conspicuous in the more constant environment. It appears that selection for delicate thalli with high productivities, as well as selection for tougher morphologies having lower photosynthetic rates due to greater proportions of structural tissues, are widespread, divergent evolutionary forces among marine algae. Experiments with captive sea urchins (*Echinometra vanbrunti* Agassiz), in conjunction with fish-preference data published for some of the same algae studied here, offer strong support for the functional-form model. Parrotfishes, rudderfishes, surgeonfishes, damselfishes and *E. vanbrunti*, in the Gulf of California, preferentially feed on delicate, early-successional, sheet-like, and filamentous algae, while rejecting or ignoring the more structured, late-successional and calcareous algae. There is no significant ($P > 0.05$) gradation in calorific content between the first four of the six functional groups (i.e., Sheet-, Filamentous-, Coarsely Branched- and Thick Leathery-Groups), but the mean value for these fleshy forms (2.6 kcal · g ash-free dry wt⁻¹) is significantly greater than that for the last two groups (0.3 kcal, Jointed Calcareous- and Crustose-Groups). The approach used in this study demonstrates a realistic technique for predicting macrophyte community composition from knowledge of the disturbance levels in a given habitat or the reverse. The form group-disturbance relationship has important implications for future biological monitoring of rocky-intertidal and subtidal systems.

INTRODUCTION

Survival mechanisms (sensu Grime, 1979) have developed in response to biotic and abiotic selective forces encountered by species throughout their evolutionary histories. Morphological and functional adaptations play critical roles in the survival and reproduction of macroalgal individuals in a given environment. For example, the turf forms of certain intertidal algae lessen mortality to herbivory and desiccation (Hay, 1981a). Specialized internal structures help withstand hydrodynamic forces (Koehl & Wainwright, 1977) or confer adaptive advantages under various light regimes (Ramus,

1978). Also, crustose alternates in the life-histories of frondose algae, such as *Gigartina* and *Scytosiphon* (Littler & Littler, 1980, 1983; Lubchenco & Cubitt, 1980; Slocum, 1980; Dethier, 1981), increase survival under conditions of high herbivory and, possibly, physical disturbances in the case of sand-scour (Littler & Littler, 1983). A similar adaptive relationship exists for heterotrachous algae, such as *Corallina officinalis* (Littler & Kauker, unpubl.), where the reproductive and more productive upright axes contrast with slower growing grazer- and disturbance-resistive prostrate axes of the same plant thallus. Each of the above studies focused on some form of environmental disturbance, from biological perturbations (e.g., herbivory) to dealing with physical forces (e.g., shearing and abrasion). Disturbances of these kinds occur sporadically throughout most rocky-intertidal communities.

In intertidal boulder fields (Littler, 1977; Osman, 1977; Sousa, 1979a; Littler & Littler, 1981), loose substrata are moved about by storm waves and patches of organisms are killed. Since small boulders are more easily overturned and battered than large ones, the frequency of disturbance is inversely proportional to boulder size (Cimberg *et al.*, 1973; Osman, 1977; Sousa, 1979a). Because the probability of substratum disturbance is spatially and temporally heterogeneous, boulder fields develop into mosaics of communities undergoing different phases of succession. Littler & Littler (1980, 1983) examined the adaptations of representative macroalgae from experimentally-determined successional stages and explored the physiological and ecological trade-offs associated with different morphologies. Distinct relationships exist between form and function that correlated with successional status, thereby implicating predictable patterns of macroalgal adaptation in response to the extremes of disturbances likely to be encountered.

Because seaweeds are recognized by their morphology, it has proven to be instructive for ecologists to quantify the morphological correlates of algal functional properties relative to the environmental factors normally experienced. The functional-form approach is of particular value in categorizing marine algae into ecologically-meaningful groups (Littler, 1980a; Littler & Arnold, 1982; Steneck & Watling, 1982; Littler *et al.*, 1983a,b). Functional-form data (e.g., unpublished productivity values of Littler) were used successfully as early as 1976 (Wynne & Norris) to compare the taxonomy of three Gulf of California species of *Colpomenia* (i.e., a thin sheet form, a thick form, and a branched form). Ecological, physiological, and developmental characteristics are intimately related through anatomical features in marine macroalgae, because structure at the lower levels of organization ultimately allows, regulates and limits every biological function. Since morphological parameters can be measured accurately and easily, they could provide a sound basis for the analysis of complex ecosystems. Here, we examine the overall postulate that the morphological, physiological, and ecological adaptations of algal functional-form groups can be related to the level of disturbance encountered in a natural environment. We predict that frequently-disturbed habitats will contain more abundant populations of the less-structured form groups (Table I, Groups A & B), whereas the more temporally-constant environments will be dominated by groups

TABLE I
Functional-form groups of predominant macroalgae; their characteristics and taxa examined.

Functional-form group	External morphology	Internal anatomy	Texture	Taxa examined
A. Sheet-Group	thin tubular and sheet like (foliose)	uncorticated, one-several cells thick	soft	<i>Colpomenia phaeodactyla</i> Wynne & J. Norris <i>Dictyota dichotoma</i> (Huds.) Lamour. <i>Ulva rigida</i> C. Ag.
B. Filamentous-Group	delicately branched (filamentous)	uniseriate, multiseriate or lightly corticated	soft	<i>Caulerpa van-bosseaee</i> Setch. & Gardn. <i>Chondria californica</i> (Collins) Kylin <i>Gelidium johnstonii</i> Setch. & Gardn. <i>Giffordia</i> sp.
C. Coarsely Branched-Group	coarsely branched, upright	corticated	fleshy-wiry	<i>Codium simulans</i> Setch. & Gardn. <i>Colpomenia sinuosa</i> (Roth.) Herb. & Sol. <i>Colpomenia tuberculata</i> Saund. <i>Euchuma uncinatum</i> Setch. & Gardn. <i>Laurencia johnstonii</i> Setch. & Gardn. <i>Lomentaria catenata</i> Harvey
D. Thick Leathery-Group	thick blades and branches	differentiated, heavily corticated, thick walled	leathery-rubbery	<i>Padina durvillaei</i> Bory <i>Sargassum herporhizum</i> Setch. & Gardn. <i>Sargassum johnstonii</i> Setch. & Gardn.
E. Jointed Calcareous-Group	articulated, calcareous, upright	calcified genicula, flexible intergenicula	stony	<i>Amphiroa van-bosseaee</i> Lemoine <i>Corallina frondescens</i> Post. & Rupr.
F. Crustose-Group	epilithic, prostrate, encrusting	calcified or uncalcified parallel cell rows	stony or tough	<i>Lithophyllum</i> sp. <i>Pyssonnella</i> sp. <i>Porolithon sonorense</i> Daws. raffisioid crust

at the opposite end of the spectrum. If the predicted correlations of morphological forms (Table I) with complementary physiological and ecological processes do not emerge from comparisons of algal assemblages on small unstable boulders with those on stable bedrock substrata, then we will deem the hypothesis falsified.

MATERIALS AND METHODS

STUDY AREA

The field work was conducted during 15–22 January 1981 in the eastern Gulf of California at Punta Las Cuevitas, Sonora, Mexico (Fig. 1, $112^{\circ}30'W$: $29^{\circ}16'N$). The general study area was selected (after reconnaissance of several hundred kilometers of shoreline) as representative of broad coastal habitat types in the upper Gulf of California, throughout which we have been conducting research for the past decade (Littler & Littler, 1981). Because this intertidal region has not been studied previously,

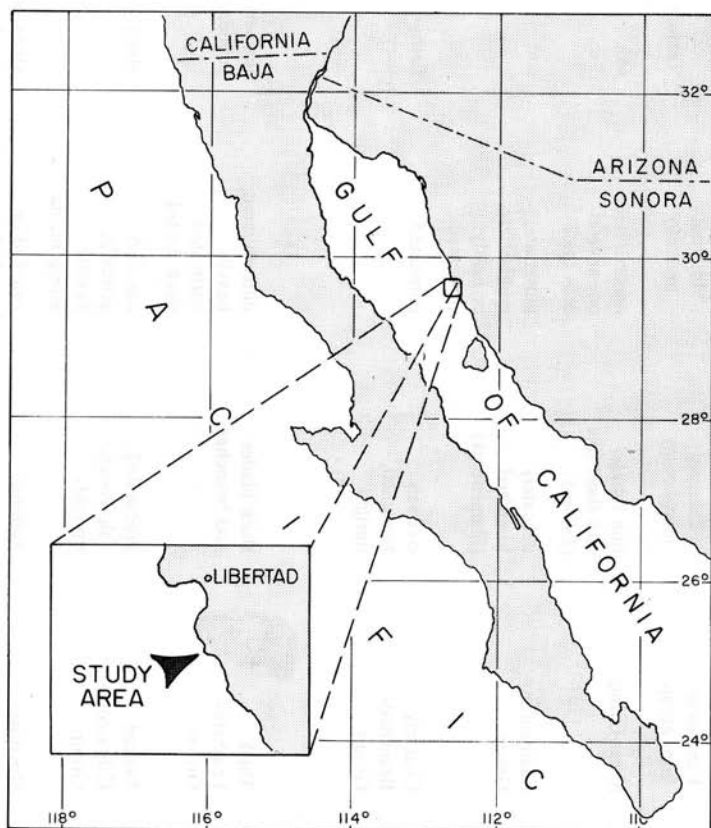


Fig. 1. Location of the study site at Punta Las Cuevitas, Sonora, Mexico.

it presented us with an unbiased means of testing our a priori predictions relating algal form groups with environmental disturbances. The study site is characterized by a shallow slope consisting of medium-sized (mostly ≈ 1.0 -m diam.) metamorphic boulders and bedrock projections. The terrestrial climate of this area is desert-like (Roden, 1964) with only 49 mm of rainfall per year (Hastings & Humphrey, 1969). Water surface temperatures vary from 15 to 30 °C yearly (Brusca, 1973) and extreme insolation, heat and desiccation stresses occur during the summer low-tide periods (Norris, 1975). Water temperatures throughout our visit ranged from 13 to 20 °C and salinity was constant at 35‰. Air temperature fluctuations were from 12 to 22 °C with 80–95% relative humidity. Variations in the maximum yearly tidal amplitude are ≈ 5.0 m. Although occurring twice daily, the tides are somewhat irregular (Dawson, 1944).

FUNCTIONAL-FORM GROUPS

We employed six of the seven functional-form groups (Table I) proposed by Littler (1980a) and used successfully by Littler & Arnold (1982), Steneck & Watling (1982) and Littler *et al.* (1983a,b). The groups transcend phylogenetic and life-history affinities, and are ranked according to external morphology, internal anatomy, texture, and hypothetical abilities to persist in undisturbed "mature" communities. Due to taxonomic and technical difficulties, developmental stages, microscopic filamentous algae, diatoms (Bacillariophyceae) and blue-green algae (Cyanophyceae) are not included. We predicted, that if the six functional-form groups are ecologically meaningful, their ranking would correlate with parameters indicative of survival mechanisms such as productivity, susceptibility to herbivores with broad diets, penetration resistance, calorific content and allocation of photosynthetic vs. structural components. The ranking of groups does not imply discrete entities, but is to be regarded as recognizable points along a continuum.

The functional-group ranking (A–F) 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 assemblages could, with equally good justification, have been reversed. For this reason we do not predict a consistent ordering of comparative data between the 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. Only the upright frond portions of this group were examined. The last group (Crustose-Group) includes the prostrate, epilithic encrusting forms that characteristically have stony (i.e., crustose Corallinaceae) or extremely tough (e.g., Peyssonneliaceae, Hildenbrandiaceae, Ralfsiaceae) textures and relatively low surface-area to volume ratios.

FIELD EXPERIMENTS

Specimens were collected while submerged and stored in polycarbonate trays of sea water until experimental examination. Voucher specimens of all species were preserved in 4.0% buffered formalin sea water, labelled, mounted and deposited with the U.S. National Herbarium, Smithsonian Institution for corroboration of identifications by Dr. J. N. Norris. The authors of the species we studied are given in Table I. We concentrated on the dominant macroalgal species of Punta Las Cuevitas and the nearby area; however, not all of the 22 taxa used could be obtained in quantities adequate for the large number of replicates required by each of our five tests. Also, time constraints permitted the examination of only five species in the captive urchin study. However, the same 16 taxa were used throughout the remaining four tests, with two additional species included in the penetration and structural studies and six taxa added to the productivity analyses.

COMMUNITY COMPOSITION

Macroalgal communities were contrasted for boulders vs. stable bedrock substrata within the same tidal interval (-0.5 to -0.8 m, MLLW). Fifteen 20×50 -cm quadrats were sampled on each of the two substratum types. All quadrats were chosen by stratified sampling at fixed intervals along a transect line laid out at the desired tidal height by means of a surveyor's transit and stadia rod. The precise location of the origin of the transect line was determined by the blind toss of a metal marker. Boulders examined ranged from 50 to 100 cm along their longest sides. Species locations were mapped on quadrat diagrams in the field and used in the laboratory as an aid in scoring infra-red and color photo-samples of each quadrat by means of the photogrammetric method (Littler, 1980b). The scored data were then used to compare per cent cover, frequency, richness (Margalef's (1968) D') and diversity (Shannon-Weaver (1949) H') between the two substratum types.

All representatives of the six groups (Table I) that could be obtained in sufficient quantities were examined experimentally in terms of their productivities, predation resistances, structural components, penetration toughnesses and calorific values in accordance with the predictions of the functional-form model as outlined below.

Productivity hypothesis

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

Measurements of net photosynthesis were made for 22 intertidal representatives of the groups (six replicates each). Incubation occurred between 0900 and 1500 on 15 and 16 January 1981 at 18 °C under skies that averaged $\approx 1600 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (range of 600 to 2100 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ Ph.A.R.). Net productivity was calculated as mg of carbon fixed per g dry algal wt per h; the dry-wt 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 & Arnold (1980).

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 least susceptibility to herbivory by generalist (i.e., having diverse diets) grazers with a gradation of increasing susceptibility toward sheets and filaments.

Although considerable effort was expended, no reliable data on fish herbivory were obtained by our suspended-line technique (Littler *et al.*, 1983b) because of extensive nearshore gill-netting. Fortunately, an excellent data set exists (Montgomery, 1980a,b; Montgomery & Gerking, 1980; Montgomery *et al.*, 1980) concerning herbivorous fish preferences in the Gulf of California for some of the same macrophytes and fishes studied here.

We did examine the susceptibilities of five species, from four of the form-groups, to grazing by the sea urchin *Echinometra vanbrunti* Agassiz. Thirty medium-sized (mean test diam.: ≈ 3 cm) *E. vanbrunti* were collected just beneath the water level at low tide. The urchins were placed in separate 2-l, wide-mouth canning jars with the hinged lids slightly open (≈ 4 cm) to prevent escape but to allow gas exchange. The 30 jars were partially submerged in trays of sea water that were frequently replenished for temperature stabilization. Paired ≈ 10 -cm discs of the five test algae were photographed and presented to individual urchins during each paired-choice feeding trial. One sample of every algal pair was always the brown alga *Colpomenia tuberculata*, which served as the basis for comparison between species. Control discs were placed in trays without urchins to determine surface area losses due to wounds or disintegration. The feeding trial lasted 24 h (on 21–22 January 1981), after which the specimens were recovered, rephotographed and quantified as above (Littler, 1980b). All urchins remained healthy during the experiment and were released into their original habitat on 22 January 1981.

Structural hypothesis

The Sheet- and Filamentous-Groups should have greater proportions of photosynthetic volume if selection has resulted in allocation of more materials to structural components in the groups near the opposite (crustose) end of the spectrum.

Cross-sections about one cell thick were made with a freezing microtome for all living thallus parts of the 18 test algae. For each species, 10 different individuals were used. Coralline algae, because of their calcification were not sectioned. Instead, the CaCO_3 content was used as a conservative estimate of the percentage of non-photosynthetic structure. Data were obtained by scoring the per cent pigmented area of fleshy forms using an ocular grid and a Wild M20 fluorescence microscope that precisely revealed the photosynthetically active areas.

Toughness hypothesis

If selection for persistence has occurred in the more highly structured forms, then the groups should show an increase in penetration resistance from sheets and filaments toward the Crustose-Group.

A penetrometer was used in the field to determine the frond penetration resistance throughout the six groups (18 species). Freshly-collected frond portions 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 of < 6.5 mm. For crustose species, flat portions of thalli were carefully separated from the underlying substratum. A cylindrical steel plunger, 6.3 mm in diameter with blunted edges, attached below a 1-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 penetrated the thallus, at which time the total weight of sand, cup, and plunger was recorded. Calcareous crustose species were so stony and tough that penetration did not occur within the capacity (8 kg) of this device and, consequently, data for the Crustose-Group are given as "offscale". Different individuals were used for each determination and 25 replicates were run for every species.

Calorific hypothesis

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

Samples of 16 representatives of all six groups were partially air dried on black polyethylene sheets. Upon their return to the laboratory, 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) semimicro, oxygen bomb calorimeter. An endothermy correction was applied to samples containing CaCO_3 . The data were expressed as $\text{kcal} \cdot \text{g ash-free dry wt}^{-1}$.

DATA ANALYSIS

The experimental design involved ranking the six functional-form groups on the basis of the five empirical parameters mentioned above. There is no reason to predict that all species should fit the model in a linear fashion since that would imply the unlikely possibility that the same factors are primarily responsible for the evolution of all algae. The differences between the means ($P = 0.05$) was assessed by both analysis of variance (ANOVA) (Sokal & Rohlf, 1969) and Duncan's Multiple Range Test (Steel & Torrie, 1960). To test objectively our overall postulate relating functional-form groups to ecological and physiological factors we performed a multiparameter cluster analysis of the 16 species common to all tests (except predation resistance). The productivity, structural vs. photosynthetic, toughness and calorific data for all possible pairs of macrophytes were compared by Bray-Curtis similarity coefficients and subjected to hierarchical cluster analysis (flexible sorting) by the unweighted pair-group method (Sokal & Sneath, 1963). This technique enabled us to identify complex multispecies groupings in an unbiased manner. 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 significant differences.

RESULTS

COMMUNITY COMPOSITION

The algal communities of the stable bedrock substrata exceeded those of the boulders in every parameter examined. For example (Fig. 2), a total of 18 species was found in the bedrock samples while only 10 occurred in the boulders, D' richness was 13.2 vs. 7.8 ($P < 0.05$, ANOVA and DMRT), H' diversity was 1.95 vs. 1.28 ($P < 0.05$)

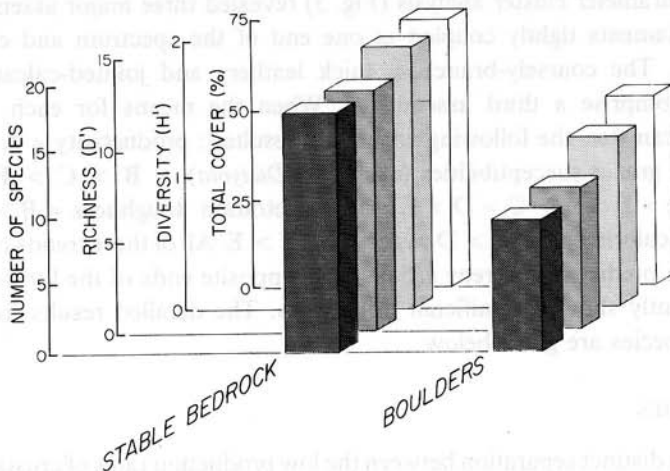


Fig. 2. Community parameters contrasting the boulder and bedrock substratum types.

and percent cover was 75 vs. 53. The primary cover organisms on bedrock are the articulated coralline algae *Amphiroa van-bossea* (24%) and *Corallina frondescens* (20%) and the crustose coralline *Lithophyllum* sp. (16%). Cover on the boulders consists predominantly of the fleshy forms *Ulva rigida* (26%) and ralfsoid crust (23%). The crustose coralline *Porolithon sonorense* is fairly abundant on both substrata (13% cover on boulders, 10% on bedrock). *Gelidium johnstonii*, while low in cover ($\approx 1\%$), also occurred frequently in samples from both habitats (14% of boulder samples, 13% of bedrock). *Valoniopsis pachynema* (Mart.) Børg. (14% bedrock frequency vs. 4% on boulders) and *Colpomenia tuberculata* (12% vs. 5%) were common only in the bedrock samples.

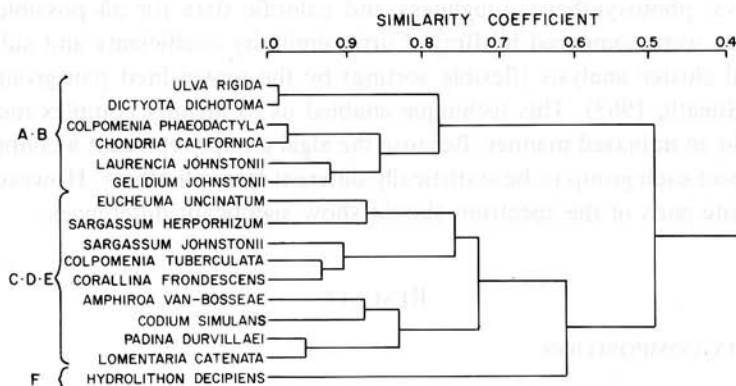


Fig. 3. Dendrogram display of differential clustering of those 16 species common to all tests (except grazer susceptibility) using combined productivity, photosynthetic volume, penetration resistance and calorific data.

The multiparameter cluster analysis (Fig. 3) revealed three major assemblages with sheets and filaments tightly coupled at one end of the spectrum and crusts at the opposite end. The coarsely-branched, thick leathery and jointed-calcareous forms grouped to comprise a third assemblage. When the means for each group were ranked by parameter, the following sequences resulted: productivity = A > B > D > C > E > F, grazer susceptibilities (excluding *Dictyota*) = B > C > F, photosynthetic volume = B > A > C > D > E > F, penetration toughness = B > A > C > E > D > F and calorimetry = B > D > A > C > F > E. All of these trends coincide with the tendencies predicted, whereby groups near opposite ends of the form-group spectrum consistently showed significant differences. The detailed results for individual groups and species are given below.

PRODUCTIVITIES

There was a distinct separation between the low production rates of crusts and jointed calcareous species (Fig. 4) and those of the remaining four groups. The means for each

group ranked from high to low as predicted by the productivity hypothesis, except Group-D was greater than Group-C (Fig. 4) due to the unexpectedly high photosynthetic rate of *Sargassum herporhizum* ($2.5 \text{ mg C} \cdot \text{g dry wt}^{-1} \cdot \text{h}^{-1}$). The means ranged as

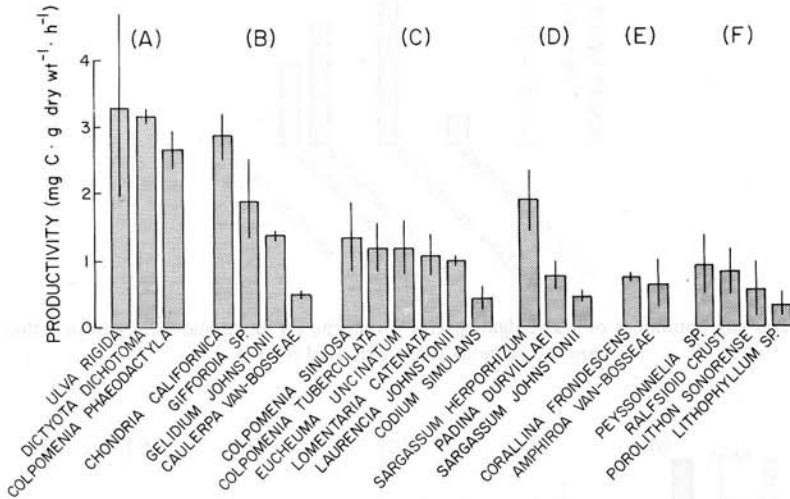


Fig. 4. Net primary productivities of macroalgal species within the six functional-form groups: A, Sheet-Group; B, Filamentous-Group; C, Coarsely Branched-Group; D, Thick Leathery-Group; E, Jointed Calcareous-Group; and F, Crustose-Group; lines indicate $\pm 95\%$ confidence intervals.

follows: Sheet-Group = $3.05 \text{ mg C} \cdot \text{g dry wt}^{-1} \cdot \text{h}^{-1}$, Filamentous-Group = 1.59 , Thick Leathery-Group = 1.26 , Coarsely Branched-Group = 1.07 , Jointed Calcareous-Group = 0.75 and Crustose-Group = 0.73 .

GRAZER SUSCEPTIBILITIES

Because our suspended-line fish-grazing experiments produced minimal results (due to gill-netting activities by local fishermen), only the data for captive sea urchins can be presented. Because of time constraints, only five species of algae representing four of the six functional-form groups could be offered in choice tests to *Echinometra vanbrunti* (Fig. 5). The data, although limited, tend to support the predation hypothesis, except for the exceptionally low susceptibility of *Dictyota dichotoma* (Group-A) to grazing by *E. vanbrunti*. The ranking of each form-group representative (Fig. 6), from high to low susceptibility, was as follows: *Caulerpa van-bosseae* (filament, 49.1% lost $\cdot 24 \text{ h}^{-1}$), *Eucheuma uncinatum* and *Codium simulans* (coarsely branched, 31.6% and 15.7% lost, respectively), *Dictyota dichotoma* (sheet, 6.0%) and ralfsoid crust (3.2%).

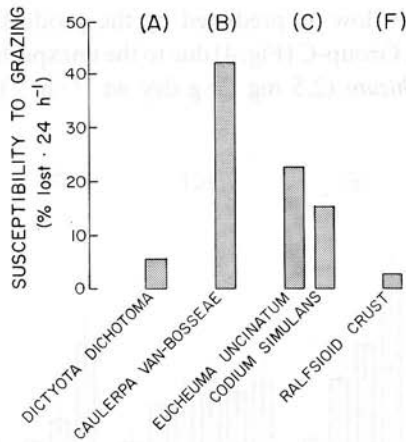


Fig. 5. Grazer susceptibilities of macroalgal species within the six functional-form groups: other features are the same as those indicated for Fig. 3.

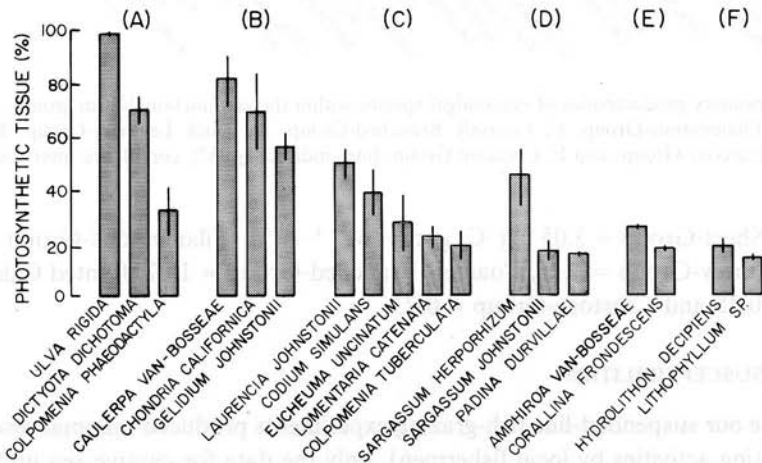


Fig. 6. Percent photosynthetic volume of macroalgal species within the six functional-form groups: other features are the same as those indicated for Fig. 3.

PHOTOSYNTHETIC VS. STRUCTURAL CONTENTS

The mean values for the six groups ranged from high to low (Fig. 6) in close agreement with the prediction, thereby supporting the structural hypothesis: Group-B = 69.0% photosynthetic volume, Group-A = 68.3%, Group-C = 31.6%, Group-D = 26.6%, Group-E = 22.5% and Group-F = 17.1%. *Ulva rigida* (sheet) contained the highest percentage (99%) of photosynthetic volume followed by *Caulerpa van-bosseae* (filament, 82%), *Dictyota dichotoma* (sheet, 71%) and *Chondria californica* (filament, 70%). The

heavily-calcified coralline forms (Fig. 6), as expected, had the lowest photosynthetic/structural volume ratios.

PENETRATION RESISTANCES

Based on the mean numbers for all 18 species examined (Fig. 7), the groups ranged from lowest to highest as follows: Sheet-Group ($10.0 \text{ g} \cdot \text{mm}^{-2}$ to penetrate thallus),

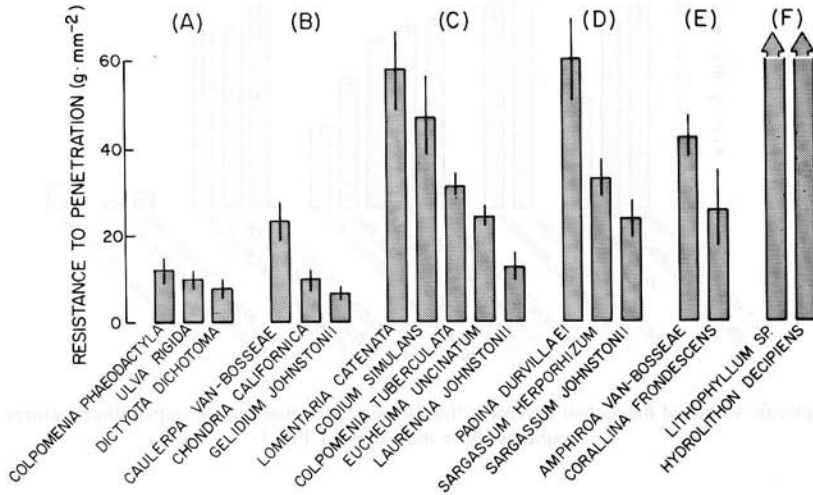


Fig. 7. Penetration resistances of macroalgal species within the six functional-form groups: other features are the same as those indicated for Fig. 3; values for crusts were offscale.

Filamentous-Group (13.3 g), Coarsely Branched-Group (34.4 g), Jointed Calcareous-Group (34.5 g), Thick Leathery-Group (38.8 g) and Crustose-Group ($> \text{offscale}$) in accordance with the prediction. All members of the Sheet- and Filamentous-Groups were less resistant to penetration than members of any of the remaining groups (Fig. 7). The crustose corallines were by far the most resistant to penetration ($> 1.5 \text{ kg} \cdot \text{mm}^{-2}$ to penetrate) followed by the thick-leathery *Padina durvillaei* ($60 \text{ g} \cdot \text{mm}^{-2}$) and the coarsely-branched *Lomentaria catenata* (58 g) and *Codium simulans* (47 g). While the relatively delicate forms of jointed-calcareous algae present at this site were not particularly resistant to penetration (Fig. 7), because of their stony texture (see Steneck & Watling, 1982) they and the crustose corallines would obviously be the most physically resistant to the scraping and rasping action of virtually all epilithic herbivores (e.g., *Collisella dalliana* Pilsbry, *Tegula rugosa* Adams, *Nerita funiculata* Menke, *Onchidella binneyi* Stearns).

CALORIFIC VALUES

There was no consistent gradation between the first four groups (A–D) based on calorific values, therefore falsifying the calorific hypothesis at this level. However, a conspicuous difference is observed when the mean for replicates within these groups

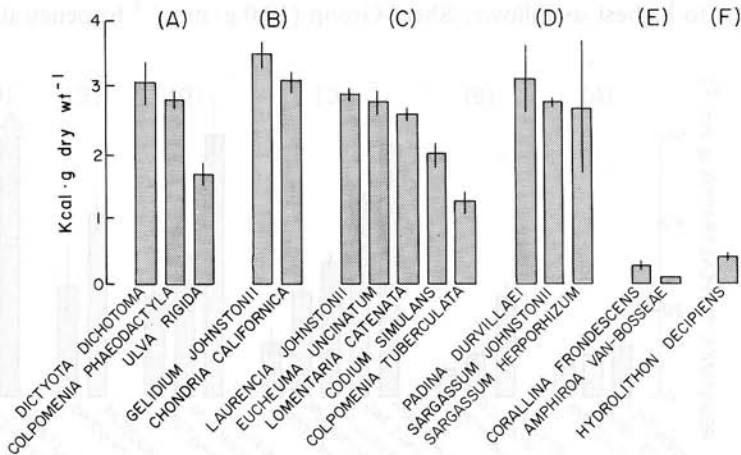


Fig. 8. Calorific values of macroalgal species within the six functional-form groups: other features are the same as those indicated for Fig. 3.

($2.6 \text{ kcal} \cdot \text{g}^{-1}$, A–D in Fig. 8) is compared with that from the Jointed Calcareous- and Crustose-Groups ($0.3 \text{ kcal} \cdot \text{g}^{-1}$, E and F) which is significantly lower ($P < 0.001$). This last point partially supports the calorific hypothesis.

DISCUSSION

Species from three of the functional groups (A, E and F) dominate boulder and bedrock biotic cover (Fig. 9). Two jointed calcareous corallines (*Amphiroa van-bosseae* and *Corallina frondescens*) and one crustose coralline (*Lithophyllum* sp.) comprise the primary portion of the community on stable bedrock substrata, whereas the thin sheet, *Ulva rigida*, covers more of the disturbed boulder habitat than any other species. Interestingly, the crustose ralfsioid is far more abundant (23% cover) on the boulders. The ralfsioid crust very likely represented a mixture of the crustose alternates (see Clayton, 1981) in the heteromorphic life-histories of the three *Colpomenia* (Scytosiphonales) species that were present.

Such *Ralfsia*-like crusts appear to be somewhat enigmatic (Dethier, 1981; Littler & Littler, 1983), when viewed from the functional-form perspective. For example, Dethier (1981) stated that *Ralfsia californica*, the alternate of another upright species of Scytosiphonales, lies in an unusual middle region between opportunistic and late-

successional forms, and our standing-stock data for the ralfsioid crust concur with this interpretation. Such ralfsioid alternates can be rapid colonizers on new surfaces (Dethier, 1981; Littler & Littler, 1983), relatively short-lived (7–12 month lifespan),

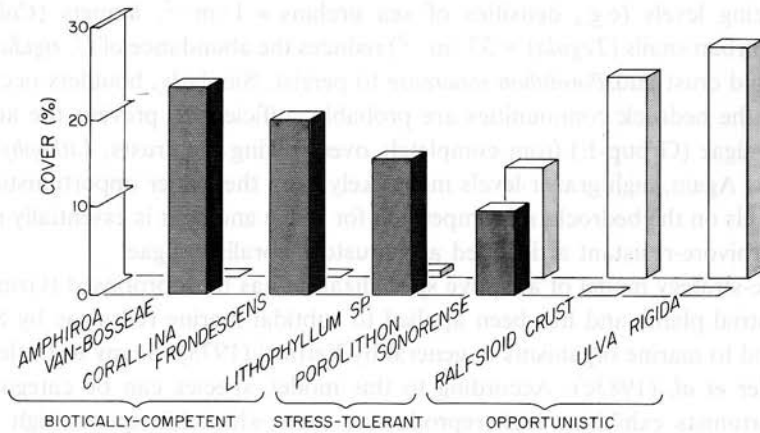


Fig. 9. Dominant cover (%) of macrophytes and their survival strategies (sensu Grime, 1979) on boulder (light histograms in rear) and stable bedrock (dark histograms in front) substrata.

continually reproductive and poor competitors (Dethier, 1981). However, as predicted and shown by Littler & Littler (1983), one ralfsioid scytosiphonalean alternate also has high herbivore resistance, low calorific values, and relatively low photosynthetic to structural tissue proportions concomitant with reduced production rates; all characteristics associated with species prevalent in mature communities.

The resolution of this seeming contradiction lies in a close morphological examination of the ralfsioid crust. While it possesses a crustose morphology, the ralfsioid crust is relatively thin ($< 300 \mu\text{m}$). Therefore, it cannot be unequivocally placed in the Crustose-Group of Littler (1980a) since most members of that assemblage are defined as heavily-calcified (e.g., crustose Corallinaceae) or much thicker (e.g., *Pseudolithoderma nigra*). Steneck & Watling (1982) dealt with this problem by including such non-calcified crusts within the intermediate Thick Leathery-Group, but, in fact, the thin morphology of the ralfsioid form could justify placement nearer the Sheet-Group (Littler 1980a), even though it has a recumbant or prostrate habit. Possibly the best interpretation is that it is specialized for habitats that are periodically disturbed and physiologically stressful (see Dethier, 1981) and such specialization has pulled it away from easy categorization in any general scheme. Consequently, the abundance of the ralfsioid crust on the unstable boulders is, in retrospect, not surprising.

The crusts (Group-F) are the only morphological form to comprise a large proportion of the cover in both habitats. Disturbances from summer stresses (Littler & Littler, 1981), grazing or rock-tumbling probably play a large role in reducing the levels of *Ulva rigida* and the articulated corallines that have the capacity to overgrow the crusts in their

respective habitats, thus allowing for coexistence. The prostrate crustose growth form is highly resistant to physical disturbances and grazing (Littler & Doty, 1975). The fact that *U. rigida* (a potential competitive dominant; Sousa, 1979b) does not completely overgrow the boulders suggests that disturbance from substratum instability or due to high grazing levels (e.g., densities of sea urchins = $1 \cdot \text{m}^{-2}$, limpets (*Collisella*) = $7 \cdot \text{m}^{-2}$, turban snails (*Tegula*) = $37 \cdot \text{m}^{-2}$) reduces the abundance of *U. rigida* allowing the ralfsioid crust and *Porolithon sonorense* to persist. Similarly, boulders occasionally abrading the bedrock communities are probably sufficient to prevent the articulated coralline algae (Group-E) from completely overgrowing the crusts, *Lithophyllum* and *Porolithon*. Again, high grazer levels most likely keep the leafier opportunistic species at low levels on the bedrock, so competition for space and light is essentially restricted to the herbivore-resistant articulated and crustose coralline algae.

A three-strategy model of adaptive specialization has been proposed (Grime, 1977) for terrestrial plants and has been applied to subtidal marine red algae by Shepherd (1981) and to marine organisms in general by Vermeij (1978), Seapy & Littler (1982), and Littler *et al.* (1983c). According to this model, species can be categorized as: (1) opportunists exhibiting high reproductive rates, short life spans, high dispersal abilities, reduced long-term competitive capacities, and occupying ephemeral or disturbed habitats; (2) stress-tolerant forms which can tolerate chronic physiological stress, exhibit low recolonization rates, tend to be long-lived with slow growth and, consequently, are generally poor competitors; and (3) biotically-competent forms that generally live in physiologically-favorable environments, have long life spans, are good competitors, and have evolved mechanisms to avoid predation. In the rocky intertidal zone, Vermeij (1978) identified stress-tolerant forms as characteristic of the upper intertidal, while biotically-competent taxa are prevalent in the lower intertidal. Opportunistic forms are ephemeral on disturbed or newly-available substrata.

The Grime model represents a workable framework within which to interpret differences between the boulder and stable bedrock populations at Punta Las Cuevitas. The boulder-field dominants at this site (Fig. 9) are *Ulva rigida* and the ralfsioid crust, characterized by our data and others as opportunistic, and *Porolithon sonorense*, documented to be a stress-tolerant strategist. The first two are most abundant and, hypothetically, are favored by the regular tumbling of the rocks by wave action. Such disturbances would lead to mortality by (1) abrasion, (2) movement from well lit to less favorable positions and (3) smothering (when communities become buried in sediments on the lower rock surfaces). The result is a continual provision of new space, analogous to sewage-induced mortalities (Littler & Murray, 1975), with a dramatic reduction in the slower recruiting biotically-competent forms.

On stable bedrock, disturbance is low but grazing by abundant sea urchins, snails and limpets is presumably high, leading to forms such as *Amphiroa*, *Corallina*, and *Lithophyllum* (Fig. 9), which are characterized as being biotically-competent (predation-resistant). *Porolithon sonorense* is uniquely abundant on both substratum types. As mentioned above, the perennial crustose genus *Porolithon* may be a stress-tolerant

strategist (sensu Grime, 1979); e.g., *P. sonorensis* (Littler & Littler, 1981) and two other species of *Porolithon* have been shown (Adey & Vassar, 1975; Littler & Doty, 1975) to be particularly resistive to environmental stresses.

The productivity data (Fig. 4) show a tendency for net apparent photosynthetic rates to be linked with morphological form. The Sheet- and Filamentous-Groups, which are more prevalent in temporally-unstable habitats, are generally more productive than the thicker and calcareous species (Groups D, E and F) that are conspicuous in more constant environments. Two exceptions to this pattern are: *Caulerpa van-bossea*, with a photosynthetic rate that is low for Group-B, and *Sargassum herporhizum*, which has high productivity for Group-D. The low rate for the former is predictable. *Caulerpa van-bossea* forms a thick turf-like mat and was incubated in its natural clumped form. Littler & Arnold (1980) and Hay (1981a) have reported markedly lower rates for turf algae when compared with incubations done on their artificially dispersed thalli. It is likely that selection for resistance to desiccation and heating, as well as herbivory (Hay, 1981a; Montgomery, 1981), by increasing density via cropping of exposed branch tips, have led to the tightly clumped habits of certain filamentous algae. The result is greatly lowered photosynthetic capacities (Dawes *et al.*, 1978; Littler & Arnold, 1980), even though such turfs have high surface/volume ratios. As pointed out by Littler & Arnold (1980), the advantages of high surface/volume ratios are negated in the clumped form by overlapping diffusion gradients and self shading. In contrast, the comparatively high photosynthetic rate of *S. herporhizum* is no doubt due to its finely dissected morphology which gives it an unusually high surface to volume ratio when compared with other members of Group-D. The relatively high photosynthetic tissue volume (47.7%), greater exchange surfaces in contact with the aquatic milieu, and the increased diversity of surface angles used to capture light throughout a given photoperiod also should increase the photosynthetic capacity.

The literature in support of the productivity hypothesis is compelling. Patterns similar to that found here have now been documented (Odum *et al.*, 1958; Kanwisher, 1966; Littler & Murray, 1974; King & Schramm, 1976; Littler, 1980a; Littler & Littler, 1981; Littler & Arnold, 1982; Littler *et al.*, 1983a) over a broad latitudinal range of diverse habitats. Therefore, it is apparent that there are two widespread, divergent evolutionary forces among marine algae: (1) selection for delicate thalli (Fig. 7) with high productivities (Fig. 4); and (2) selection for tougher morphologies, having lower photosynthetic rates due to greater proportions of structural tissues (Fig. 6).

Our limited sea urchin susceptibility data (Fig. 5) suggest a trend supportive of the predation hypothesis except for the exceptionally low preference values for *Dictyota dichotoma*. *Dictyota* (and other Dictyotales) contains large quantities of unique secondary compounds (Gerwick, 1981; Norris & Fenical, 1982) that disrupt fish metabolism in artificial situations. *Dictyota cervicornis* has been documented (Hay, 1981b; Littler *et al.*, 1983a) as having exceptional resistance to fish grazing on a Belizian barrier reef. In addition, herbivorous damselfishes, rudderfishes, parrotfishes, and surgeonfishes all avoid eating *Dictyota* under natural conditions in the Gulf of California (Montgomery 1980a,b; Montgomery *et al.* 1980).

The extensive fish-preference data obtained by Montgomery (1980a,b), Montgomery & Gerking (1980) and Montgomery *et al.* (1980) for some of the same fishes and algae studied here, afford strong independent support for our predation hypothesis, as well as for the functional-form model (Littler & Littler, 1980). One example, the giant blue damselfish, *Microspathodon dorsalis*, feeds almost exclusively on the small extremely-delicate, nutritionally-rich and highly-productive, ephemeral red alga *Polysiphonia*, which it maintains by weeding slower-growing, late-successional, tough algae from its territories (Montgomery, 1980a). In the case of the highly-selective Cortez damselfish, *Eupomacentrus rectifraenum*, the thin early-successional *Ulva* is preferred along with fleshy red algae, while late-successional brown algae such as *Dictyota*, *Sargassum*, and *Padina*, as well as calcareous Rhodophyta, are shunned (Montgomery, 1980b).

Similar results, in strong support of the functional-form model, have been noted for other herbivorous reef fishes as well. Tropical rabbitfishes (Siganidae; Tsuda & Bryan, 1973; Von Westernhagen, 1974) and temperate blennioids (*Cebidichthys violaceus* and *Xiphister mucosus*, Montgomery, 1977; Horn *et al.*, 1982) also select fleshy red forms and delicate, early-successional, sheet-like and filamentous green algae, while rejecting or ignoring brown and calcareous algae. Preference patterns in accordance with the above findings additionally have been shown (Montgomery *et al.*, 1980) for parrotfishes, rudderfishes and the surgeonfish, *Prionurus punctatus*, in the southern Gulf of California. The avoidance of *Dictyota* sp., *Padina* sp., *Sargassum* sp. and *Liagora* sp. by herbivorous fishes produces refuges for opportunistic delicate algae under their canopies.

The ranking of percent photosynthetic volumes (Fig. 6) strongly supports the structural hypothesis. It would appear that seaweeds in the more structured groups have gained persistence in time at the cost of decreased primary productivity (Fig. 4) by diverting substantial resources to non-photosynthetic structural tissues. The tougher algae (Fig. 7), in addition to being less susceptible to the feeding mechanisms of most herbivores (Steneck & Watling, 1982), have the added ability to withstand abrasion and wave-shearing (Littler & Littler, 1983). The larger tough forms (e.g., *Lomentaria catenata* and *Sargassum johnstonii*) may be able to interfere with their more delicate competitors by the brushing or lashing effect shown (Dayton, 1975) for some temperate zone kelps.

There was no significant ($P > 0.05$) gradation between the first four groups (A–D) based on calorific data, contrary to earlier interpretations (Littler & Murray, 1978; Littler & Littler, 1980) for fleshy cold-temperate zone seaweeds, but in agreement with recent findings (Littler *et al.*, 1983a) for tropical algae. The significant difference ($P < 0.001$), when the mean for fleshy algae ($2.6 \text{ kcal} \cdot \text{g ash-free dry wt}^{-1}$, A–D in Fig. 8) was contrasted with that for calcareous species (0.3 kcal), at least partially, is consistent with the calorific hypothesis. We conclude that the range of ash-free calorific values among the algae, with the exceptions of the very low values for Corallinaceae and some high values for a few ephemerals, does not appear great enough for selection to have acted upon it to the degree postulated by Paine & Vadas (1969) and Littler & Littler (1980).

The presence of the ralfsioid crust, *Ulva rigida* and the coralline algae in their

respective habitats (Fig. 9) supports the overall prediction that opportunistic species should predominate in the disturbed boulder area, while biotically-competent late-successional forms should be the primary species of the bedrock habitat. Opportunistic and biotically-competent life forms lie at the perturbational-successional extremes outlined by Littler & Littler (1980, shown in their Table I), while, as demonstrated above, encompassing the complementary costs and benefits postulated in their Table II. This functional-form model bears superficial resemblance to *r*- and *K*-selection concepts (Pianka, 1970) and to R-C-S strategies proposed (Grime, 1977) for land plants. The opportunistic portion (Groups A and B) of the functional-group spectrum is relatable to these concepts (cf. R-strategists of Grime, 1977; ephemeral functional groups of Dayton, 1975). However, in addition to physiologically-tolerant and competitive strategists (S- and C- sensu Grime, 1977), the functional-form paradigm incorporates (1) physically-resistant forms (disturbance-tolerant, D-strategists) as well as (2) predation-tolerant forms (P-strategists) at the opposite end of the spectrum to improve robustness. It is apparent that the array of form groups in Table I is not based on "carrying capacity" (K-selection sensu Pianka, 1970). For example, organic standing stocks of crustose and jointed calcareous algae tend to be potentially small per unit of area relative to those for Groups D or E.

Our results demonstrate it is now within the realm of possibility to predict community compositions from knowledge of disturbance levels in given environments, or the reverse. Further, the approach is applicable anywhere the predominant algal abundances are known without being restricted by phylogenetic group, habitat, or geological era (e.g., see Steneck & Watling, 1982). The form-group disturbance relationship has important implications for establishing future biological monitoring programs for rocky-intertidal and subtidal systems.

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