LITTLER, MARK M. AND LITTLER, DIANE S.: A RELATIVE-DOMINANCE MODEL FOR BIOTIC REEFS, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

We propose a relative-dominance paradigm (Fig. 1) that predicts which of the following four major space-occupying groups of sessile photosynthetic organisms will dominate as a function of long-term nutrient levels and herbivore activity: (1) corals, (2) coralline algae, (3) fleshy macroalgae, and (4) microfilamentous algae.

All of these sessile organisms compete vigorously for space and light and each group can predominate given specific environmental conditions. Variations in the levels of grazing and wave shock (physical disturbance) and limiting or toxic nutrient levels (physiological stress), hypothetically, lead to spatial segregation of coral-, coralline-, or fleshy algal-dominated communities between or within habitats (Fig. 1), or they may lead to temporal separations important during succession and reef biogenesis.

Corals, while preyed upon by certain omnivorous fishes and sea urchins, generally gain primacy under intensive herbivory, moderate levels of wave shear, and very low nutrient concentrations. With an increase in the amount of nutrients, the growth of short-lived filamentous and leafy algae is favored over the slower-growing corals and the latter become susceptible to competition for space unless they can attain a refuge in size.

Conversely, coralline algae predominate in areas of moderate to heavy grazing (or heavy wave shear) and are generally not inhibited by moderate to high levels of nutrient enrichment.

Eutrophic waters, where grazing and wave ripping are low, tend to favor large standing stocks of frondose macroalgae that can overgrow and kill both coralline algae and corals. When nutrient levels are low and grazing activity low to moderate, microfilamentous forms with greater surface area to volume ratios tend to predominate.

The relative-dominance paradigm (Fig. 1) appears superficially related to the 3-strategy model of Grime (1979) for terrestrial plants. Grime postulated that land plant biomass and evolutionary trends are controlled primarily by physiological stress (factors that limit metabolic production) and physical disturbance (factors that remove biomass). Evolutionary interactions have led to (1) opportunists (= ruderals; R-adapted) under conditions of low stress and high disturbance, (2) stress tolerant forms (S-adapted) under high stress and low disturbance, and (3) good competitors (C-adapted) where both stress and disturbance are low. Littler and Littler (1984) added (4) predation-tolerant and (5) physically-resistant forms (P- and D-adapted, respectively) where stress is low and disturbance high. Our paradigm for biotic reefs (Fig. 1) differs from Grime's (1979) by (a) including the last two survival mechanisms as exemplified by long-lived calcifying corallines and corals and (b) by emphasizing the variable (limiting vs. toxic) role of nutrients as stress factors. Therefore, nutrient levels in our model do not coincide with the unidirectional stress gradient of Grime (1979), and evolutionary outcomes (i.e., P- and D-adaptations) other than opportunism are possible under high levels of disturbance on reefs.

The role of stochastic events must be considered in any model of relative dominance for reef systems. For example, extremely heavy herbivore pressure may keep even well-defended organisms at inconspicuous levels within predominantly microfilamentous communities due to inadvertent grazing. If, however, some chance environmental factor alters herbivory long enough, populations of unpalatable organisms may bloom and reach a critical mass. Such individuals then attain a "refuge in abundance" and potentially remain constant over long periods under the same environmental conditions that formerly maintained them as rare components of a completely different community. Also, in the case of unpalatable organisms, removal of epibiota and microfilamentous competitors by "optimal" levels of predation may increase local standing stocks. The predictions of the relative-dominance model should be regarded only as general tendencies. Obviously. the same selective factors have not operated on all major reef organisms to the same extent and there may be more than one possible solution to a given evolutionary problem.

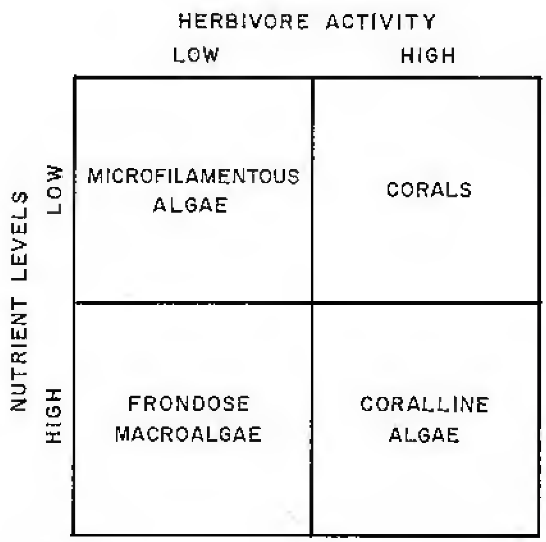

Figure 1. Relative dominance model--Four potentially predominant space-occupying groups of sessile reef organisms are hypothesized to interact as a function of (1) long-term nutrient levels and (2) disturbances such as herbivore activity. The latter is considered the more important direct controller of standing stocks on undisturbed reefs.

Literature Cited

Grime, J.P., 1979. Plant strategies and vegetation processes. John Wiley & Sons, New York, 222 pp.

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