

FACTORS CONTROLLING RELATIVE DOMINANCE OF PRIMARY PRODUCERS ON BIOTIC REEFS

FACTEURS QUI CONTROLENT LA DOMINANCE RELATIVE DES PRODUCTEURS PRIMAIRES DANS LES RECIFS CORALLIENS

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ABSTRACT

Tropical reefs represent some of the most luxuriant natural ecosystems known and stand out as productive "gardens" in many of the world's nutrient-poor warm oceanic systems. We present a relative-dominance paradigm that predicts which of four major space-occupying groups of sessile photosynthetic organisms will tend to dominate on reefs as a function of long-term nutrient levels and herbivore activity: (a) symbiotic zooxanthellae within hermatypic corals, (b) coralline algae, (c) frondose macroalgae and (d) microfilamentous algae. All of these groups of sessile primary producers compete vigorously for space and light and each 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 or coral-, coralline-, or fleshy algal-dominated communities between or within habitats or they may result in temporal separations important during succession and reef biogenesis.

Corals 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. 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 algae with greater surface area to volume ratios tend to predominate; however, these forms also appear opportunistically in any system where physical disturbances make newly cleared free space available.

RESUME

Les récifs coralliens des régions tropicales sont parmi les écosystèmes naturels les plus exubérants et apparaissent comme des "jardins" très productifs dans nombre de systèmes océaniques à température élevée mais pauvres en éléments nutritifs. Nous donnons un paradigme de la dominance relative qui permet de prévoir lequel des 4 groupes principaux d'organismes photosynthétiques sessiles qui occupent l'espace considéré, tendra à être dominant sur les récifs en fonction des taux de substances nutritives et de l'activité des herbivores : (a) les zooxanthelles symbiotiques à l'intérieur des coraux hermatypiques, (b) les corallinacées, (c) les macro-algues à grandes frondes ou (d) les micro-algues filamenteuses. Tous ces groupes de producteurs primaires sessiles sont en compétition pour la place et la lumière, et chacun d'eux peut devenir dominant selon les conditions spécifiques de l'environnement. Les variations dans l'action des herbivores, dans l'impact de la houle, et dans la limitation ou même la toxicité d'éléments nutritifs, aboutissent théoriquement à une ségrégation spatiale, entre différents habitats ou au sein d'un même habitat, des biotopes dominés soit par les coraux, soit par les corallinacées, ou par les algues à thalle charnu, ou bien, ces variations peuvent amener une importante séparation dans le temps au cours de la succession écologique et de la biogénèse récifale. En général, les coraux deviennent dominants lorsque l'activité des herbivores est intense, en cas de faible arasement par la houle et lorsque le milieu est pauvre en éléments nutritifs. Si la concentration en éléments nutritifs augmente, la croissance des algues filamenteuses ou foliacées à courte durée de vie est favorisée. Au contraire, les corallinacées dominent là où l'activité herbivore est moyenne ou très développée (ou là où l'effet de la houle est très important) et ne sont en général pas retardées dans leur développement par des taux moyens ou élevés d'apports nutritifs. Les eaux eutrophiques, où l'activité herbivore et l'action des vagues sont minimes, tendent à favoriser de grandes populations d'algues foliacées géantes qui peuvent recouvrir et tuer les corallinacées aussi bien que les coraux. A des niveaux nutritifs plutôt bas, avec une action des herbivores limitée ou modérée, les micro-algues filamenteuses, au rapport surface/volume plus élevé, prédominent; toutefois, ces formes peuvent apparaître dans tout système où des changements physiques dégagent de nouveaux espaces accessibles à ces opportunistes.

Tropical reefs represent some of the most luxuriant natural ecosystems known (Westlake 1963; Lewis 1977) and stand out as productive "gardens" in many of the world's nutrient-poor warm oceanic systems. The photosynthetic organisms responsible are (a) symbiotic zooxanthellae within hermatypic corals, (b) coralline algae, (c) large frondose macroalgae and (d) small frondose algae (microfilamentous forms and thin sheet forms).

On reefs not dominated by corals, non-articulated coralline algae or various frondose algae usually comprise the majority of plant cover. Larger frondose algae occur abundantly on shallow reef flats (Doty 1971; Wanders 1976; Connor and Adey 1977), unstructured sand plains (Earle 1972; Dahl 1973; Hay 1981a) or deep-water sites (Littler et al. 1985) where herbivory is very low. Frondose macroalgae are generally restricted from reef slopes by high rates of grazing (Littler and Doty 1975; Wanders 1976; Hay 1981b; Hay et al. 1983; Hatcher and Larkum 1983). The sparseness of microfilamentous algae on shallow reef-front systems dominated by corals and corallines also is thought (Randall 1961; Wanders 1977; Borowitzka 1981) to primarily result from intensive grazing by the numerous herbivores and omnivores inhabiting these spatially heterogeneous systems. Where spatial rugosity is minimal or wave turbulence is high on tropical reefs, herbivore activity is reduced (Brock 1979; Hay et al. 1983; Adey and Vassar 1975) and reasonably large standing stocks of the bigger macrophytes (*Sargassum*, *Turbinaria*, *Acanthophora*) often develop (Doty 1971; Connor and Adey 1977; Wanders 1976).

The predominance of the coralline genus *Porolithon* as a builder of algal ridges (Littler 1973, Adey and Vassar 1975) seems to be directly determined by interspecific competition under the indirect influences of wave force, grazing and high light intensity. Transplant and ecophysiological experiments indicated (Littler 1973; Littler and Doty 1975) that the dominance of *Porolithon* on algal ridges is due to a combination of (1) its physiological tolerance and (2) physical nature. First, its stress-resisting physiology gives it competitive advantage over corals and other corallines intertidally in direct sunlight. Secondly, it is relatively insensitive to the ripping forces of waves, and resistant to grazing by echinoderms, gastropods and fishes that tend to remove the fleshy algae and delicate corals that overgrow it under other circumstances.

Model of relative dominance -- We herein present a relative-dominance paradigm (Fig. 1) whereby four major space-occupying groups of sessile photosynthetic organisms are emphasized as a function of long-term nutrient levels and physical disturbances (i.e., processes that reduce biomass): (1) corals, (2) coralline algae, (3) large fleshy macroalgae and (4) the smaller frondose algae (including the juvenile stages of macroalgae). Dominance here refers to the acquisition and preemption of the major resource of horizontal space. All of the above sessile organisms compete vigorously for space (e.g. Littler and Doty 1975; Wanders 1977; Buss and Jackson 1979; Hay et al. 1983) and each group can dominate under specific environmental conditions (Fig. 1).

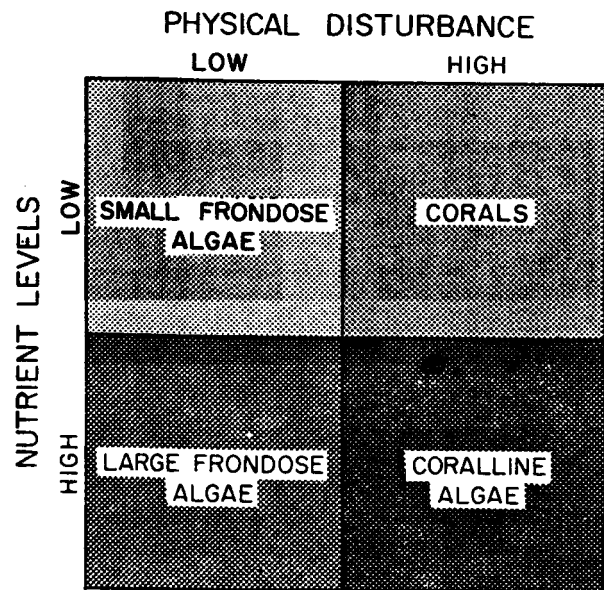


Figure 1. Diagrammatic representation of the relative-dominance model. Potentially predominant space-occupying groups of photosynthetic reef organisms are emphasized as a function of long-term nutrient levels and disturbance. Hermatypic corals are hypothesized to be the competitive dominants, while coralline algae are projected as the poorest competitors but the most physically resistant group. Grazing is considered the more important direct controller of algal standing stocks on undisturbed reefs, whereas nutrients set the potential upper limits to biomass.

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 micro- and macroalgal dominated communities between or within habitats (Fig. 1), or they may lead to temporal separations important during succession and reef biogenesis. The predictions of the relative-dominance model, elaborated below, 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 (e.g. toxicity) to a given evolutionary problem.

Corals are the hypothetical competitive dominants on pristine reefs according to our model (Fig. 1). Their massive growth forms, longevity and symbiotic relationships allow them to compete strongly for space, light and low levels of nutrients. Corals, while preyed upon by certain omnivorous fishes (Neudecker 1977) and sea urchins (Glynn et al. 1979), generally should gain primacy under intensive herbivory (Brock 1979), moderate levels of wave shear and very low nutrient concentrations (e.g. Kealakekua Bay, Fig. 2). However, high nutrient levels are inhibitory allowing competitive interactions between macroalgae, microfilamentous algae and corallines. Townsley (cited in Doty 1968, 1969) found that some

Hawaiian corals (e.g. *Porites compressa*) are extremely susceptible to increased phosphate concentrations, which are known (Simkiss 1964) to inhibit calcium deposition. The decrease in coelenterate coral cover, relative to macroalgae (Doty 1971) and corallines (Littler 1971), such as has occurred on the reef flat at Waikiki, Oahu (Fig. 2) over a 45-yr span has been correlated (Littler 1973) with increases in nutrients from eutrophication due to municipal sewage effluents that impinged upon the reef (Laevastu et al. 1964).

Macroalgae are predicted to dominate in undisturbed situations where nutrient levels are sufficient to maintain a large biomass. Eutrophic waters, where grazing and wave ripping are low should favor large standing stocks of frondose macroalgae that can overgrow and kill both coralline algae (Littler and Doty 1975; Wanders 1977; Adey et al. 1977) and corals (Banner 1974; Potts 1977; Antonius 1982).

Interactions between sewage eutrophication and fish grazing appeared (Banner 1974; Smith et al. 1981) to alter the competitive dominance of the macrophyte *Dictyosphaeria cavernosa* over corals (particularly *Porites compressa*). This green alga overgrew and killed many of the formerly luxuriant coral communities, in association with nutrient enrichment due to sewage effluents, throughout Kaneohe Bay, Hawaii. As mentioned earlier (Birkeland 1977), filamentous and fleshy algae outcompete corals

(which may be inhibited) under elevated nutrient levels. Perturbation studies concerning the effects of fertilization on reef communities have been conducted (Kinsey and Domm 1974; Kinsey and Davies 1979; Smith et al. 1979) that showed substantial enhancement of photosynthesis but, because of methodological limitations, no significant changes could be detected in the standing stocks of plants or corals.

When nutrient levels are low and grazing activity low to moderate, macroalgae do poorly and microalgal forms (i.e. filaments and sheets, including the juvenile forms of macroalgae) with greater surface area to volume ratios should tend to predominate. Also, one would expect these highly productive forms (Littler et al. 1983) to appear opportunistically in any system where extreme physical disturbances make newly cleared free space available.

Conversely, non-articulated coralline algae are predicted to be the poorest competitors (Fig. 1) and should prevail only in consistently disturbed areas of moderate to heavy grazing or heavy wave shear. They are not expected to be inhibited by moderate to high levels of nutrient enrichment.

Extremely high wave shear forces and aerial exposure, such as present on the intertidal leading edges of reef crests, presumably result in the reduction of physiologically susceptible corals, and provide a refuge for gastropod grazers from their predators. This allows the physiologically and physically resistant forms of corallines such as *Porolithon* and *Lithophyllum* to predominate and form algal ridges (Littler and Doty 1975).

Significant erosion of the algal ridge by the scraping and rasping actions of echinoderms, sipunculid worms, mesogastropod limpets and other organisms has been recorded at Raroua Atoll (Doty 1954; Doty and Morrison 1954; Newell 1954), St. Croix (Adey and Vassar 1975), Oahu Island (Littler 1973) and Guam (Littler 1976); however, this may be more of a mutualistic relationship than is readily apparent. Hypothetically, rasping and scraping organisms may be acting to prevent "fouling" of the coralline crusts by reducing softer organisms. For example, limpet grazing, by removing blue-green algal epiphytes and inhibitory epithelial cells (Adey 1973), may be required for successful growth of the coralline *Clathromorphum circumscriptum*. Also, the tunneling action of chitons, limpets and sea urchins may provide wetting spouts (miniature blowholes) of water to portions of the reef crest that might dry out and die otherwise (Littler 1976).

Of the two factors, nutrients and grazing, the latter is probably most important in directly controlling dominance in natural situations. However, so little is known about nutrient uptake responses in reef algae that our hypotheses are at best preliminary in this regard. The recent Caribbean-wide decline of the grazer *Diadema antillarum* (Lessios et al. 1984) thus far has resulted in increases of relatively small forms (sheets and filaments) of frondose algae. When human over-exploitation of gastropods, urchins or fishes occurs, then frondose macroalgal stocks can become quite extensive (e.g. the 1-2 m deep Waikiki reef flat; Doty 1971; Fig. 2).

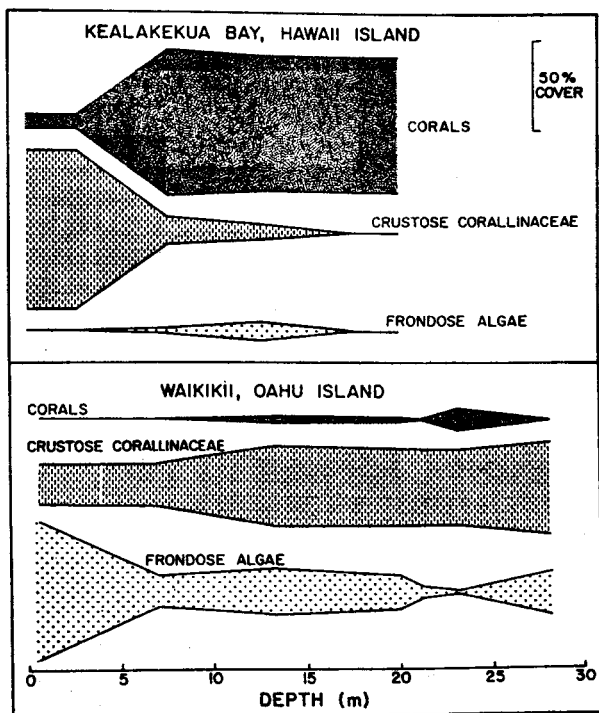


Figure 2. Cover of sessile primary producers as a function of depth in two contrasting Hawaiian reef systems. Kealakekua Bay is characteristic of geologically young and oligotrophic Hawaiian reefs (Doty 1968) with large populations of sea urchins and herbivorous fishes. The older Waikiki reef flat has been overfished and is relatively eutrophic (Doty 1971).

Grime (1979) 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) disturbance-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 corals and corallines, and (b) by emphasizing the variable (toxic as well as limiting) 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 recent nutrient enrichment experiment of Hatcher and Larkum (1983) affords a partial test of the relative dominance model. Although, corallines were not considered, this work revealed that the limits to algal standing stocks on reefs are set by an interacting complex of physical-chemical and biotic factors that show considerable temporal and spatial variability. Nutrient levels determine the potential size of algal standing stocks (Gaines and Lubchenco 1982; Hatcher and Larkum 1983), but herbivores can maintain macroalgal biomass well below the limits set by nutrients. Consequently, we believe that macroalgae can reach their maximum standing stocks only when herbivory is reduced and nutrient levels elevated (Fig. 1).

One appropriate test of the relative-dominance paradigm (Fig. 1) would be to extend the experimental design of Hatcher and Larkum (1983). Long-term (at least 3-yr) competitive, inhibitory and other interactions between various species of transplanted corallines and corals, as well as large versus small fleshy algal populations could be examined by staging competitive bouts, while simultaneously manipulating nutrient levels and key herbivore densities in various habitats such as the reef slope, reef-crest and back-reef. This is technically feasible using a non-toxic artificial underwater epoxy substrata in conjunction with slow release nutrient diffusers and herbivore exclusion cages, along with appropriate control treatments.

The role of stochastic events must be considered (Lighty 1982; Hatcher 1984) in any model of relative dominance for reef systems. For example, extremely heavy herbivore pressure could keep even well-defended macroalgae at inconspicuous levels within predominantly microfilamentous communities, owing to inadvertent grazing. If, however, some chance environmental factor alters herbivory long enough, populations of unpalatable macroalgae can bloom and reach a critical mass (Lighty 1982; Hatcher 1984). Such algae then attain a

"refuge in size or 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 macroalgae (Norris and Fenical 1982; Hatcher and Larkum 1983), removal of epiphytes and microfilamentous competitors by "optimal" levels of herbivory may increase local standing stocks.

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