

solve, I suspect that young biologists will continue to be drawn to the magical tidal margins of the sea. ♦

2.1.2 Essay: Tropical reefs as complex habitats for diverse macroalgae

Mark M. Littler and Diane S. Littler*

Beneath the vast expanse of warm azure waters, tropical biotic reefs comprise spectacularly complex ecosystems on limestone bases, derived mainly from the fossilized remains of calcareous algae and coelenterate corals. Such reefs occur around the globe within the 22°C isotherms (north and south). Reef systems have evolved an extremely high level of biological diversity, including many uniquely specialized macroalgae. The calcite (CaCO₃) cement produced by coralline algae consolidates calcareous (aragonitic) skeletons of coral animals and other calcifiers, along with terrigenous debris, and leads to reef formation. The nonarticulated coralline algae may also form a seaward intertidal ridge that buffers wave shock, thereby reducing erosion and destruction of the more delicate corals and softer organisms typical of reef-flat habitats. A diverse group of calcified green algae deposit the aragonite form of calcium carbonate, which is responsible for much of the sand and lagoonal sediments within the reef-flat and deeper fore-reef areas. For example, skeletal sand-sized components from some tropical Atlantic reef sediments are composed of up to 77% *Halimeda* fragments. Tropical reefs are remarkable for their development of massive structure in conjunction with high primary productivity; algae are responsible for much of the former and all of the latter.

In 1966, while completing degrees at the University of Hawaii, we became intrigued by the challenges of understanding the complex interactions structuring tropical reefs. Our studies of biotic reefs have taken us on adventures to Micronesia (Guam, Palau, Enewetak), the Australian Great Barrier Reef, the Galapagos Islands, Tahiti, Republic of the Seychelles, Kenya, Panama, Brazil, Belize, Mexico, Greater Antilles, Lesser Antilles, French Guyana, Bahamas, Florida, and Bermuda. Most of our ongoing research is centered in the Florida Keys and in Belize where we are investigating algal-animal interactions and the long-term interactions of nutrients and herbivory in reference to the Relative Dominance Model we developed (Fig. 2.3).

* Mark and Diane Littler have spent much time studying tropical reefs worldwide. They are cited in the *Guinness World Book of Records* for their discovery of the deepest plant life on earth. In addition to their major contributions to ecological and systematics research on reef algae, they have an interest in underwater photography and have published a color guidebook to Caribbean seaweeds (D. Littler et al. 1989).

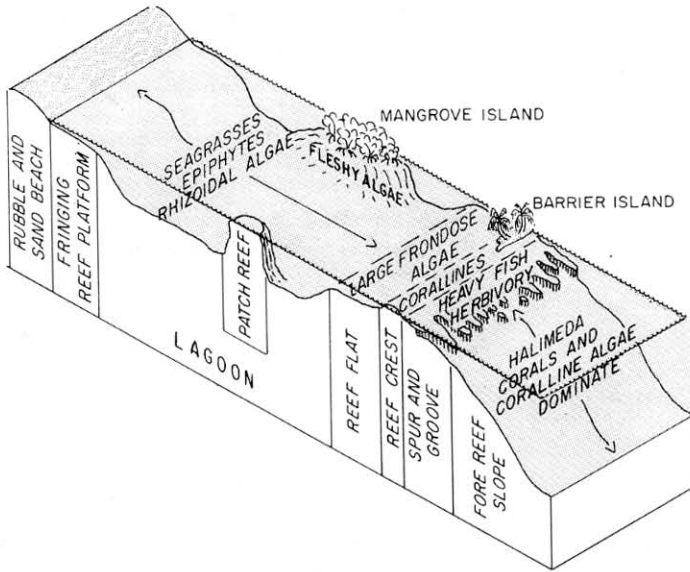
There are three major reef types, based on their location – fringing, barrier, and atoll – and all have basically the same ecological zones (Fig. 2.2a). The most seaward portion of a typical reef is the fore-reef slope that grades upward to the reef crest. Where wave action is consistently high, the reef crest develops into an intertidal algal ridge generally dominated by *Porolithon* and *Lithophyllum* (Fig. 2.2a,b). The most massive algal ridges are found on Pacific atolls, although they are present intertidally on any reef system consistently exposed to high wave energy. Shoreward of the algal ridge is the shallow reef flat where limestone-boring organisms rework the calcareous matrix. In this habitat, slower-growing corals, various coralline algae, and frondose algae dominate. The reef flat usually grades upward toward the shoreline to form an intertidal reef platform dominated by Cyanophyta, where storms may cast calcareous sediment, rubble, and boulders. This material accumulates, particularly on windward barrier and atoll reefs, to form low islands (known as cays/keys in the Caribbean, motus in the South Pacific).

Various calcareous and noncalcareous groups of algae tend to predominate within different reef habitats. The relative dominance of frondose algae, calcareous algae, and corals appears to be related directly to biological factors such as competition and grazing, in addition to being influenced indirectly by abiotic factors, including nutrient levels, wave action, irradiance, desiccation, and temperature. Where herbivory is reduced or nutrient levels are elevated, biotic reefs shift from coral to algal domination. Such shifts from coral dominance to fleshy algal dominance have been related to excess nutrient increases and other stresses for reefs off Venezuela (Weiss and Goddard 1977), on the Abaco reef system, Bahamas (Lighty et al. 1980), and in Kaneohe Bay, Hawaii (Banner 1974; Smith et al. 1981). Unfortunately, the effect of modern mankind on tropical reefs has been to decrease herbivorous fishes through netting and trapping while simultaneously adding nutrients via sewage and agricultural pollution. Unless curbed, this anthropogenically induced shift from coral to algal domination on reefs will continue at an accelerating pace.

Noncalcareous algae. Frondose macroalgae normally are rare on reefs because of grazing by herbivorous fishes and sea urchins. Filamentous algae on the shallow fore-reef slope are also kept inconspicuous by intensive grazing in these spatially heterogeneous habitats. Where there is much turbulence or little topographic shelter from higher-order carnivores on tropical reefs, herbivore activity is reduced, and larger standing stocks of macrophytes develop (e.g., *Sargassum*, *Turbinaria*, *Acanthophora*, *Eucheuma*). Deeper sand plains often contain isolated rubble fragments that provide suitable substrata for strikingly attractive frondose gen-

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(a)



(b)

Figure 2.2. Coral reefs. (a) Sectional view through a tropical continental shelf containing characteristic barrier reef and mangrove systems. Dominant macrophyte groups are indicated for the various habitats. (b) Photograph of *Porolithon-Lithophyllum* ridge at Pago Bay, Guam. (Part a from D. S. Littler et al., 1989, with permission of Cambridge University Press; b by María Scheffer, © 1992, María Scheffer.)

era such as *Halymenia*, *Kallymenia*, *Dasya*, and *Gracilaria*, which can reach considerable size in these refuges. Chemical defenses among macroalgae reach their greatest diversity and frequency in tropical-reef habitats (Hay & Fenical 1988), and some genera (e.g., *Halimeda*, *Stypopodium*, *Laurencia*, *Dictyota*) often are abundant even where grazing is high. Such algal populations may contribute a major portion of the total primary productivity to some tropical reefs. However, it is the sparse mats of fast-growing, opportunistic filamentous algae (see Fig. 1.15b) that usually are responsible for the very high primary productivity per unit area in most biotic reefs. Proportionately, sparse filamentous mats are considerably more productive per unit of algal biomass than are dense stands of the larger macroalgae,

because of their high surface-to-volume ratios. Herbivorous fishes, by their scraping mode of feeding, continuously provide new substrata and thereby select for opportunistic microalgal forms, as well as long-lived scrape-tolerant coralline algae.

Fixation of atmospheric nitrogen by blue-green algae such as *Calothrix crustacea* (e.g., Wiebe et al. 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 is in large part due to this nitrogen fixation, as well as to unusually efficient nitrogen and phosphorus recycling within the symbiotic populations (Johannes et al. 1972). Macroalgae and corals may also be closely associated with blue-

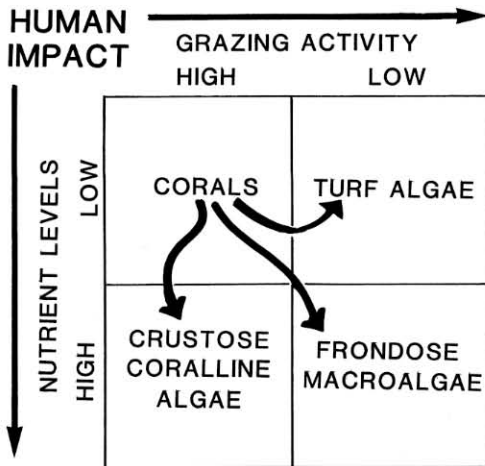


Figure 2.3. Diagram of the relative dominance paradigm. Potentially predominant space-occupying groups of primary producers are emphasized as a function of long-term nutrient levels and disturbance. Human activities tend to reduce grazing animals and increase nutrient levels, thereby shifting reefs from coral to algal domination (arrows). (Modified from Littler & Littler 1984).

green algae. These blue-green-algal associations fix nitrogen at rates equal to those recorded for the richest nitrogen-fixing terrestrial systems (e.g., alfalfa fields).

Other important algae in reef ecosystems are erosive agenic species that contribute to the breakdown of reef structure. Such penetrating or boring algae play an important role in bioerosion. The commonest rock-boring algae are Cyanophyta that attack skeletal materials differentially; the aragonitic coral skeletons are more susceptible, and the denser calcitic deposits of coralline algae are more resistant. One systematic study of penetrating algae in the Indo-Pacific recorded 20 species distributed among Cyanophyta, Chlorophyta, Phaeophyta, and Rhodophyta (Weber-van Bosse 1932), and 33 species of carbonate-boring algae have been reported from tropical China (Chu & Wu 1983). Much research remains to be done on the biology of this interesting group of endolithic marine plants.

Calcareous algae. Calcareous algae have long been recognized as predominant 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 brought the calcifying seaweeds to the attention of geologists, paleobiologists, and ecologists.

The order of prominence for the reef-forming organisms that provided bulk during the development of the reef at Funafuti Atoll, Tuvalu (formerly Ellice Islands) (8° 30' S, 179° 10' E), was as follows: (1) non-articulated coralline algae, (2) *Halimeda*, (3) foraminifera,

and (4) corals (Finckh 1904). Subsequent ecological work (e.g., Littler 1971) and paleontological studies (e.g., Easton & 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 (reef-building) corals.

Some of the adaptive advantages of calcification in reef algae include mechanical support and minimization of damage from sand scour, wave shock, and herbivory, as well as reduction of fouling epiphytes (by means of carbonate sloughing). 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, but reach maximum abundances in shallow, physically disturbed areas. There is evidence that some corallines require physical disturbances such as wave shock or herbivory to prevent their overgrowth by fleshy algae. Coralline algae, in contrast to most fleshy algae, have relatively low primary productivity because of their high structural commitment. Interestingly, calcification rates appear to differ little among reef-flat communities consisting of diverse kinds of calcifiers (Wanders 1976), whether they be corals, nonarticulated coralline algae, or turfs of articulated corallines. Reef-building Corallinales are able to grow at greater depths in weaker light than other primary producers (Littler et al. 1986). *Porolithon* and certain *Lithophyllum* species that dominate algal ridges (e.g., *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 (which are unsuited for most other macroalgae), and they occur only in subtropical and tropical regions, often in association with seagrasses. *Halimeda* is also common on the deeper fore-reef slopes. Psammophytic (sand-dwelling) algae such as *Udotea*, *Penicillus*, and some *Halimeda* species can translocate nutrients from rich sediment-pore waters by means of their unique bulbous rhizoidal systems (Williams & Fisher 1985). Few quantitative studies have been done on any aspect of the ecology of the calcareous Chlorophyta, with the exception of the widely studied genus *Halimeda*. Numerous *Halimeda* species are abundant on protected reef-flat and fore-reef habitats, occurring over a broad depth range on both hard and soft substrata. Other psammophytic forms are associated with shallow seagrass beds and mangroves. Recently, impressive banklike mounds composed of living *Halimeda* and its sediments (dating back to 5,000 years B.P.) have been discovered in back-reef regions of the Great Barrier Reef, Australia (Davies & Marshall 1985).

Deep-water reef algae. Submersible vessels have greatly expanded our knowledge of the distributional limits for marine organisms, but macroalgae have received only incidental attention until recently. The record depth (268 m) for an attached living marine macrophyte was discovered during our own ecological surveys of a seamount off San Salvador Island, Bahamas (Littler et al. 1985). These studies from a submersible, in conjunction with shore-based productivity measurements, revealed unsuspected abundances and potential importances of other deep-water tropical macroalgae. Four zonal assemblages were present on the seamount over the depth range from 81 to 268 m: a *Lobophora*-dominated group (81–90 m), a *Halimeda* assemblage (90–130 m), a *Peyssonnelia* group (130–189 m), and a crustose coralline zone (189–268 m). The zonation pattern observed (i.e., reds > greens > browns with increasing depth) is quite similar to that recorded in Malta by Larkum et al. (1967).

Dominant members of the diverse multilayered macrophyte community on top of the San Salvador seamount (at 81 m) showed net productivity levels comparable to those for shallow-water seaweeds, although receiving only 1–2% of the light energy available at the surface. Deep-water macroalgal communities produce at rates comparable to those for some shallow reef systems, but lower than those for most seagrasses or typical carbonate reef-flat habitats. Calcification rates in deep-water *Halimeda* species are, significantly, similar to those reported for shallow forms of the genus.

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. Until recently, few workers had directed their efforts toward determining the functional and ecological roles of algae on living reefs. We are at a stage where descriptive (correlative) and mechanistic (experimental/causative) approaches must be combined to produce more conceptual theoretical perspectives, which will accelerate our predictive understanding of algal roles in reef biology. General ecological theories are already being modified as a result of experimental studies of tropical algal biology.

The lure of tropical reefs lies in their unsurpassed natural beauty. There is no terrestrial counterpart to the underwater scenery of a rich biotic reef; the vibrant colors and intricate structures of the plants and animals are unique to the marine environment. Reefs are among the few places where one can observe a complex community of plants and animals interacting naturally, seemingly little disturbed by human presence. A burgeoning awareness of the attractiveness of tropical marine plants as experimental organisms for the elucidation of ecological and reef-building processes offers exciting prospects for the future of reef research. ♦

2.1.3 Essay: Kelp forests

Paul K. Dayton*

My interest in kelp communities grew from my thesis work in the intertidal habitat where I studied algal ecology. I considered several types of biological relationships in the intertidal communities, including canopy effects and the roles of herbivores and their predators. Competitive dominance was important, but the expression of the dominance was much affected by wave exposure. I became intrigued by kelp forests, which seemed to offer many important parallels with terrestrial forests, while still allowing some of the manipulative opportunities of intertidal systems.

The sublittoral zone on most temperate rocky shores is dominated by kelps – large brown algae of the Order Laminariales – or the morphologically similar furoids (Figs. 2.1 and 2.4). Both canopy types include fronds suspended in the water column by some form of flotation, fronds supported above the substratum by semirigid stipes, and fronds lying on or immediately above the substratum. Their high productivity and the often-extensive vertical structure formed by their fronds provide food and habitat for many of the species that occur in these regions. Because of this, they are also quite important to human fishermen and divers (Dayton 1985; Chapman 1986; Schiel & Foster 1986). Large kelp forests can considerably reduce alongshore currents and cross-shore water motion (Jackson & Winant 1983).

Like all other populations, kelps are affected by many biotic and abiotic factors. Biotic influences usually include several types of grazers and competition. Kelp systems have many grazers, including polychaetes, arthropods, molluscs, and vertebrates, but they seem to differ from most other plant associations in that the predominant plants can be severely overgrazed by a single type of herbivore (strongylocentrotid sea urchins). The potentially devastating impact of urchins must have a strong influence on evolutionary trends in kelps.

Important abiotic factors include nutrients, appropriate substrata for settlement, and, most important, light. Kelps compete among themselves and with other kinds of algae for limiting resources, especially when they are small. The effect of this competition is highly variable, but it is always potentially there and must be considered. In most situations, one species (usually with floating canopies) can conspicuously dominate the kelp community. One of the most interesting research

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Seaweed communities

2.1 Seaweed communities

Seaweeds exist as individuals, but they also live together in communities with other seaweeds and animals – communities that affect and are affected by the environment. In Chapter 1 we reviewed the morphologies, life histories, and developmental processes of seaweeds as species. In this chapter we consider the patterns and processes in marine benthic communities as a starting point for later factor-by-factor dissection of the environment. We open with overviews of three major habitats and the seaweeds in them: rocky intertidal zone, tropical reefs, and kelp forests. We hope that these personal essays by some noted algal ecologists will also give the reader a glimpse of the phycologist at work and a sense of the excitement of physiological ecology. Near the end of the chapter, three more ecologists tell about some less well known habitats: salt marshes, seagrasses, and the Arctic.

2.1.1 Essay: The rocky intertidal zone *Trevor A. Norton**

Few habitats are so frequently visited by ecologists as the rocky intertidal zone, for it offers intermittent access to a fascinating variety of organisms. It must be unique, however, in that it is invariably examined when most of its inhabitants are out of their element. The number of ecologists who study the shore at high tide when its residents are active and operational could, I suspect, be counted on the arms of a starfish. This is

a pity, for it is the shore when underwater that is the shore in action (Fig. 2.1).

The term “rocky intertidal zone” may slightly mislead the reader, for shores are rarely composed exclusively of bedrock. Many have pebble-littered gullies or sand-carpeted pools, and below the low water mark the rock often gives way to sand or mud. The proximity of such mobile substrata greatly enhances the abrasiveness and therefore the ecological importance of waves.

Even where stable bedrock predominates, the effective substratum may not be rock at all. The mid-shore region is usually covered with closely packed barnacles, with little rock visible between them. Tide pools are often lined with encrusting pink and purple Corallinaceae, which may also carpet the lowermost levels of the shore. By occupying the rock so comprehensively, these organisms replace it. They become the substratum to which other organisms must attach, and yet little is known about their ecological significance as substrata. Do the propagules of other organisms settle preferentially on some crusts and shun others? Can the crusts shed the settled propagules of some fouling species, but not all? The interactions between these little-studied substrata and other shore dwellers may be major influences on the patterns of intertidal vegetation.

Water motion has long been recognized as a major determinant of intertidal communities. A stroll along the coast will reveal striking differences in the vegetation of exposed promontories and that of sheltered bays. An awakening of interest in biomechanics has demonstrated that seaweeds do not confront the waves, but rather yield to them. Immense mechanical strength is less useful than pliability, elasticity, and an ability to conform to the flow (Norton et al. 1982; Koehl 1986; Denny 1988).

Ecologists talk glibly of exposed or sheltered shores, but even the most wave-battered shores may have some relatively protected places. The drama of the

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Seaweed ecology and physiology

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