

2. Structure and role of algae in tropical reef communities

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I. Introduction

Tropical reef ecosystems consist of spectacular biological communities on limestone bases, derived mainly from the fossilized remains of coelenterate corals and calcareous algae, and are found within the 22°C (north-south) isotherms throughout the world's oceans (Fig. 2-1). Because of the long geological history of environmental constancy within tropical zones, reef systems have developed an extremely high level of biological diversity, including many specialized organisms. The calcareous skeletal material of coral animals (aragonite) supplies much of the structural bulk, and the calcite cement produced by coralline algae (Rhodophyta) consolidates this material and other debris to contribute to reef formation. In addition, nonarticulated coralline algae may form an outer intertidal algal ridge that buffers wave forces and prevents erosion and destruction of the more delicate corals and softer organisms typical of back-reef habitats. A diverse group of calcified green algae (Chlorophyta) belonging to the orders Caulerpales and Dasycladales deposit the aragonite form of calcium carbonate, which is responsible for much of the sand and lagoonal sediment within the back reef and deeper areas. Tropical reefs are remarkable for their development of massive structure and high primary productivity. As we will show, algae are responsible for much of the former and all of the latter.

On a global scale, reef ecosystems comprise a quantitatively significant geographical, geochemical, and biological resource. Their total area, fisheries yield, calcium mass balance, and primary productivity have been calculated (Lewis 1977; Smith 1978) and found to be substantial. For example, total reef area is approximately 6×10^5 km², which is about 0.17% of the world's ocean area and about 15% of the shallow sea floor within the 0-30 m depth range (Smith 1978). Although taken from this relatively small region of the world's oceans, the reef fisheries potential is estimated (Smith 1978) to be about 9% (approximately 6×10^9 kg·y⁻¹) of the total oceanic fisheries yield. Further, shallow reefs are conservatively estimated (Smith 1978) to precipitate about 6×10^{12} mol CaCO₃ annually, which is equal to about 50% of the yearly calcium input to the world's oceans. Reefs retain a signif-

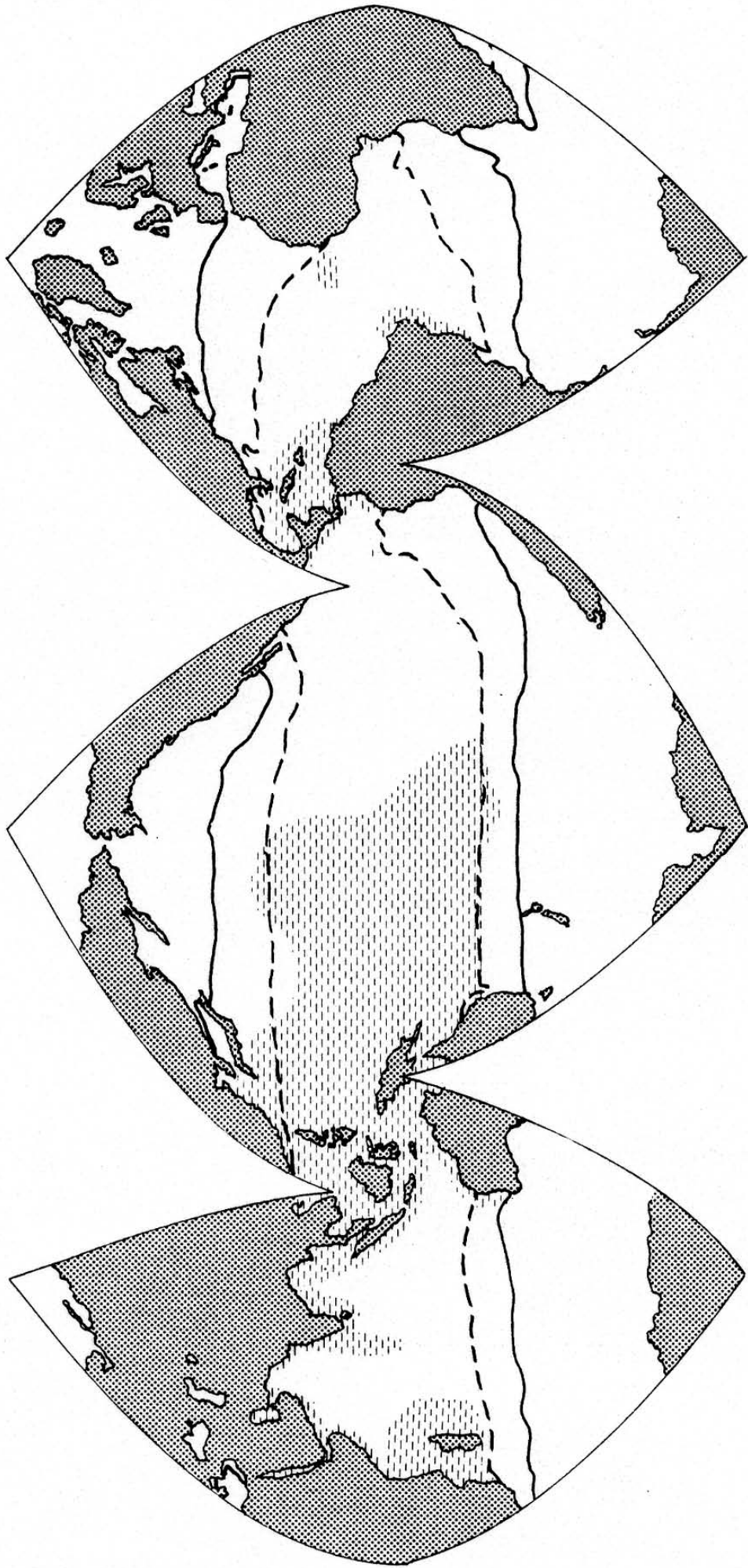


Fig. 2-1. Distribution of reefs and relation to controlling sea surface temperature. Solid bold line is extended 21°C isotherm, broken bold line is restricted 21°C isotherm, and lightly shaded areas are generalized areas containing the majority of coral reefs. (Modified from Wells 1957.)

Table 2-1. *Productivity figures for open ocean phytoplankton vs. reef populations*

Type of algae	Productivity ($\text{g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$)
Open-sea phytoplankton	0.1–0.35
Reef community	5.0–10.0
Encrusting coralline algae	2.7
Fleshy and filamentous algae	3.3
Coral zooxanthellae	11.0

Source: Marsh 1976; Wanders 1976.

icant fraction of precipitated sediments by means of their wave-resistant structures and lagoons and constitute a major global sink for calcium sediments.

Biotic reefs represent some of the most productive natural ecosystems known (Westlake 1963; Lewis 1977), although they mainly occur in nutrient-poor waters. Shallow reef flats characteristically have gross production rates 50 to 100 times higher than the productivity of the adjacent open ocean (Table 2-1). The anomalously high organic productivity of reefs is attributable to: (a) extensive spatial rugosity (dramatically increasing metabolic surface area), (b) continual nutrient input from water currents flowing across these surfaces, (c) specialized benthic nitrogen-fixing blue-green algae and bacteria, and (d) biological systems that efficiently retain nutrients by recycling. Four major groups of sessile photosynthetic organisms are responsible for the bulk of reef productivity (Fig. 2-2A–F): (1) microfilamentous turf algae, (2) symbiotic unicellular algae within hermatypic corals, (3) frondose macroalgae, and (4) coralline algae. In some soft bottom habitats, seagrasses, algal epiphytes, and siphonaceous Chlorophyta (Fig. 2-2F) contribute substantially to overall productivity.

The average living coral colony on Eniwetok atoll contains three times as much plant as animal tissue (Odum and Odum 1955), of which only about 6% is contributed by zooxanthellae, the remainder being composed of microfilamentous green algae within the coral skeletal structure. On reefs not dominated by corals, coralline algae and various small filamentous algae usually compose the majority of cover (e.g., standing stocks of $< 0.27 \text{ kg} \cdot \text{m}^{-2}$; Brawley and Adey 1977). Recolonization of new substrata by microfilamentous algae is extremely rapid on reefs. For example, after corals were killed by the predatory starfish *Acanthaster* on Guam reefs, blue-green algae became established within 24 hours, and a diverse filamentous community of algae was dominant after 26 days (Belk and Belk 1975). Larger frondose algae occur abun-

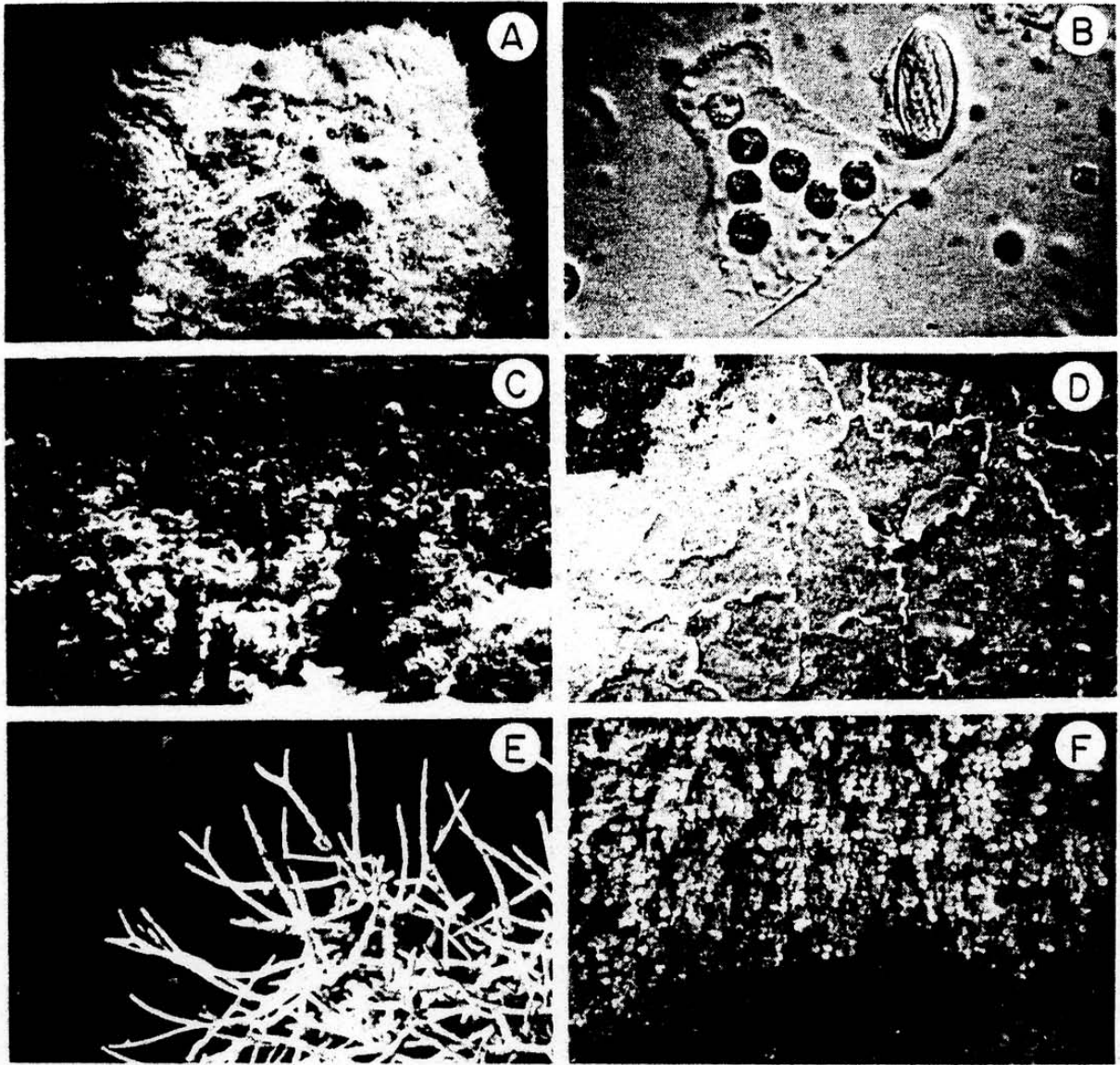


Fig. 2-2. A. Microfilamentous algal turf scraped by herbivorous parrotfish. B. Symbiotic zooxanthellae within a hermatypic coral (photo courtesy of William Fitt and Robert Trench). C. Frondose algal populations of *Turbinaria* and *Sargassum*. D. Nonarticulated (crustose) coralline alga. E. Articulated coralline alga. F. The siphonaceous calcifying chlorophyte *Halimeda*.

dantly on reef flats (Doty 1971; Wanders 1976), unstructured sand plains (Earle 1972; Hay 1981a), or deepwater sites (Littler et al. 1985), with typical mean algal standing stocks of $3.0\text{--}3.5\text{ kg}\cdot\text{m}^{-2}$ (Doty 1969) and unusually rich locations (e.g., Martinique: Connor and Adey 1977) ranging up to $10\text{ kg}\cdot\text{m}^{-2}$. Thus, although temperate algal standing stocks tend to be higher (Taylor 1960), some tropical reef habitats can support algal biomass levels of a comparable high magnitude.

All of the coral and algal groups compete for space, nutrients, and light (e.g., Littler and Doty 1975); any one assemblage can predominate under specific environmental conditions. For this reason, and despite its wide usage, the popular term *coral reef* can be misleading unless it

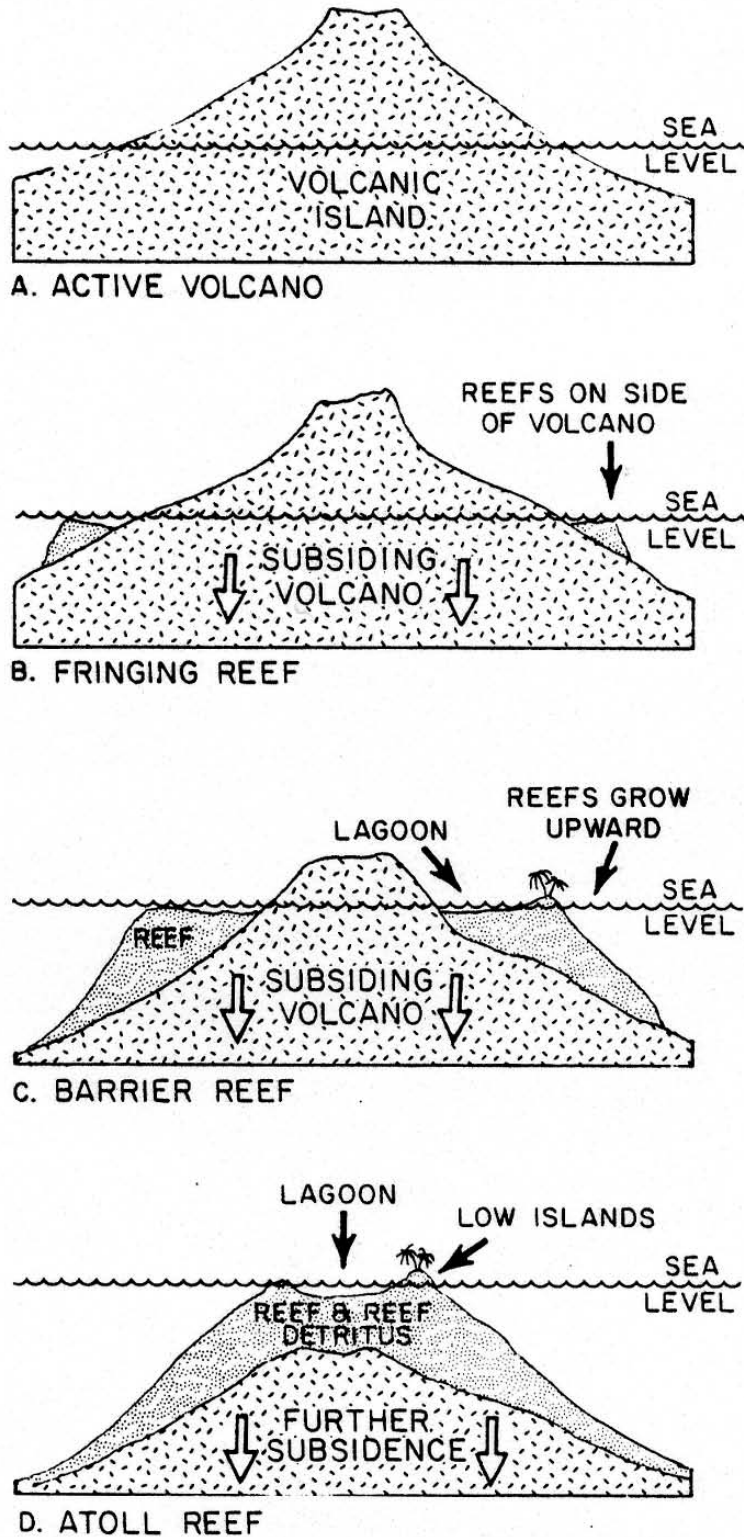


Fig. 2-3. Subsidence sequence proposed by Darwin leading from B (fringing reef) to C (barrier reef) to D (atoll reef formation).

refers specifically to those systems dominated by coelenterate corals. Consequently, in the general sense, *biotic reef* (Womersley and Bailey 1970) or simply *reef system* is preferable.

There are three reef types, based on their location – fringing, barrier, and atoll (Fig. 2-3) – and all have the same basic ecological zones.

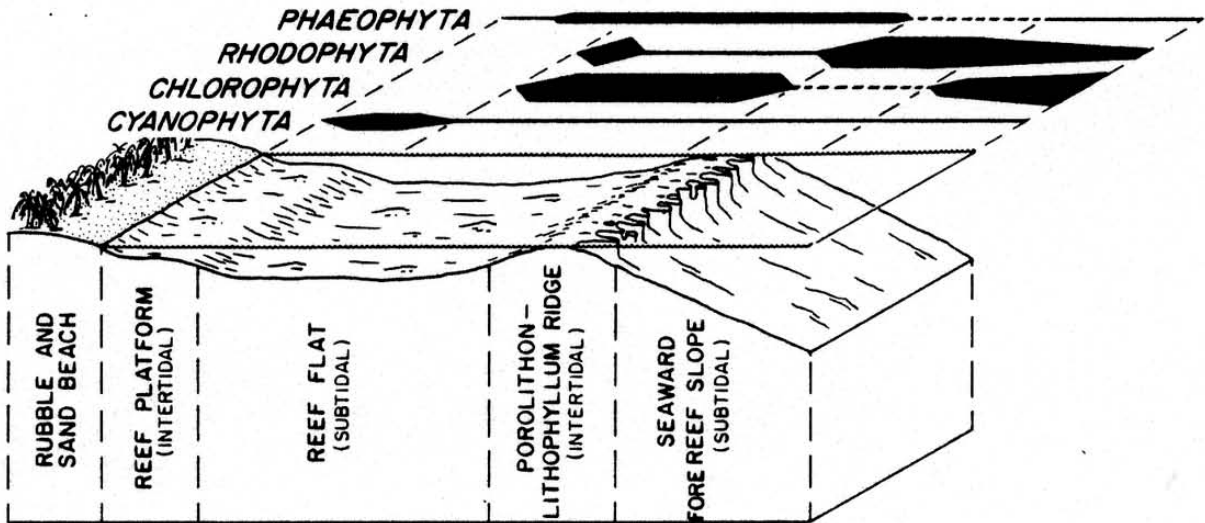


Fig. 2-4. The generalized primary habitats of the tropical marine divisions of calcareous macroalgae. The relative extents of zonal configurations vary markedly from reef to reef.

Related to these basic reef configurations are patch reefs, barrier bank reefs, and table reefs. The most seaward portion of a typical reef (Fig. 2-4) is the outer fore reef slope, which grades upward to the shallow fore reef and the reef crest. Where wave action is consistently high, the reef crest develops into an intertidal algal ridge (often including a spur-and-groove configuration) generally dominated by the coralline algal genera *Porolithon* and *Lithophyllum*. The most massive algal ridges are found on Pacific atolls although they are present intertidally on any reef system consistently subjected to high wave action. Behind the algal ridge is the shallow back reef, which is the product of limestone-boring organisms that cause the disintegration of calcareous material. In this habitat are the slower-growing corals, various coralline algae, and frondose algae. The shallow back reef immediately behind the algal crest usually grades upward toward the shoreline to form a reef flat and/or platform where storms may cast calcareous sediments, rubble, and boulders. This material accumulates, particularly on windward reefs, to form consolidated terrestrial surfaces on which islands can develop.

II. An overview of shallow-water algae

Although it is difficult to generalize, there is a tendency for the various calcareous and noncalcareous groups of algae to predominate within different reef habitats. The distribution of frondose algae, calcareous algae, and corals appears to be related directly to biological factors such as competition and grazing as well as physical factors, including nutrient levels, wave action, irradiance, and temperature. As will be discussed, much of the pattern seems to be generated by competition mediated by

the interaction of variations in nutrient availability and disturbances by herbivorous fishes and wave action.

A. Noncalcareous forms

Fronlose macroalgal abundances (Fig. 2-2C) are normally reduced on reefs by herbivorous fishes and sea urchins (Littler and Doty 1975; Hay 1981b; Hatcher and Larkum 1983). The inconspicuousness of microfilamentous algae (Fig. 2-2A) on shallow reef-front systems also is thought (Littler and Doty 1975; Borowitzka 1981) to result primarily from intensive grazing by the numerous herbivores and omnivores inhabiting these spatially heterogeneous habitats. Where there is much turbulence or little topographic relief on tropical reefs, herbivore activity is reduced (Brock 1979; Hay, Colburn, and Downing 1983), thereby enabling reasonably large standing stocks of macrophytes (*Sargassum*, *Turbinaria*, *Acanthophora*) to develop (Doty 1971; Wanders 1976). Some chemically well-defended macroalgae (e.g., *Halimeda*, *Styopodium*, *Dictyota*; see Norris and Fenical 1982) can be abundant where grazing is high. Such macroalgal populations may contribute a major portion of the total primary productivity of tropical reefs (Rogers and Salesky 1981). However, most evidence (Odum and Odum 1955; Marsh 1976; Carpenter 1985) indicates that the sparse mats of fast-growing, opportunistic filamentous algae result in the very high primary productivity per unit area of biotic reefs. For example, on St. Croix reefs dominated by the coral *Acropora palmata* (where larger macrophytes are rare), filamentous algae, although present only in very low biomass ($180\text{--}270\text{ g}\cdot\text{m}^{-2}$), are responsible (Brawley and Adey 1977) for 70–80% of the productivity of the shallow fore and back reefs ($5\text{--}7\text{ g net C fixed}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). Proportionately, sparse filamentous mats are considerably more productive per unit of algal biomass than are dense stands of the larger macroalgae. This can be related to functional morphological differences (Littler 1980; Littler, Littler, and Taylor 1983a) where opportunistic species with high surface-to-volume ratios typically outproduce those having a coarser morphology. Variations of this sort are due (Littler and Littler 1980) to differential allocation of materials to photosynthetic versus structural tissues. Herbivorous fish, by their scraping mode of feeding, continuously provide new substrata and thereby select for opportunistic microalgal forms (Fig. 2-2A), as well as long-lived scrape-resistant coralline algae (Littler and Doty 1975; Wanders 1976).

Fixation of atmospheric nitrogen by blue-green algae such as *Calothrix crustacea* (Wiebe, Johannes, and Webb 1975; Mague and Holm-Hansen 1975) within filamentous microalgal assemblages also is an important feature that enhances reef productivity and nutrition. The greater productivity of benthic reef communities versus planktonic oceanic systems (Table 2-1; Lewis 1977), is in large part due to such

nitrogen fixation within mixed filamentous algal communities (Wiebe et al. 1975; Mague and Holm-Hansen 1975), as well as unusually efficient nitrogen and phosphorus recycling within the symbiotic populations (Johannes et al. 1972). Other reef organisms, also closely associated with blue-green algae and showing high nitrogen fixation rates, include various macroalgal populations (Capone, Taylor and Taylor, 1977) and corals (Crossland and Barnes 1976). Such blue-green algal associations fix nitrogen at levels ($985 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$; Wiebe et al. 1975) equal to those recorded for the richest nitrogen-fixing terrestrial systems known (e.g., alfalfa fields).

Another important component of reef biology includes algae that cause breakdown of reef structure. Duerden (1902) recognized that penetrating or boring algae play a critical role in bioerosional processes. The commonest of diagenic algae are blue-green algae (see Nadson 1900; Purdy and Kornicker 1958) that attack skeletal materials differentially; the aragonitic coral skeletons are most susceptible, and the denser calcitic deposits of coralline algae are most resistant. Several distributional surveys of rock boring by microalgae (Green 1975; May, Macintyre, and Perkins 1982) documented the importance of this group on Caribbean reef systems. Weber-van Bosse (1932), during an extensive systematic study of penetrating algae in the Indo-Pacific, recorded 20 species distributed among the Cyanophyta, Chlorophyta, Phaeophyta, and Rhodophyta. Thirty-three species of carbonate-boring tropical algae have been reported from China (Chu and Wu 1983), two of which are active at depths exceeding 100 m. Much research remains to be done with this very interesting group of endolithic marine plants.

B. Calcareous algae

Calcareous algae are universally recognized (James and Macintyre 1985) as important contributors to both the bulk and frame structures of the majority of reef limestone deposits. Such deposits often have been associated with petroleum reserves, and this relationship has drawn the attention of geologists, paleobiologists, and others to calcifying seaweeds. Important historical roles of algal taxa as sediment producers and reef builders have been chronicled thoroughly by Wray (1971, 1977).

The order of prominence for reef-forming organisms in providing bulk during the development of the reef at Funafuti atoll, Ellice Islands ($8^{\circ}30'S$, $179^{\circ}10'E$), was estimated as follows (Finckh 1904): (1) nonarticulated coralline algae (Rhodophyta), (2) the green alga *Halimeda* (Chlorophyta), (3) foraminifera, and (4) corals. Subsequent ecological work (e.g., Womersley and Bailey 1970; Littler 1971) and paleontological studies (e.g., Easton and Olson 1976) have substantiated the predominant role of coralline algae in cementing coarse and fine-grained

sediments produced by calcareous green algae, molluscs, and foraminifera, along with the bulkier deposits provided by hermatypic corals (see also James and Macintyre 1985).

Some of the advantages of algal calcification postulated by Littler (1976) include mechanical support, resistance to sand scour, wave shock, and grazing, as well as protection against fouling epiphytes (by means of carbonate sloughing) and photoinhibition due to intense irradiance. Also, by providing their own substrata, calcareous algae may increase the stability and quality of their attachment sites.

The calcifying Rhodophyta grow on solid substrata intertidally and subtidally down to at least 268 m (Fig. 2-4; Littler et al. 1985, 1986) but attain maximum abundances in shallow turbulent areas. Coralline algae (Fig. 2-2D, E), in contrast to most fleshy algae, are relatively low primary producers, as documented by studies of their functional morphology (Littler and Littler 1980, 1984a; Littler, Littler, and Taylor 1983). Marsh (1970) was the first to note the low productivity of nonarticulated coralline populations ($0.66 \text{ g net C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ at Eniwetok atoll) and surmised that these algae are more important in reef building than in primary production. In his review, Lewis (1977) concluded that coralline algae have rates (Table 2-1) of primary production that are much lower than mean values for reefs as a whole. It is interesting to note that calcification rates appear to differ little among reef-flat communities consisting of diverse kinds of calcifiers (Smith 1973; Wanders 1976), whether they are corals, nonarticulated coralline algae, or turfs of articulated coralline algae. For the frame-building Corallinaceae, the available information (Littler et al. 1985, 1986) indicates an algal group able to grow at greater depths in weaker light than other primary producers. *Porolithon* and certain *Lithophyllum* species that dominate algal ridges (Fig. 2-4; e.g., *P. onkodes*, *P. pachydermum*, *P. craspedium*, *P. gardineri*, *L. kotschyianum*, *L. congestum*, *L. moluccense*) are somewhat exceptional in that they can withstand considerable desiccation and exposure to the highest sunlight irradiances.

The calcareous Chlorophyta predominate mainly in protected shallow areas on soft bottoms, often in association with seagrasses, as well as on the deeper reef slopes in the case of *Halimeda* (Hillis-Colinvaux 1977; Littler et al. 1985). In summarizing the ecological research on reef-building algae, the published data for the sediment-producing shallow Chlorophyta indicate an assemblage adapted to calm, soft-bottom habitats (which are unsuited for most other macroalgae) throughout subtropical to tropical zones. Few quantitative studies exist on any aspect of the ecology of the calcareous Chlorophyta with the exception of the widely studied genus *Halimeda* (see review by Hillis-Colinvaux 1980). Numerous *Halimeda* species are abundant on protected back-reef and fore-reef habitats, occurring over a broad depth range on both hard

and soft substrata. Other psammophytic (sand-dwelling) forms are associated with shallow seagrasses and mangroves. Natural *Halimeda* populations of 100 plants \cdot m⁻² are common (Hillis-Colinvaux 1980), and densities up to 500 m⁻² are found on some Jamaican reefs. Recently, spectacular, large banklike mounds composed of living *Halimeda* and its sediments (dating to 5,000 years B.P.) have been discovered (Davies and Marshall 1985) in the back-reef portion of the Great Barrier Reef, Australia. Skeletal sand-sized components from some tropical Atlantic peripheral reef and lagoonal sediments are composed of up to 44% and 77% *Halimeda* fragments, respectively (Milliman 1974; Orme 1977). An excellent, but largely overlooked, review of the importance of *Halimeda* as a reef-forming organism throughout the tropical Pacific was published (Chapman and Mawson 1906) over 80 years ago.

C. Coral-algal symbiosis

The major reef-building invertebrates belong to the phylum Cnidaria, classes Anthozoa and Hydrozoa, and have dinoflagellate microalgae (zooxanthellae) living within their tissues as primary producers (Fig. 2-2B). This symbiosis usually results in a net daily excess in primary productivity for shallow colonies (e.g., about 11 net g C \cdot m⁻² \cdot d⁻¹: Wanders 1976). Zooxanthellae are derived from at least two genera of dinoflagellates, including *Symbiodinium* and *Amphidinium* (see review by Trench 1981), and by their symbiosis gain protection from zooplankton predators and obtain a wide variety of nutrients from the coral host. The nutrients obtained directly include phosphate and a variety of nitrogenous compounds such as ammonium, uric acid, guanine, alanine, and adenine. The coelenterate acquires algal photosynthates in the form of glycerol (currently estimated at up to 98% of the total carbon produced; see Muscatine, Falkowski, and Dubinsky 1983) and glucose (Battey and Patton 1984) as well as oxygen. Transfers of nutrients and energy sources between algal symbionts and their hosts (e.g., many corals, foraminifera, sponges, and molluscs) are important pathways in reef community recycling, representing a major mechanism enabling survival in oligotrophic waters (Muscatine and Porter 1977). The contribution of organic carbon from zooxanthellae to their hosts is significant, often estimated (Muscatine et al. 1983) at over 100% of the level of carbon required to meet the host's metabolic requirements. Under adverse conditions (i.e., low light), the amount of photosynthetically fixed carbon available to the host decreases, in spite of photoadaptation by the zooxanthellae (Muscatine et al. 1983; Porter et al. 1984). Algal symbiosis is energetically of great benefit when food is scarce but of less benefit when food resources are plentiful (Hallock 1985). Filamentous, boring green algae (Chlorophyta), mostly of the genus *Ostreobium*, also occur within the calcified coral skeletons and together with the zoox-

anthellae provide a very significant portion of the living biomass of a coral. For example (Muscatine et al. 1983), zooxanthellae contribute as much as 15% of total protein of coelenterate symbioses, and boring algal biomass can exceed that of the animal host (Odum and Odum 1955). However, the biology of the boring forms is poorly known. Endozoic algae embedded in the skeletons of living corals have not proven (Kanwisher and Wainwright 1967) to be significant primary producers on reefs.

III. An overview of deepwater algae

Submersible vessels have greatly expanded our knowledge of distributional limits for marine organisms; however, macroalgae have received only incidental attention until recently. For example, crustose red and filamentous green algae were seen by Lang (1974) as deep as 175 m at Discovery Bay, Jamaica. Adey and Macintyre (1973) cite the unpublished observations of J. C. Lang and J. W. Porter for the maximum depths for crustose coralline algae (200 m) on steep Belizean and Bahamian reef walls.

Recently, a record depth (268 m) for an attached living marine macrophyte was reported (Littler et al. 1985) during an extensive floristic-ecological survey of a seamount off San Salvador Island, Bahamas (Fig. 2-5). Studies from a submersible in conjunction with shore-based productivity measurements (Jensen et al. 1985; Littler et al. 1985, 1986) revealed unsuspected abundances and potential importances of other deepwater tropical macroalgae. Four zonal assemblages occurred over the depth range from 81 m to 268 m and consisted of a *Lobophora*-dominated group (Phaeophyta, 81–90 m), a *Halimeda* assemblage (Chlorophyta, 90–130 m), a *Peyssonnelia* group (Rhodophyta, 130–189 m), and a crustose coralline zone (Rhodophyta, 189–268 m).

The overall deepwater flora of the Bahamas is composed of unique deepwater taxa combined with shallow-water species characteristic of shaded low-light conditions. Species of Chlorophyta (e.g., *Johnson-sealinkia profunda* at 200 m) are the deepest-growing frondose algae, followed by Phaeophyta (e.g., *Lobophora variegata* at 100 m). Encrusting calcareous Rhodophyta extend below all other forms of macrophytes. The zonal pattern observed (Fig. 2-5) – namely, reds > greens > browns with increasing depth – is quite similar to that recorded (Larkum, Drew, and Cosset 1967) on the south coast of Malta. Off Malta, the shallower zone to 15 m is dominated by brown algae; green algae (mainly *Halimeda*) are then most abundant down to 75 m, and red algae (particularly *Peyssonnelia* and *Lithophyllum*) dominate below the 80–90 m transitional depth.

Dominant members of the diverse multilayered macrophyte commu-

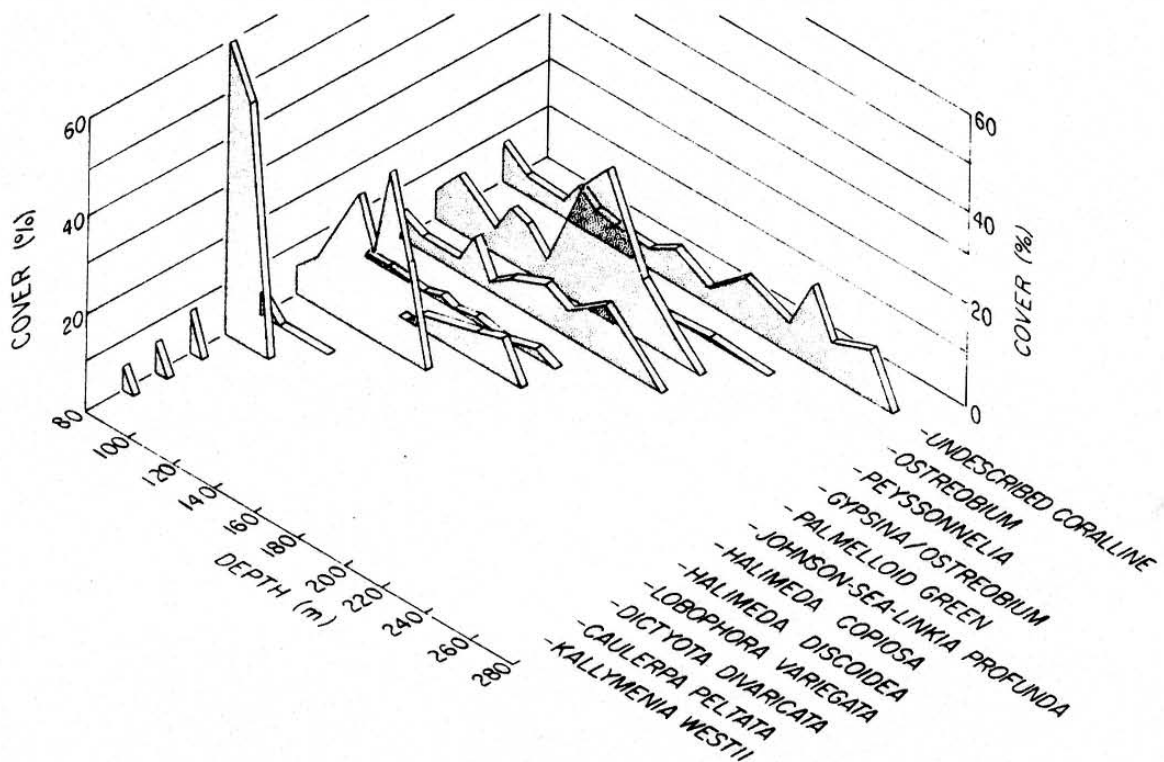


Fig. 2-5. Distribution and abundance patterns of the major deepwater plant cover on San Salvador seamount, Bahamas.

nity on top of San Salvador seamount (81 m depth) showed net productivity levels comparable to shallow-water seaweeds although receiving only 1–2% of the light energy available at the surface. Productivity rates reported for shallow carbonate reef systems range from 0.06 to 0.72 g C · m⁻² of substratum · h⁻¹ (approximated from daily rates) as follows: intertidal, blue-green algal-dominated substrate at Eniwetok atoll = 0.06–0.22 g C · m⁻² · h⁻¹ (Bakus 1967); macroalgal-dominated habitats in the Canary Islands = 0.15–0.30 (Johnston 1969); photosynthetic coral and algal turfs at Eniwetok = 0.16–0.72 (Smith 1973); a coralline algal-dominated fringing reef in French Polynesia = 0.38 (Sournia 1976); and fore- and back-reef algal turf systems = 0.5–0.7 (Brawley and Adey 1977). The mean rate for the seamount plateau, 0.066, falls within the lower end of this range. Littler et al. (1986) conclude that deepwater macroalgal communities produce at rates comparable to some shallow reef systems but lower than most seagrass beds (see Littler et al. 1985) or typical carbonate reef-flat habitats. It is significant that other physiological processes (i.e., calcification) for four deepwater *Halimeda* species (Jensen et al. 1985) also showed similar rates to those reported (Borowitzka and Larkum 1976) for shallow forms of the genus.

The great abundance and considerable productivity of macroalgae in the previously unknown deep-sea realm underscores their potential

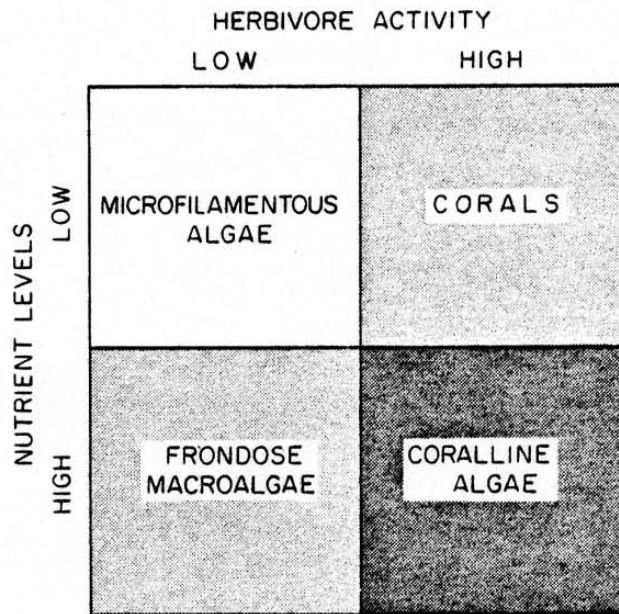


Fig. 2-6. Diagrammatic representation of the relative dominance paradigm. Potentially predominant space-occupying groups of photosynthetic reef organisms are emphasized as a function of long-term nutrient levels and disturbance. Hermatypic corals are hypothesized to be the competitive dominants, and 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. (From Littler and Littler 1985.)

widespread importance to the marine food web and reef biogenesis in other clear tropical waters. As more plant specialists gain access to deep-sea communities, the role of benthic algae will become clearer and new botanical theories and concepts based on *in situ* research will replace older ones derived from shipboard studies and remote sensing.

IV. Factors regulating algal distribution

Variations in the levels of grazing and wave shock (physical disturbance) and limiting or toxic nutrient levels (physiological stress) hypothetically are major factors that lead to spatial segregation of coral-, coralline-, or fleshy algal-dominated communities between or within habitats, or they may lead to temporal separations important during succession and reef biogenesis (Fig. 2-6). Corals, though preyed upon by a few omnivorous fishes and sea urchins, generally gain primacy under intensive herbivory (Brock 1979), moderate levels of wave shear, and very low nutrient concentrations (Bakus 1969). The decrease in coelenterate coral cover, relative to macroalgae (Doty 1971) and coralline algae (Littler 1971), on the reef flat at Waikiki, Oahu, over a 45-year span may be attributable to increases in nutrients from eutrophication due to municipal sewage effluents. 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 endangered by competition for space unless they can attain a refuge in size (Birkeland 1977). Townsley (cited in Doty 1969) found that some Hawaiian corals (e.g., *Porites compressa*) are extremely sensitive to increased phosphate concentrations. Orthophosphates are known (Simkiss 1964) to inhibit CaCO_3 crystal formation at concentrations as low as $0.01 \mu\text{M}$ and can inhibit production of external skeletal material in marine animals. The 50% reduction in calcification rate observed (Kinsey and Domm 1974; Kinsey and Davies 1979), following experimental fertilization of a patch reef on the Great Barrier Reef, was partly attributed to phosphate poisoning.

Coralline algae, on the other hand, predominate in areas of moderate to heavy grazing (or heavy wave shear) and are not inhibited by moderate to high levels of nutrient enrichment (Fig. 2-6). However, high phosphate concentrations also are known (Brown, Ducker, and Rowan 1977) to reduce calcification and growth of some temperate articulated coralline algae.

Eutrophic waters, where herbivory and wave-shearing forces are low, tend to favor large populations of frondose macroalgae that can ultimately overgrow and kill both coralline algae (Littler and Doty 1975) and corals (Banner 1974). When nutrient levels are low and grazing activity is low to moderate (Fig. 2-6), microfilamentous forms with greater surface area to volume ratios tend to predominate (e.g., as in damselfish territories [Vine 1974; Brawley and Adey 1977; Hixon and Brostoff 1982]). Birkeland (1977) also noted that filamentous and fleshy algae outcompete corals (which are inhibited) under elevated nutrient levels. He concluded that small, fast-growing algae are not just opportunists that depend on disturbances to release space resources from established longer-lived populations but, rather, become the superior competitors when provided with abundant nutrients. Shifts from coral dominance to fleshy algal dominance have been related to excess nutrient increases for reefs off Venezuela (Weiss and Goddard 1977), on the Abaco reef system, Bahamas (Lighty, Macintyre, and Neumann 1980), and in Kaneohe Bay, Hawaii (Banner 1974; Smith et al. 1981).

Nitrogen is generally thought (Hatcher and Larkum 1983) to be the nutrient most often limiting tropical marine algal growth rates. Phosphorus, due to its effective recycling, traditionally has been considered less likely to be in short supply (Pilson and Betzer 1973). However, recent evidence (Lapointe 1983) is beginning to reveal that phosphorus is limiting under more widespread conditions than previously thought. The reason for phosphorus limitation (Simkiss 1964) is phosphate binding by calcium carbonate particles that are abundant in nearly all reef environments and the presence of nitrogen-fixing blue-green algae, making nitrogen relatively plentiful in many benthic reef environments.

Table 2-2. *Herbivore resistance mechanisms shown by benthic macrophytes*

Resistance mechanisms	Examples	References
Noncoexistence escapes		
1. <i>Temporal escapes</i> Short or alternating life histories	Annuals (e.g., <i>Liagora</i> , <i>Trichogloea</i>) and seasonally alternating heteromorphic forms (<i>Porphyra</i> , <i>Gigartina</i>)	Littler and Littler 1980; Lubchenco and Cubit 1980
Opportunistic colonization of unpredictable new substrata	Thin, sheetlike, and filamentous forms (e.g., <i>Polysiphonia</i> , <i>Centroceras</i> , <i>Enteromorpha</i>)	Littler and Littler 1980
2. <i>Spatial escapes</i> Refuge habitats	Intertidal habitats (<i>Ahnfeltia</i> , <i>Chnoospora</i>), high-energy environments (<i>Sargassum</i>), sand plains (<i>Gracilaria</i>), and crevices (<i>Amansia</i>)	Earle 1972; Ogden et al. 1973; Brock 1979; Hay 1981a; Hay et al. 1983
Association with unpalatable organisms	Next to toxic or stinging organisms such as <i>Styopodium</i> , <i>Gorgonia</i> and <i>Millepora</i> (<i>Liagora</i> , <i>Laurencia</i>)	Littler, Taylor, and Littler 1986; Littler et al., 1987b
Association with carnivorous predators	Next to grouper or snapper lairs (<i>Acanthophora</i>)	Randall 1965; Ogden et al. 1973
Association with territorial animals	Within damselfish territories (e.g., <i>Polysiphonia</i>)	Brawley and Adey 1977; Hixon and Brostoff 1982
Coexistence defenses		
1. <i>Crypsis</i>	Inconspicuous forms (some <i>Gracilaria</i>) and small forms (<i>Plectonema</i>)	Gaines and Lubchenco 1982
2. <i>Mimicry</i>	Coral mimics (<i>Eucheuma arnoldii</i>)	Kraft 1972; Littler, Taylor and Littler 1983

Table 2-2. (cont.)

Resistance mechanisms	Examples	References
<i>3. Structural defenses</i>		
Morphologies that minimize accessibility	Upright large algae (e.g., <i>Turbinaria</i>), branched crustose corallines (<i>Neogoniolithon</i>), and turf-forming colonies (<i>Halimeda</i>)	Steneck and Watling 1982; Hay 1981a
Textures that inhibit manipulation and feeding	Encrusting species (<i>Lobophora</i>) and spiny forms (<i>Turbinaria</i>)	Nicotri 1980
Materials that lower food quality	CaCO ₃ in corallines (<i>Porolithon</i>) and calcareous green algae (<i>Penicillus</i> , <i>Neomeris</i>)	Littler 1976
<i>4. Chemical defenses</i>		
Toxins, digestion inhibitors, unpalatable substances	<i>Halimeda</i> , <i>Caulerpa</i> , <i>Styopodium</i> , <i>Dictyota</i>	Norris and Fenical 1982; Paul and Fenical 1983
Lowered energetic content	Coralline algae (<i>Amphiroa</i>)	Paine and Vadas 1969; Littler, Littler, and Taylor 1983
<i>5. Satiation of herbivores</i>	Rapid replacement of lost tissues (<i>Ulva</i>)	Littler and Littler 1980; Borowitzka 1981

Enrichment studies (i.e., fertilization) of reef communities have shown (Kinsey and Domm 1974; Kinsey and Davies 1979) substantial enhancement of photosynthesis, but because of methodological limitations no significant changes could be detected in macrophyte standing stocks.

Of the two factors, nutrients and grazing, the latter is probably most important in directly determining algal distributions. Several herbivore-resistance mechanisms are often expressed by a given algal species and are summarized in Table 2-2. The synthesis of toxic secondary organics by algae increases dramatically in herbivore-rich subtropical and tropical reef systems (Fenical 1980) compared to temperate coastal environments. This correlation has fostered the rather speculative literature on algal chemical defenses, as pointed out by Norris and Fenical (1982). With the exceptions of several studies on temperate algae (e.g., Steinberg 1985), these contentions have rarely been evaluated by ecologically

relevant experiments. The stage has now been set for more precisely controlled field studies involving hypothetical chemical-defense compounds used on natural reef populations at normal levels, with artificial problems eliminated, to establish the adaptive significance of algal secondary metabolites.

V. Human influences

Reefs have developed over long geological time periods under relatively constant conditions. This stability has resulted in the evolution of an astounding abundance and diversity of specialized plant and animal life, which makes these areas fascinating subjects for research. Human interest is readily stimulated by the beauty, mystique, and complexity of reef organisms, and in the past human activities have caused little damage as they have been, for the most part, in harmony with reef ecosystems. However, this condition in recent years has undergone rapid change.

Reef formations have a long history of use by humans as a source of food, materials, and recreation. Ciguatera poisoning, frequently associated with reefs throughout the tropical world, often results in death to humans who have eaten carnivorous fishes that contain ciguatera toxins. It is now known that the ciguatera-type toxins are derived from the benthic dinoflagellate *Gambierdiscus toxicus* (Bagnis et al. 1979). The flattened cells of this organism are most often attached to highly branched filamentous algal thalli but also occur on primary substrata. When such cells are inadvertently eaten by grazing fish, the result is that two toxic substances, maitotoxin and ciguatoxin, tend to be accumulated and retained in the food chain. The toxins, with time, become greatly concentrated in the higher trophic levels, particularly by carnivorous fishes.

Because of its complex nature, the reef environment is particularly vulnerable to deleterious external influences. There are two basic environmental concerns: resource utilization and pollution. The most obvious activities of humans that affect the marine algae of tropical reefs are indirect and include the harvesting of fish, the gathering of molluscs, the collecting of sea urchins, and the hunting of herbivorous marine turtles. These activities, where excessive, may reduce the populations of key species of herbivores, thereby eliminating the constraints on certain algal populations and leading to unusual predominances by one or several forms. However, ecological release from competition or predation and compensatory expansion of a particular herbivore group following the reduction of another can occur. For example (Hay and Taylor 1985), on overfished reefs, disturbance is ameliorated when sea urchin populations increase and expand, keeping localized ratios of corallines, frondose macroalgae, microfilamentous forms, and corals near

their previous levels. When human overexploitation of gastropods and urchins as well as fishes occurs, frondose algal stocks can become quite extensive (e.g., the 1–2 m deep Waikiki reef flat: Doty 1971). Perturbations are usually restricted to those sections of the reef and adjoining coastal habitats most conveniently accessible to man.

The construction of seawalls and the building of groins, platforms, and extensions of the land over reef flats for human habitation all affect the normal current patterns and sedimentological processes. The cutting of terrestrial forest communities greatly increases sediments that wash onto reef systems. Such sedimentation effects include scouring, smothering, and lowering of light levels, all of which are deleterious to both plant and animal stocks. Ship groundings occur frequently (Hatcher 1984; Littler et al. 1987a) with devastating physical results. Algal community structure resulting from such stochastic physical disturbances (including hurricanes: Mah and Stearn 1985) may be permanently changed to some alternate steady state (Hatcher 1984).

Tropical algae have been utilized by man as food, medicines, poultices on wounds, ceremonial objects, and for ornaments. In the Philippines, Malaysia, Indonesia, China, and Japan, farming of seaweeds on shallow reef flats is now undertaken on a relatively broad scale (see Lewis, Stanley and Quist, Chapter 9). However, it is not known what effects such increases in algal standing stocks and shading have on the natural biota. Also, numerous wild algal populations are commercially harvested as local food sources and for colloidal extracts (see Abbott, Chapter 6). The gathering of calcareous coralline algal nodules, dredging, or dynamite blasting of sizable reef blocks as land fill, to be transformed and used as mortar, or for liming acidic tropical soils has obvious (but unmeasured) detrimental effects.

Protection of reefs is becoming increasingly difficult because the areas in which they are found, particularly near the coast, are used as sites for tourism, industry, and resource exploitation. There appear to be several ways in which excess nutrient enrichment (i.e., eutrophication due to fertilizer runoff, sewage, etc.) can decrease coral fitness causing reef biogenesis to decrease and bioerosion to increase. For example, declines in water transparency due to phytoplankton blooms may limit photosynthetic production and growth (Tomascik and Sander 1985), phosphate may inhibit calcification (Simkiss 1964; Kinsey and Domm 1974), and suspension-feeding reef borers may become disproportionately abundant (Smith et al. 1981). In association with nutrient enrichment due to sewage effluents, *Dictyosphaeria* and other algae overgrew and killed many of the more luxuriant coral communities throughout Kaneohe Bay, Hawaii (Banner 1974; Smith et al. 1981). Six years after termination of the sewage discharge (Maragos, Evans, and Holthus 1985), *D. cavernosa* declined whereas corals showed a remarkable recov-

ery, corroborating the prediction that sewage eutrophication is a major stress to lagoon corals but a stimulant to algal growth.

Already many of the world's reefs have been exposed to different degrees of sewage pollution and oil spills; spear fishing and fish trapping have been so intensive that the larger reef fishes have almost disappeared near many of the heavily populated regions. Despite extensive research, human influence on reef environments continues to outpace our understanding of the ecological changes that are taking place.

VI. Future outlook

We still know very little about the physiological ecology, population biology, and community dynamics of algae that affect the ecology and biogenesis of biotic reefs. Especially lacking have been biological studies of reef-boring macroalgae and deepwater macrophytes. As pointed out by Littler (1972), and still true almost two decades later, areas of investigation concerning the role of bioenergetics, heterotrophy, allelopathy, interspecific and intraspecific competition, recruitment, natality, and mortality phenomena remain virtually untouched for most tropical algae. Until we begin to understand processes at these levels, it will be difficult to make definitive statements concerning the role of algae, or other organisms, in the dynamics of tropical reef communities.

Submersibles have greatly expanded our knowledge of the distributional patterns and abundances of deep-sea organisms; however, macroalgae have, until recently, received only anecdotal attention. As more phycologists gain access to deep-sea communities, the diversity, abundances, and production levels of benthic algae will be revealed and new oceanographic theories based on *in situ* research will replace older dogma derived from less efficient remote sampling from shipboard.

Until recently, few workers had directed their efforts toward determining the functional and ecological roles of algae on living reefs. Philosophical approaches that yield mechanistic and predictive insights are needed to supplement the more traditional descriptive approaches and methodologies. Taxonomically sound, reproducible, conceptually based, experimental analyses of ecological processes in the field have been particularly few. Historical reasons for this scarcity would seem to be taxonomic difficulties, an intimidating array of life-history complexities, and a lack of quantitative ecological techniques with sufficient resolution. Fortunately, taxonomic difficulties are now surmountable (Adey and Macintyre 1973), and various descriptive (Stoddart and Johannes 1978; Rützler and Macintyre 1982) as well as experimental (e.g., Wanders 1976; Hay 1981a; Littler, Littler, and Taylor 1983; Littler, Taylor, and Littler 1983; Hatcher and Larkum 1983; Littler and Littler 1984b) ecological methods are available. With these obstacles

posing less difficulty, advancement beyond the observational descriptive level toward more theoretical issues is rapidly taking place, although our knowledge of algal biology still lags behind that available for most other reef organisms.

Because seaweeds are recognized by their external and internal morphology, it has proven instructive to relate morphological groups (Littler 1980) with measurements of functional properties, relative to the environmental parameters normally experienced. Recently, research focusing on the functional significance of morphology has provided the focal point for the postulation of testable new theory concerning the ecological significance of anatomical variability and has enabled reef ecologists to consider a broad array of evolutionary phenomena for tropical seaweeds. Structure at all levels of organization ultimately governs all biological activities, and since morphological/anatomical features can be measured relatively accurately and easily, functional/morphological groups have proven to be extremely useful (Littler and Littler 1980, 1984a; Steneck and Watling 1982; Littler, Littler, and Taylor 1983; Littler, Taylor, and Littler 1983) for the interpretation of complex biotic reef ecosystems.

We are at a stage where descriptive (correlative) and mechanistic (i.e., experimental/causative) approaches must be combined to produce more conceptual theoretical themes, which will accelerate our predictive understanding of algal roles in reef biology. Experimental approaches are increasingly being utilized with the result that general ecological theories now are being modified by studies of tropical algal biology (see reviews by Lubchenco and Gaines 1981; Gaines and Lubchenco 1982; Littler and Littler 1984b). A burgeoning awareness of the attractiveness of tropical marine plants as experimental organisms for the elucidation of ecological and biogenic processes offers exciting prospects for the future of reef research.

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