Progress in Phycological Research, Vol. 3. (Round/Chapman, eds.)
Biopress Ltd., 1984

7

Models of Tropical Reef Biogenesis: The Contribution of Algae

MARK M. LITTLER
and
DIANE S. LITTLER
Department of Botany National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 U.S.A.

---

1. INTRODUCTION

Calcareous algae are universally recognized 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 has drawn attention to calcifying seaweeds from a spectrum of disciplines (e.g. geology, phycology and paleobiology). Important historical roles of algal taxa as sediment producers and reef builders have been chronicled thoroughly by Wray (1971, 1977). While nearly all specialists agree that calcifying algae of modern depositional habitats are abundant, diverse and ecologically significant, critical quantitative information is scarce and these organisms are in nearly every respect poorly known.

For example, the bulk of data concerning biological calcification comes from studies of bone and shell producing animals. Present information on calcareous macroalgae mostly concerns the location, appearance and degree of calcification, but the mechanisms (Borowitzka 1982a) and ultrastructural features (Borowitzka 1982b) are still in the exploratory phase (see for examples Wilbur *et al.* 1969; Marszalek 1971; Borowitzka *et al.* 1974; Böhm 1978; Borowitzka 1979; Digby 1977a, 1977b, 1979). Reasons for this lack of knowledge are varied, but the intractability of the problem, as well as the polyphyletic and variable nature of marine plants that deposit calcium carbonate, have contributed.

One historical debate (e.g. Howe 1912; Setchell 1926, 1928; Crossland 1939) concerned the relative importances of the different groups of calcareous organisms to tropical reef ecosystems. Biologists usually tended to stress the significance of biotic abundances, while geologists emphasized fossil remains from sediment and drilling measurements. By using both approaches, the scientists on the Funafuti Atoll expeditions (Finckh 1904; David *et al.* 1904) made a major advance in understanding the contributions of the various kinds of reef builders. The order of prominence of reef-forming organisms in providing bulk during the development of the reef at Funafuti was as follows (Finckh 1904): (1) non-articulated coralline algae, (2) the green alga *Halimeda*. (3) foraminifera and (4) corals. Subsequent ecological work (e.g. Lee 1967; Womersley and Bailey 1970; Littler 1971, 1973a, 1973b; Stearn *et al.* 1977; see also Cribb 1973) and paleontological studies (e.g. Easton and Olson 1976; Macintyre and Glynn 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. Additional deep drillings into atoll reefs [e.g. Bikini Atoll (Emery *et al.* 1949); Enewetak Atoll (Ladd *et al.* 1953); Midway Atoll (Ladd *et al.* 1967, 1970)] as well as high-island reefs (Easton and Olson 1976) have confirmed the preponderance of calcareous algae as both bulk producers and consolidators.

Until recently, few workers had directed their efforts towards determining the functional and ecological roles of calcareous algae on living reefs. Stronger philosophical emphases that stress mechanistic and predictive viewpoints are needed to supplement the more traditional descriptive approaches and methodologies. Particularly lacking are taxonomically-sound, reproducible field studies of production and calcification processes and experimental analyses of environmental factors that determine the rates of such processes. Historical reasons for this scarcity would seem to be taxonomic difficulties and a lack of applicable quantitative ecological techniques (Littler 1972). As a result, the ability of paleoecologists to utilize the extensive fossil record remains severely limited and, as pointed out by Adey and Macintyre (1973), serious taxonomic and ecological misinterpretations are entrenched in the literature. Fortunately, taxonomic problems are no longer insurmountable (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 *et al.* 1983a, 1983b; Hatcher and Larkum 1983) ecological methods are available. While extensive ongoing ecological field programs have been initiated throughout the Caribbean on living reef algae (Adey and Vassar 1975; Steneck and Adey 1976; Wanders 1976, 1977; Adey 1978a, 1978b; Van den Hoek *et al.* 1978; Hay 1981a, 1981b, 1981c, 1984; Littler *et al.* 1983a, 1983b) and research activities are intensifying in that region, comparable algal research projects on tropical Pacific reefs are disproportionately few (see Borowitzka 1981a; Hatcher 1982; Hatcher and Larkum 1983).

2. CHARACTERISTICS OF REEF ALGAE

2.1. *Organic productivity and N_2 fixation*

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. This anomalously high organic productivity is related to: (1) increased spatial heterogeneity (dramatically increasing metabolic surface area), (2) continual nutrient input from water flowing across these surfaces, (3) specialized benthic nitrogen-fixing blue-green algae and bacteria and (4) biological systems that tend to retain nutrients by recycling. The photosynthetic organisms responsible are symbiotic zooxanthellae within hermatypic corals, microfilamentous algae (e.g. *Polysiphonia, Herposiphonia, Centroceras, Ceramium* and blue-green algae; Fig. 1a), frondose macroalgae (e.g. *Laurencia, Sargassum, Dictyota, Caulerpa*; Fig. 1b) and coralline algae (Fig. 1c). In certain soft bottom habitats, seagrasses contribute significantly and provide attachment sites for epiphytic seaweeds (McRoy and McMillan 1977). On reefs not dominated by corals, non-articulated coralline algae and various small filaments usually comprise the majority of cover. Larger frondose algae occur abundantly on reef flats (Doty 1971; Wanders 1976; Connor and Adey 1977), unstructured sand plains (Earle 1972; Dahl 1973; Hay 1981c) or deep-water sites (personal observation) 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 inconspicuousness of microfilamentous algae on shallow reef-front systems also is thought (Randall 1961; Wanders 1977; Borowitzka 1981a) to primarily result from intensive grazing by the numerous herbivores and omnivores inhabiting these spatially heterogeneous systems. Where spatial rugosity is minimal on tropical reefs, herbivore activity is reduced (Brock 1979; Hay *et al.* 1983) and reasonably large standing stocks of macrophytes (*Sargassum, Turbinaria, Acanthophora*) often develop (Doty 1971; Connor and Adey 1977; Wanders 1976). Such macroalgal populations may contribute a major portion of the total primary productivity of some reefs (Rogers and Salesky 1981). However, most evidence (e.g. Wanders and Wanders-Faber 1974; Bunt 1975; Marsh 1976; Dahl 1976; Larkum 1981; Rogers and Salesky 1981) indicates that it is the fast-growing and opportunistic filamentous algae of sparse mats that result in the very high primary production rates per unit area of biotic reefs. Conversely, tightly-compacted mats of algae (turfs) usually show reduced productivity due to overlapping diffusion gradients and self shading (Littler and Arnold 1980; Hay 1981a).

On *Acropora palmata* Lamarck reefs of St. Croix where larger macrophytes are rare, filamentous algae, which are present only in very low biomass, are responsible for 70 to 80 per cent of the productivity ($5–7\,\mathrm{g\,C\ fixed} \cdot \mathrm{m}^{-2} \cdot \mathrm{d}^{-1}$) of the shallow fore and back reefs (Brawley and Adey 1977). Proportionately, sparse filamentous mats are considerably more productive per unit weight of algal biomass than are dense stands of the larger macroalgae. This can be related to functional morphological differences where opportunistic species with high surface to volume ratios typically outproduce those having a coarser morphology (Littler 1980a; Littler

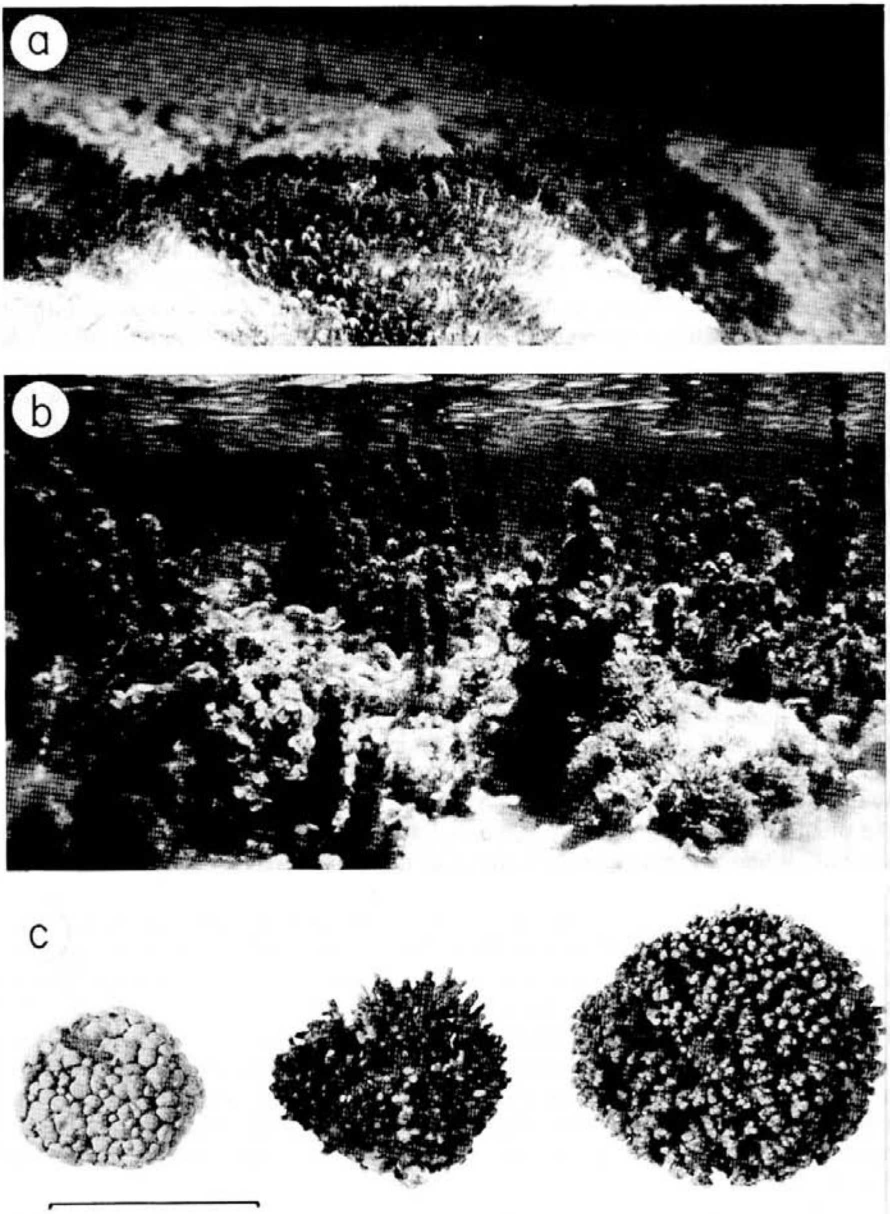

Figure 1. (a) Microfilamentous turf dominated by *Wrangelia argus* Montagne. Length of individual fronds are about 1 cm. (b) Macroalgal community dominated by *Sargassum polyceratium* Montagne and *Turbinaria turbinata* (L.) Kuntze. Length of largest thallus is approximately 25 cm. (c) Examples of unbranched and branched coralline rhodoliths. From left to right *Hydrolithon reinboldii*, *Neogoniolithon frutescens* and *Lithothamnium glaciale*. Scale = 5 cm in length.

and Arnold 1982; Littler *et al.* 1983a). 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 select for and maintain opportunistic microalgal forms (Montgomery 1980), as well as long-lived resistant coralline algae (Littler and Doty 1975; Wanders 1976).

Fixation of atmospheric nitrogen by blue-green algae (Wiebe *et al.* 1975; Mague and Holm-Hansen 1975) within filamentous microalgal assemblages also is an important feature that enhances reef productivity and nutrition. The increased productivity of benthic reef communities, versus planktonic oceanic systems, is very likely due in large part to such nitrogen fixation within filamentous algal communities (Wiebe *et al.* 1975; Webb *et al.* 1975; Mague and Holm-Hansen 1975). Oceanic water flowing across a shallow, windward, inner island reef at Enewetak Atoll (Wiebe *et al.* 1975) became markedly enriched with various forms of dissolved and particulate fixed nitrogen. The source of this localized enrichment ($985\,kg \cdot ha^{-1} \cdot yr^{-1}$) was several nitrogen-fixing algae, the most abundant and important of which was *Calothrix crustacea* Thuret. This epiphytic blue-green alga occurs intermingled as a turf former (Bakus 1967) among other filamentous microalgae; a similar system was described (Webb and Wiebe 1978) for the Great Barrier Reef (see also Burris 1976). Other reef organisms that contain blue-green algae and show high nitrogen-fixation rates are various macroalgal populations (Capone 1977; Capone *et al.* 1977) and corals (Crossland and Barnes 1976). Such blue-green algal associations fix nitrogen at levels equal to those recorded for the richest nitrogen-fixing terrestrial systems known (Wiebe *et al.* 1975).

Coralline algae, on the other hand, are notoriously low primary producers as documented by studies of their functional morphology (Littler and Littler 1980, 1981, 1984; Littler and Arnold 1982; Littler *et al* 1983a). Marsh (1970) was the first to note the low production rates of non-articulated coralline populations ($240\,g$ net $C \cdot m^{-2} \cdot yr^{-1}$ at Enewetak Atoll) and concluded that these algae are more important in reef building than in primary production. A comparable net production value of $370\,g\,C \cdot m^{-2} \cdot yr^{-1}$ was obtained (Wanders 1976) for a shallow Caribbean reef flat at Curacao, Netherlands Antilles where frondose algal and coral production rates exceeded those for coralline communities. Marsh (1974) felt that the algal zone of Enewetak Atoll was about equal to the coral zone in terms of daily primary productivity, which is in contrast to the finding of Smith and Marsh (1973) and Rogers and Salesky (1981), who noted that the coral portions of coral/algal communities had significantly lower net productivity than algal components.

Five coralline species on Hawaiian reefs also tended to show (Littler, 1973c) low rates (0.5–$2.6\,g$ net $C \cdot m^{-2}$ of thallus $\cdot\, d^{-1}$), however, because of the large standing stocks, coralline contributions to overall net primary productivity were substantial ($5.7\,g\,C \cdot m^{-2}$ of reef$\cdot d^{-1}$). A Pacific fringing reef community in French Polynesia dominated by the coralline *Neogoniolithon frutescens* (Fosl.) Setch. and Mason had a gross productivity of $1{,}387\,g\,C \cdot m^{-2} \cdot yr^{-1}$ (Sournia 1976), whereas the value for the entire reef system was nearly double that figure ($2{,}682\,g\,C \cdot m^{-2} \cdot yr^{-1}$). In his review, Lewis (1977) concluded that coralline algae have rates of primary productivity that are much lower than those for reefs as a whole.

Production of the calcareous green algae *Halimeda incrassata* (Ellis) Lamour., *H. monile* (Ellis and Solan.) Lamour., *Penicillus capitatus* Lamarck, *Rhipocephalus phoenix* (Ellis and Solan.) Kütz. and *Udotea flabellum* (Ellis and Solan.) Lamour. in a Florida lagoon (Bach 1979) averaged $8.6\,g$ ash-free dry wt $\cdot\, m^{-2} \cdot yr^{-1}$ and $4.2\,g\,CaCO_3 \cdot m^{-2} \cdot yr^{-1}$, of which *H. incrassata* accounted for more than half.

Sediment production was considered (Bach 1979) to be the most important biological function of these chlorophytes.

Additionally, $CaCO_3$-boring algae may have the potential to play an important role in primary productivity (Wanders 1976) once the upper algal stories are removed by grazing. However, endozoic algae embedded in the skeletons of living corals have not proven to be significant primary producers on reefs (Kanwisher and Wainwright 1967; Franzisket 1968; Halldal 1968). Much research remains to be done with this very interesting group of endolithic marine plants.

2.2. *Calcification*

There are about 100 genera of calcareous algae known. By far, the majority and the most heavily calcified of the reef species belong to the family Corallinaceae [proposed for removal from Cryptonemiales as Corallinales (Silva and Johansen 1982)] within the Division Rhodophyta. Several members of the Ceramiales (Crouanieae, Wollaston 1968) also calcify. *Titanophora* is the sole calcifying genus of the Gigartinales (Rhodophyta), whereas calcareous Nemaliales include approximately seven genera. The Chlorophyta rank next in number of calcareous forms (~10 genera), while the Phaeophyta contain only one genus (*Padina*) with calcification. Some marine Cyanophyta (Nostocales) also are capable of calcium deposition.

2.2.1. *Physical precipitation*

Physical deposits of calcium salts may arise on reefs through processes of mechanical accretion by filamentous Cyanophyta. For example, stromatolite accretions in Bermuda (Gebelein 1969) are produced by the interaction of two blue-green algae. During the daylight growth period, the mucilaginous upright filaments of *Schizothrix calcicola* (C.Ag.) Gomont trap particulate matter, and at night the horizontal development of *Oscillatoria* firmly binds these trapped grains. Carbonates also are precipitated physically and lithified inside mats to form stromatolite-like laminations within tidal pools in the Red Sea (Friedmann *et al.* 1972) and subtidally in the Bahamas (Dravis 1983).

Cryptocrystallization is of considerable importance to the geological building of reefs, even though only indirectly associated with living organisms (Milliman 1973; Alexandersson 1977). Submarine lithification is a very complicated geochemical topic with an extensive literature that cannot be reviewed here. The process involves the internal cementation that takes place in shallow subsurface spaces or voids in carbonate structures where the local environment contains organics and is conducive to crystal precipitation. Cryptocrystallization occurs in calcareous algae when carbonate precipitates within empty cells, conceptacles or any place where boring organisms have excavated cavities. The surfaces of a living reef are composed of biological tissues that seal off the internal non-living bulk of the reef. The countless internal voids and chambers, once having lost contact with the surrounding seawater, become suited for $CaCO_3$ precipitation and cementation. Consequently, submarine cementation takes place beneath living calcareous reefs and this as well as other lithification processes are important in producing massive structures. Alexandersson (1977) has suggested that organic extracellular products, released by living algae at the surface of the reefs, influence the internal chemistry of a reef. Such organics may be carried into the reef interstices, facilitating mineralization under conditions that would not otherwise be favorable. In this regard, the decay of organic matter in these subsurface habitats, by releasing ammonia by-products, could be the mechanism (Macintyre, 1984) triggering the precipitation of $CaCO_3$.

2.2.2. *Physiological deposition*

Mechanisms. The deposition of $CaCO_3$ in most calcareous macroalgae is a physiological process (Borowitzka 1982a) in intimate association with the cells or thallus surface (Borowitzka 1982b). The two proposed mechanisms of skeletal deposition are: (1) cellular metabolic processes (not yet elucidated) and (2) removal of carbon dioxide and bicarbonate during photosynthesis, thereby raising the pH to levels where $CaCO_3$ precipitation occurs. Photosynthetic precipitation within intercellular spaces is the mechanism suggested (Borowitzka 1981b) to explain aragonite deposition in marine algae such as *Halimeda, Udotea* and *Galaxaura*. Lewin (1962) proposed that carbon dioxide uptake alone is insufficient to explain calcification because of the fact that calcified and non-calcified photosynthetic algae live side-by-side in nature. A second point is the presence of uncalcified photosynthetic joints or flex-points, in some of the erect and heavily-calcified algae, which is difficult to explain if photosynthetic precipitation is the mechanism. Thirdly, algal calcification in the absence of light has been documented (Goreau 1963; Stark *et al.* 1969; Smith 1973). However, the presence of extracellular organic inhibitors of calcification could explain (Borowitzka 1982a) the lack of calcification by photosynthetic cells, whereas dark calcification might result from strictly non-metabolic physical precipitation. Once calcite crystal nuclei have formed, further precipitation of $CaCO_3$ (epitaxial nucleation) proceeds without metabolic activity (Borowitzka 1979) and is probably important in the continued deposition in older parts of coralline thalli.

The physiological mechanisms and cellular processes of calcite calcification continue to loom as major gaps in our understanding of tropical reef biology. Research demonstrating that light stimulates calcification rates and that photosynthesis is intimately related to $CaCO_3$ deposition in coralline algae includes that of Goreau (1963), Ikemori (1970), Okazaki *et al.* (1970), Pearse (1972), Pentecost (1978), Böhm (1978), Smith and Roth (1979), LaVelle (1979) and Borowitzka (1979). One related example, albeit from freshwater (Lucas and Smith 1973), involves segments of the internodal cells of the alga *Chara corallina* Klein ex Willd. That extrude hydroxyl ions in the presence of light, and it is on these alkaline regions of the cell wall that calcium-carbonate deposition occurs. This mechanism also is suggested (Borowitzka 1982a) to account for the unique pattern of aragonite deposition in the marine alga *Padina*. The planktonic coccolithophorids have been examined in greatest detail (see review by Borowitzka *et al.* 1974) and show involvement of the Golgi apparatus and very high light/dark ratios of calcification. Some Rhodophyta and Chlorophyta exhibit two to three times as much calcium fixation in light as compared to dark, whereas other red and green algae show no difference between light and dark fixation (Goreau 1963; Stark *et al.* 1969; Ikemori 1970; Böhm and Goreau 1973). It would seem, at least in *Bossiella* (Pearse 1972), that the rate of calcification is stimulated by translocated photosynthetic products which serve as structural components or energy sources rather than simply by the ionic changes surrounding ongoing photosynthesis. Calcification in *Halimeda opuntia* (L.) Lamour. results from two opposing processes; both calcium uptake and calcium release were shown (Böhm and Goreau 1973) to be metabolically controlled.

An early attempt (Littler 1973c) to determine the total carbon and calcium budgets for four non-articulated coralline algae suggested a considerable exchange between the internal inorganic and organic carbon pools within individuals. Related to this is the finding (Böhm and Goreau 1973) that in *Halimeda opuntia*, skeletal calcium is simultaneously deposited and remobilized by opposing metabolic processes. Measurement of calcification rates in calcareous algae using radioactive tracers (e.g. Stark *et al.* 1969; Littler 1973c; Borowitzka 1977; Böhm and Goreau 1973; Böhm 1978; Borowitzka and Larkum 1976a, 1976b, 1976c, 1977) as well as with corals (e.g. Barnes and Crossland 1977) is complicated, particularly in the case of ^{45}Ca, by interactions with two compartments other than the calcium carbonate crystals. These compartments are (Borowitzka 1979) intercellular spaces, cell wall mucilages and polysaccharides. An improved kinetic method, developed and discussed by Böhm (1978), has been used successfully to measure calcification in several species of calcareous algae. In this technique, the uptake of isotope is plotted over time and the calcification rate is calculated using only the linear portion of the curve. Consequently, errors of the single point technique, due to initial curvilinear uptake as a function of isotopic exchange, organic binding to cell walls and intercellular absorption (Borowitzka, 1982a), are avoided.

Among the more novel calcification theories is the electrochemical model of Digby (1977a, 1977b, 1979) that places emphasis on chemical events controlled by photosynthesis and cellular manipulations of pH. This model postulates the first step to involve the photosynthetic splitting of water whereby oxygen atoms and hydrogen ions are released from the cell, while the electrons are retained to reduce organic metabolites. As these metabolites become oxidized, excess hydroxyl ions (and hydrogen atoms) are produced due to reduction of the hydrogen ions by electrons during photosynthesis. Other electrons derived from photosynthesis react with bicarbonate ions that have diffused in from the seawater to yield carbonate ions (and hydrogen atoms). The presence of hydroxyl ions could also result in the production of carbonate from bicarbonate in a reaction possibly involving carbonic anhydrase. The second step proposes the outward diffusion of carbonate ions and their internal replacement by bicarbonate diffusing inward. The carbonate ions once outside the cell, partially hydrolyze thus raising the pH in the cell walls where carbonate is being deposited. Consequently, conditions of saturation of both calcium (from seawater) and carbonate ions (from the cells) are reached in the walls with the result that calcium carbonate precipitates. Finally, in step three, the internal hydrogen atoms, resulting from the production of hydroxyl and carbonate ions, must be removed, which could be accomplished by reaction with oxygen. In summary, the diffusion of hydrogen ions outward through the tips of the cells, and the inward diffusion of bicarbonate ions and outward diffusion of carbonate ions at the sides of the cells, would result in calcification. Hydrogen ions moving out through the cell apex would be lost to the surrounding seawater. The above electrochemical model (Digby 1977a, 1977b) does not exclude the idea that an organic matrix (Borowitzka 1977) in the cell wall plays an important role in deposition. Borowitzka (1982a) has taken exception to this model and stresses that the intimate connection between calcification and photosynthesis is of paramount importance. The low productivity and slow growth of coralline algae may reflect the fact that a great proportion of photosynthetic energy is channeled into carbonate precipitation.

It is interesting to note that calcification rates appear to differ little among communities consisting of diverse kinds of calcifiers (Smith 1973), whether they are corals, non-articulated coralline algae or turfs of articulated coralline algae on reef flats.

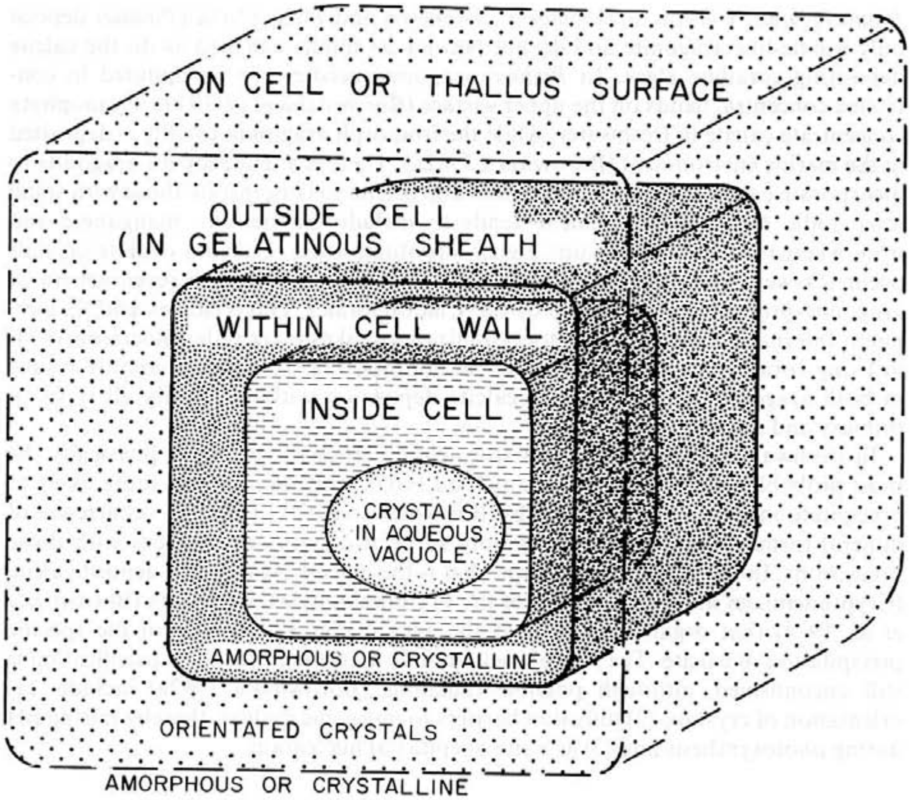

Figure 2. Diagrammatic view of the four locations of calcium carbonate deposition in algae (modified from Arnott and Pautard 1970). Only the unicellular coccolithophorids (Prymnesiophyta) show intracellular calcification.

Sites. The possible sites of deposition (Fig. 2) vary greatly among algae belonging to different taxonomic groups. The blue-green algae (Nostocales) and red algae (Cryptonemiales, Corallinales) are the only groups having deposition associated with the cell wall or its organic sheath. Caulerpales, Dasycladales, Nostocales, Nemaliales, Cryptonemiales, Corallinales and Ceramiales deposit calcium carbonate both inter-cellularly and on the thallus surface. The Gigartinales and Dictyotales exhibit only surficial calcification.

Mineralogy. In algae, crystalline calcium carbonate occurs principally in either the aragonite form (orthorhombic) or calcite form (hexagonal-rhombohedral), but rarely as a mixture of the two in the same species. Magnesium carbonate is often incorporated (7 to 50 per cent of the skeleton by weight) along with algal calcite (Moberly 1968), while 4–5 per cent magnesium hydroxide (brucite) has been reported for *Neogoniolithon* (as *Goniolithon*. Weber and Kaufman 1965). The faster the growth rate of the alga (Moberly 1968), the greater the percentage of magnesium. Most calcareous species (i.e. Corallinaceae) deposit only calcite, while calcifying Rhodophyta other than Corallinaceae (e.g. *Titanophora, Peyssonnelia, Ptilocladia, Galaxaura, Liagora, Trichogloea, Trichogloeopsis, Izziella, Dotyophycus*), all calcareous Chlorophyta (e.g. *Penicillus, Cymopolia, Halimeda, Tydemania,* *Rhipocephalus, Udotea, Acetabularia, Neomeris*) and Phaeophyta (*Padina*) deposit only needle-like aragonite and do not become as solidly calcified as do the calcite depositing coralline algae. In *Padina*, aragonite needles are precipitated in controlled concentric bands on the upper surface (Borowitzka *et al.* 1974). Cyanophyta concentrate calcite in freshwater, while the isomorph aragonite usually is deposited in the marine environment (Borowitzka 1982a). There is a tendency for aragonite to incorporate cations with large ionic radii and calcite to concentrate those with small ionic radii. Consequently, calcite tends to include magnesium, manganese and iron, whereas aragonite contains higher strontium levels. Calcium oxalate crystals occur (Dawes 1969; Friedmann *et al.* 1972; Böhm *et al.* 1978) in seven genera of aragonite-producing green algae of the Cladophorales, Dasycladales and Caulerpales. Internal lithification (cryptocrystallization) takes place (Alexandersson 1974) in living coralline rhodoliths (=spherical nodules, Fig. 1c) that apparently results in both aragonite and magnesium-calcite deposition within virtually all types of primary and secondary cavities.

In freshwaters super-saturated with calcium carbonate, calcite is physically the most probable form to be deposited (Cloud 1965), while aragonite is more likely to precipitate in seawater. As noted by Borowitzka *et al.* (1974), the occurrence of mineral forms among algae having only surficial deposition coincides with those predictions. In the exceptional groups, that is the marine algae which deposit calcite (Cryptonemiales and many genera of the Prymnesiophyta), it appears (Borowitzka *et al.* 1974) that organic matrices at the sites of deposition control the specific precipitation of calcite. The role of such organic matrices in coralline calcification is still unconfirmed, although possible functions (Borowitzka 1982a) include: (1) orientation of crystals, (2) diffusion barriers to inorganic carbon, thereby raising pH during photosynthesis and (3) as a site of epitaxial nucleation.

3. DISTRIBUTION AND ABUNDANCE OF REEF ALGAE

3.1. *Geological records*

Wray (1971, 1977) reviewed ample evidence showing conclusively the degree to which marine calcareous algae have contributed to the formation of ancient and modern reef sediments and frameworks. The major trends (Fig. 3) are as follows (mainly abstracted from Wray 1971). Filamentous encrusting Cyanophyta and Chlorophyta were the dominant forms on Paleozoic reefs, occasionally in conjunction with abundant primitive calcareous Rhodophyta (solenopores and ancestral corallines). Filamentous Cyanophyta mostly contributed laminated calcareous structures, usually in the reef flat habitat but also subtidally. Calcifying Chlorophyta consistently have been abundant producers of sediments since they appeared in the late Cambrian. Their contributions primarily have been whole or broken segments or muds deposited in back-reef and lagoonal habitats. The predominance of calcareous organisms in the late Cambrian fossil record has been postulated (Lowenstam and Margulis 1980) as due to the evolution of intracellular mechanisms of calcium-ion concentration in conjunction with natural selection by predators.

During the Mesozoic, solenopores were predominant (Wray 1971), while non-articulated coralline algae were conspicuous reef components from the late Cretaceous through the Cenozoic. The Solenoporaceae appeared in the Cambrian as encrusting rhodoliths, reached their peak diversity and abundance during the Ordovician, declined through the remainder of the Paleozoic, attained a second

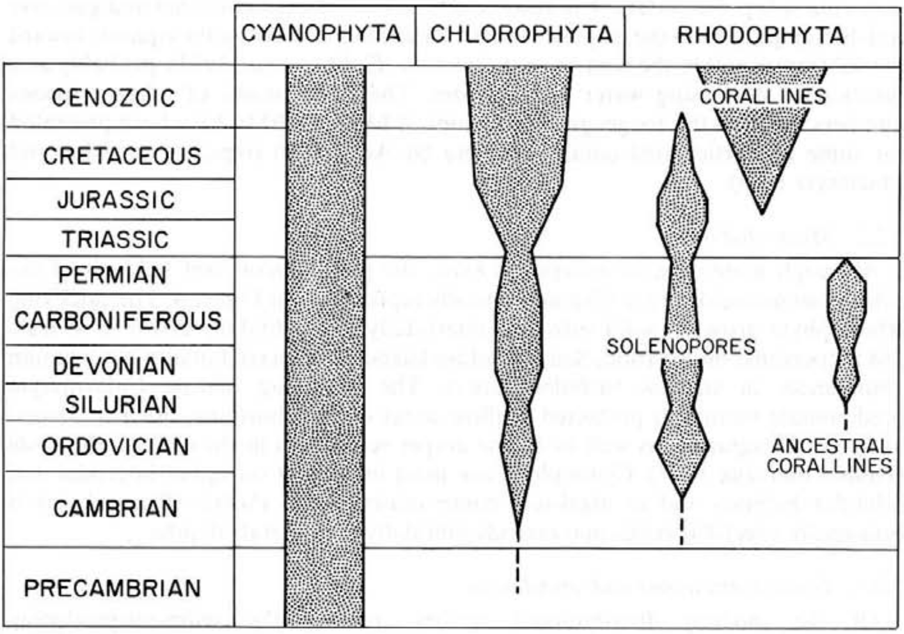

Figure 3. Geological distributions of algal groups recorded in reef structures (from Wray 1971).

peak within the Jurassic, finally becoming extinct during the Paleocene. A group of distinctive calcareous algae, possibly ancestors of the late Mesozoic and Cenozoic corallines, appeared between the Devonian and Permian.

A large-scale evolutionary trend toward more intense grazing by gastropods, sea urchins and fishes (Steneck 1983) may have given the Corallinales a distinct advantage over the relatively herbivore-susceptible solenopores. Although coralline algae were first recorded in the Jurassic, probably descending from both the Solenoporaceae and the 'ancestral corallines', they did not begin to diversify and increase rapidly until the Cretaceous and early Cenozoic. The extinction of Solenoporaceae and the adaptive radiation of coralline algae (Steneck 1983) parallel a gradient of escalating herbivory over time. Corallinales have sustained an extremely rapid expansion into shallow marine communities in association with increased grazing intensity throughout the Cenozoic to the present. Today corallines are the only algal group to thrive under, and often require, intensive herbivory (Littler and Doty 1975; Wanders 1976).

3.2. *Modern records*

3.2.1. *World-wide patterns*

In addition to association with intensity of herbivore grazing, the abundance of calcareous algae can be correlated to some extent with the concentration of dissolved calcium carbonate in seawater. Calcareous organisms, in general, are most diverse and abundant in tropical waters, which are supersaturated with calcium carbonate. This saturation decreases towards the poles due to lower temperatures and a higher partial pressure of carbon dioxide. Notable exceptions to the above distributional pattern are the occurrences (Kjellman 1883; Foslie 1895; Lebednik 1977) of massive calcareous banks of non-articulated coralline algae in very cold sub-polar waters. The relative dominance of calcareous macroalgae over reef-building corals in the tropical western Pacific increases from the equator toward the subtropics and in the west-to-east direction (Golikov *et al.* 1973), probably as a function of decreasing water temperatures. The distributions of relative species numbers, fitted to the zoogeographic regions of Ekman (1953), have been presented for some non-articulated coralline genera by Adey 1970 (repeated in Adey and Macintyre 1973).

3.2.2. *Macro-habitats*

Although many specific exceptions exist, the predominant reef habitats of the calcareous macroalgae are diagrammatically represented in Figure 4. The calcifying Rhodophyta grow on solid substrata intertidally and subtidally down to at least 268 m (personal observation, San Salvadore Island, Bahamas), but attain maximum abundances in shallow turbulent areas. The calcifying marine 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). Cyanophyta are most important on upper intertidal and tidal-flat habitats and in algal-turf communities, while *Padina* (Phaeophyta) is principally a reef-flat genus that extends subtidally to moderate depths.

3.2.3. *Local distributions and abundances*

Of the modern distributional studies treating the sediment-producing macroalgae, among the most noteworthy are the assessments of distribution and abundance patterns in the tropical Atlantic (see for examples, Stockman *et al.* 1967; Land 1970). Non-articulated coralline algae and *Halimeda* have been noted (Ginsburg 1956; Neumann and Land 1969, 1975; Stearn *et al.* 1977; Hillis-Colinvaux 1980, 1982) as major elements of tropical Atlantic and Pacific reefs. *Halimeda* is the most abundant component of Atlantic reef sands and dominates the back reef and nearshore algal banks. For example, the Bight of Abaco (Little Bahama Bank) contains standing stocks of *Halimeda, Rhipocephalus* and *Penicillus* averaging 20 thalli $\cdot$ m^{-2} of substratum (Neumann and Land 1969). It was estimated that, perhaps for the entire Bahama Banks, green algae have produced more aragonitic lime mud during the past 5,500 yrs than could be accommodated on the bank tops (about 24 g $CaCO_3 \cdot m^{-2} \cdot yr^{-1}$, Neumann and Land 1975). An excellent, but largely overlooked, review of the importance of *Halimeda* (and other calcareous algae) as a reef-forming organism throughout the tropical Pacific was published by Chapman and Mawson (1906) nearly 80 years ago.

The coralline algae are not as impressively conspicuous on Indian Ocean and Atlantic reefs as they are in the Central and Indo-Pacific (Wells 1957; Stoddart and Yonge 1971) and, until relatively recently, well-developed algal ridges were thought (Stoddart 1969; Milliman 1973) to be absent in these regions. The notable lack of studies by coralline specialists was responsible for this biased picture for Caribbean areas and it is now known (Glynn 1973; Adey 1978a, 1978b) that massive algal ridges are plentiful where wave shock is consistently high. Wave turbulence, such as that generated by trade winds, is critical (Littler and Doty 1975; Adey 1978a) to the maintenance of ridge-building coralline species.

Extensive work in Hawaii (Littler 1971, 1973a, 1973b, 1973c; Doty 1974; Littler and Doty 1975) on the distributions of reef-building organisms has revealed a predominance of non-articulated coralline algae in both fringing reef (Fig. 5) and SCUBA-depth (Fig. 6, 7–28 m) reef habitats. Drilling studies at Midway Atoll

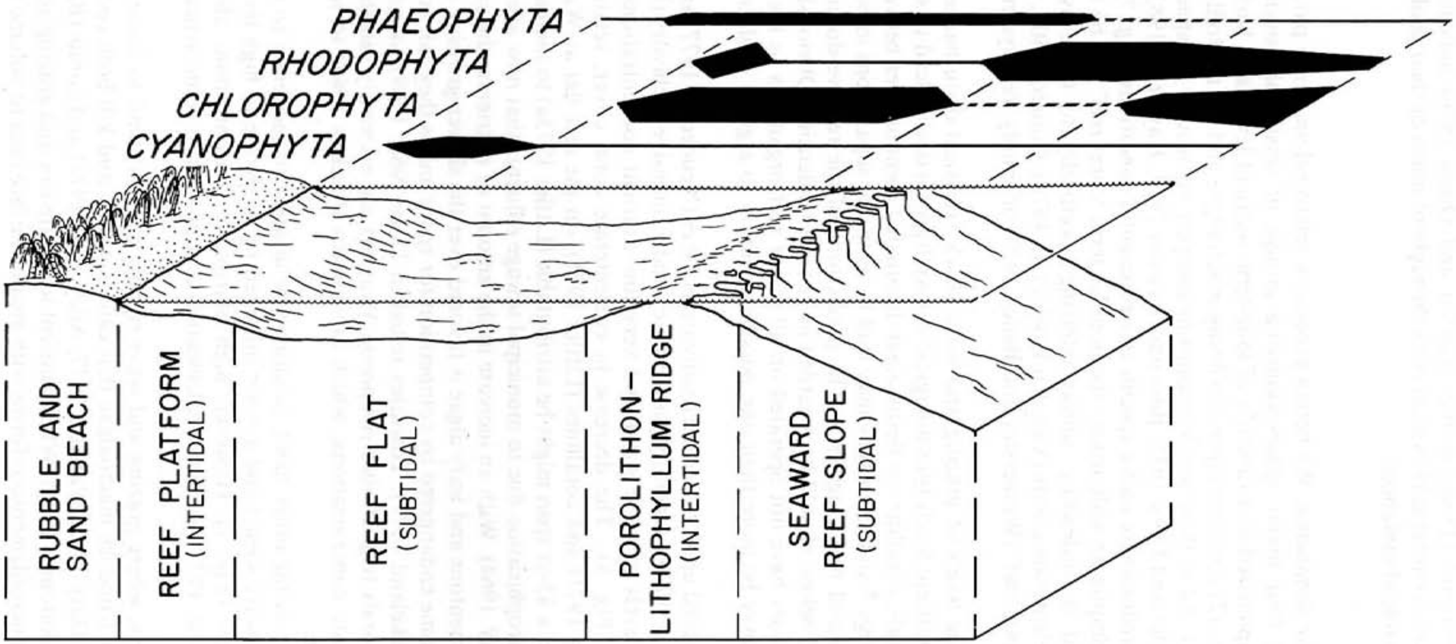

Figure 4. The generalized primary habitats of the tropical marine divisions of calcareous macroalgae. The relative extents of platform and flat habitats vary markedly from reef to reef.

(Gross *et al.* 1969) and Hanauma Bay (Easton and Olson 1976) indicate that coralline algae have dominated Hawaiian reefs throughout much of their geological history in comparable abundances.

3.2.4. *Ecology*

Model of relative dominance. We herein propose a relative-dominance paradigm (Fig. 7) whereby four major space-occupying groups of sessile photosynthetic organisms are emphasized as a function of long-term nutrient levels and herbivore activity: (1) corals, (2) coralline algae, (3) fleshy macroalgae and (4) microfilamentous algae (Fig. 1). All of these sessile organisms compete vigorously for space and light (e.g. see Littler and Doty 1975; Buss and Jackson 1979; Hay *et al.* 1983) and each group can predominate under specific environmental conditions (Fig. 7). For this reason, and despite its wide usage, the popular term 'coral reef' can be highly inappropriate and is misleading, unless referring specifically to those systems dominated by coelenterate corals (Van den Hoek *et al.* 1975). Consequently, in the general sense, 'biotic reef' (Womersley and Bailey 1970) or simply 'reef system' are preferable terms.

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 (Figs 7 and 8), 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 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.

Corals, while preyed upon by certain omnivorous fishes (Neudecker 1977) and sea urchins (Glynn *et al.* 1979), generally gain primacy under intensive herbivory (Brock 1979), moderate levels of wave shear and very low nutrient concentrations (e.g. Kealakekua Bay, Fig. 8)., The decrease in coelenterate coral cover, relative to macroalgae (Doty 1971) and corallines (Littler 1971), on the reef flat at Waikiki, Oahu (Fig. 8) over a 45-yr span might be attributable (Littler 1973a) to increases in nutrients from eutrophication due to municipal sewage effluents that now affect the reef (Laevastu *et al.* 1964). 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 1968, 1969) found that some Hawaiian corals (e.g. *Porites compressa* Vaughn) are extremely sensitive to increased phosphate concentrations, which are known (Simkiss 1964) to inhibit calcium deposition.

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. 7). However, high phosphate concentrations also are known (Brown *et al.* 1977) to reduce calcification and growth of some articulated coralline algae.

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 (Littler and Doty 1975; Wanders 1977; Adey *et al.* 1977) and corals (Banner 1974; Potts 1977; Antonius 1982). When nutrient levels are low and grazing activity low to moderate, microfilamentous forms with greater surface area to volume ratios

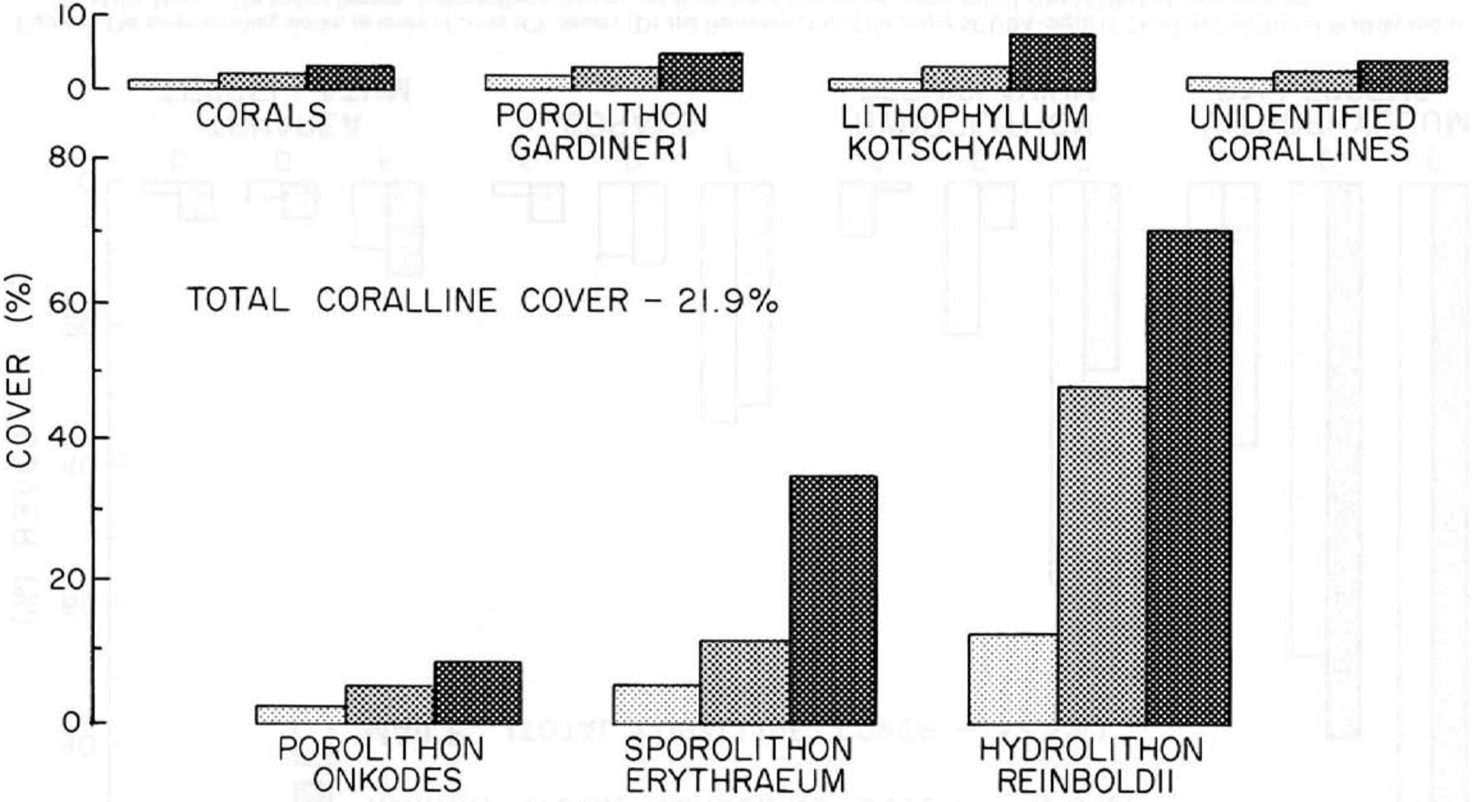

Figure 5. The mean standing stocks of the major reef builders over the entire Waikiki, Hawaii fringing reef. In each histogram, per cent cover is given in the left column, relative density (per cent of individual thalli sampled) by the middle column and frequency (per cent of samples in which a given species was present) by the right column.

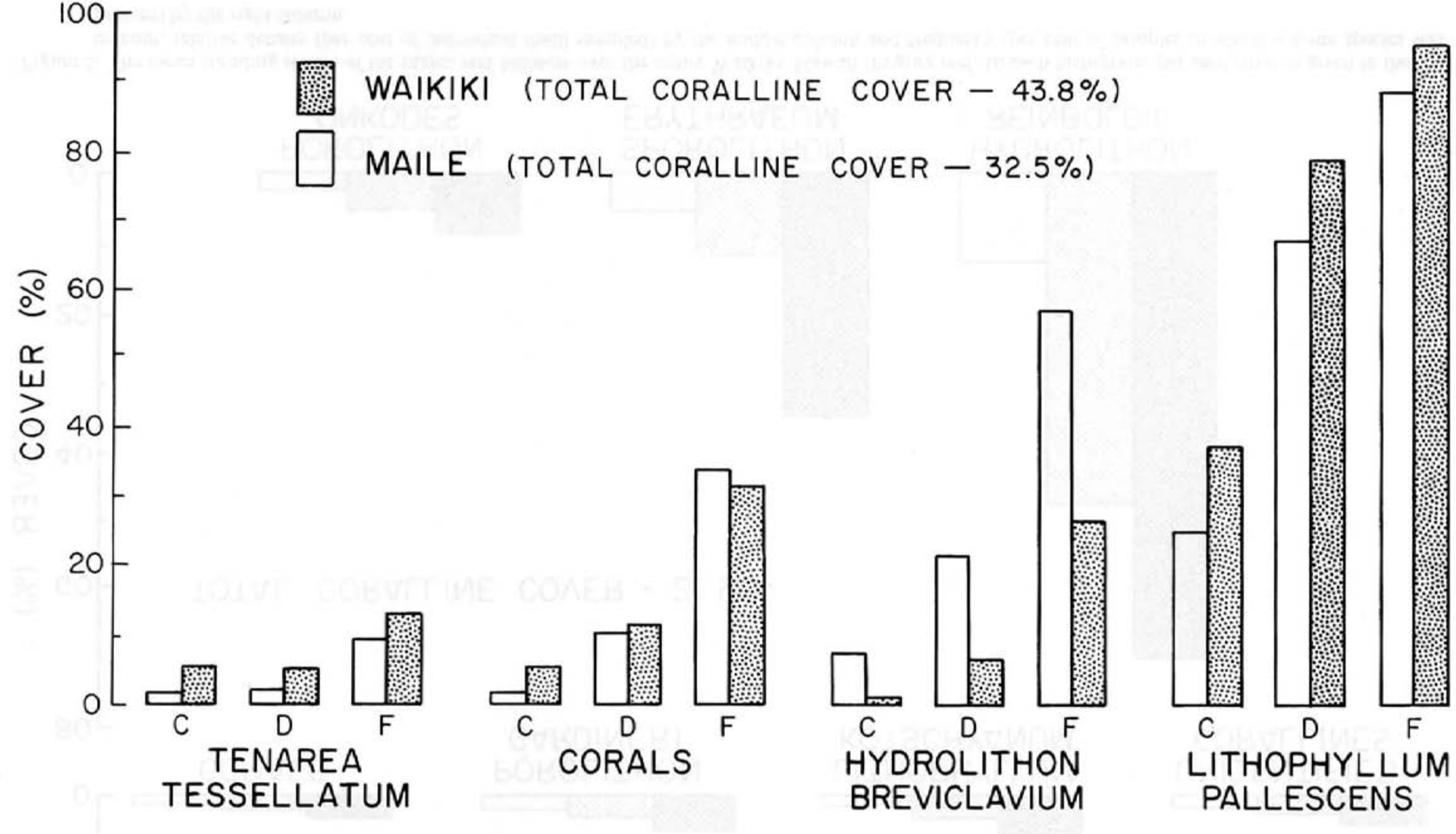

Figure 6. The mean standing stocks, in terms of cover (C), density (D) and frequency (F), of the major SCUBA-depth (8–28 m) reef builders at Waikiki and at Maile, Hawaii, The nodule formers, *Lithophyllum pallescens* and *Hydrolithon breviclavium*, previously (Littler 1973b) had been combined.

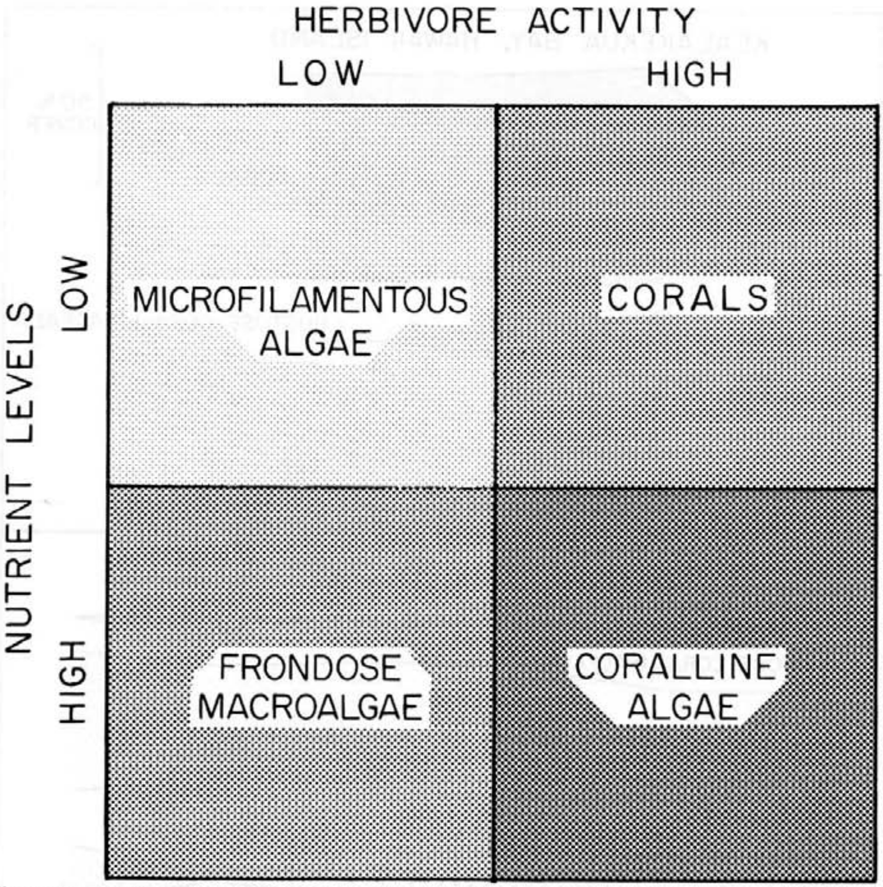

Figure 7. Diagrammatic representation of the relative-dominance paradigm emphasizing four potentially predominant space-occupying groups of sessile reef organisms as a function of long-term nutrient levels and herbivore activity. The latter is considered the more important direct controller of standing stocks on undisturbed reefs.

tend to predominate [e.g. as in damselfish territories (Vine 1974; Brawley and Adey 1977; Kaufman 1977; Potts 1977; Montgomery 1980; Hixon and Brostoff 1982)].

Although only correlative data are available (Banner 1974; Smith *et al.* 1981), interactions between sewage eutrophication and fish grazing appear to alter the competitive dominance of the macrophyte *Dictyosphaeria cavernosa* (Forsk.) Boerg. over corals (particularly *P. compressa*). This green alga has overgrown and killed many of the more 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 are inhibited) under elevated nutrient levels. Nitrogen is generally thought (Hatcher and Larkum 1983) to be the nutrient most often limiting algal growth rates. Whereas, phosphorus, due to its effective recycling, traditionally has been considered less likely to be in short supply (Pilson and Betzer 1973; Atkinson 1982; Entsch *et al.* 1983). However, recent evidence (Lapointe 1983) is beginning to reveal that phosphorus is limiting under more widespread conditions than previously

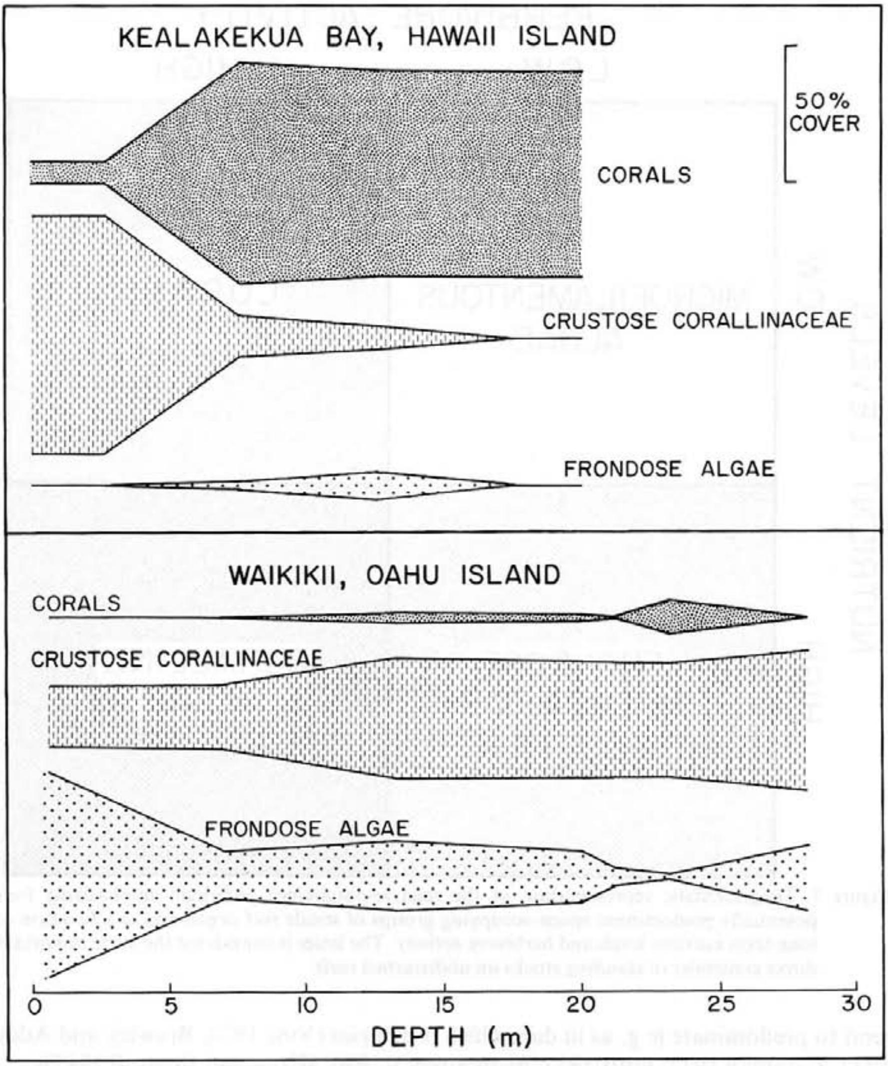

Figure 8. Cover of benthic primary producers as a function of depth in two markedly different, Hawaiian reef systems. Kealakekua Bay is geologically young and pristine (Doty 1968) with low nutrients and large populations of sea urchins and herbivorous fishes, while the older Waikiki reef flat has been overfished and is relatively eutrophic (Doty 1971).

thought. The reason for this (Simkiss 1964) is the removal of phosphate by binding to calcium carbonate particles which are abundant in nearly all reef environments, and the presence of nitrogen-fixing blue-green algae, making nitrogen relatively plentiful in many benthic reef communities. 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.

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

The recent experimental study of Hatcher and Larkum (1983), conducted with appropriate controls and replication over a long term, affords a partial test of the relative-dominance model. 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 may 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, macroalgae are abundant only when herbivory is reduced and nutrient levels elevated (Fig. 7). When production and biomass are not closely interrelated or grazing is selective (Hatcher and Larkum 1983), production-limiting factors other than herbivory must be considered in explaining differences in distribution and abundance patterns between benthic algal communities. The way is now paved for extending the experimental design of Hatcher and Larkum (1983) to testing the relative-dominance paradigm (Fig. 7) by simultaneously examining competitive, inhibitory and other interactions between corallines and corals, as well as fleshy algal populations.

Of the two factors, nutrients and grazing, the latter is probably most important. Ecological release from competition or predation and compensatory expansion of a particular herbivore group following the reduction of another is possible (Hay *et al.* 1983; Hay 1984). For example, on overfished reefs, sea urchin populations could conceivably increase and expand, keeping localized ratios of corallines, frondose macroalgae, microfilaments and corals near their previous levels. When human over-exploitation of gastropods and urchins as well as fishes occurs, then frondose algal stocks can become quite extensive (e.g. the 1–2 m deep Waikiki reef flat; Doty 1971; Fig. 8).

The relative-dominance paradigm (Fig. 7) appears superficially related to the 3-strategy model of Grime (1979) for terrestrial plants. Grime (1979) postulated that land plant biomass and evolutionary strategies are controlled primarily by physiological stress (factors that limit metabolic production) and physical disturbance (factors that remove biomass). Evolutionary interactions have led to opportunists (=ruderals; R-strategists) under conditions of low stress and high disturbance, stress tolerant forms (S-strategists) under high stress and low disturbance and good competitors (C-strategists) where both stress and disturbance are low. Littler and Littler (1984) added predation-tolerant and physically-resistant forms (P- and D-strategists, respectively) where stress is low and disturbance high. Our model for biotic reefs (Fig. 7) differs from Grime (1979) by (1) including the last two strategies among long-lived calcifying corallines and corals and (2) by emphasizing the variable (limiting vs. toxic) role of nutrients as stress factors. As an example of the latter, low nutrient levels limit production in microfilamentous, frondose and coralline algae (Hatcher and Larkum 1983); whereas, an abundance of nutrients could have toxic effects on coelenterate coral production (Townsley in Doty 1968, 1969; Banner 1974). Therefore, nutrient levels in our model do not coincide with the unidirectional stress gradient of Grime (1979) and evolutionary solutions (i.e. P- and D-strategies) other than opportunism (ruderal strategies) are possible under high levels of disturbance on reefs.

Hypothetical adaptations. The adaptive significance of skeletal carbonate in reef-forming algae is not well understood. Several functions postulated (Littler 1976) include the following. (1) Resistance to fouling epiphytes. There are published electron-micrographs (Bailey and Bisalputra 1970) that clearly show rapid erosion and sloughing-off of the calcified outer layers of coralline algae that may function much in the manner of some antifouling paints used on boat hulls. (2) Mechanical support. Aside from allowing upright, rigid thallus-forms to compete more effectively for light and nutrients, some heavily-calcified algae may be able to overgrow and physically abrade more delicate organisms during competition for space. (3) Persistence under abrasive stress. For example, many rhodolith formers appear (Littler 1973a) resistant to abrasion and tumbling and, thus, can occupy unstable habitats (e.g. sand pockets) not available to other algae. Rhodoliths, when exposed to increased abrasion and damage to delicate branch apices, show arrested growth at the tips and increased expansion of undamaged perithallial cells below the tips. Instead of elongation, this results in the thickening of branches by protected meristematic activity leading ultimately to a tougher laminar type of morphology (Bosellini and Ginsburg 1971). (4) Resistance to wave shock. Littler and Doty (1975) presented experimental evidence that the ripping forces of waves, by removing frondose algal competitors, are critical in maintaining *Porolithon onkodes* (Heydrich) Fosl., *P. gardineri* (Fosl.) Fosl. and *Lithophyllum kotschyanum* Unger as dominants (Figs. 5 and 9a) on the seaward margins of Pacific fringing reefs. (5) Inhibition of grazing. Numerous studies (e.g. Paine and Vadas 1969; Littler and Doty 1975; Wanders 1977; Littler *et al.* 1983a, 1983b) have shown the special resistances of calcareous algae to herbivory. Some species even depend on grazing to prevent mortality due to fouling organisms (Littler and Doty 1975; Wanders 1977; Steneck 1983). Also, calcareous algae tend to be (a) dramatically lower in calorific content than fleshy forms (Littler *et al.* 1983a), which may also (b) render them unpalatable to many herbivores as well as (c) inhibit the action of digestive fluids. (6) Protection against intense light. The genus *Porolithon*, among non-articulated coralline algae, is able to withstand light intensities above 120,000 lux without photo-destruction (Littler 1973c). However, interpretation of the calcareous matrix as a protective light screen is speculative because other heavily-calcified corallines, e.g. *Sporolithon erythraeum* (Rothpletz) Kylin, are shade adapted. (7) Modification of habitat suitability. By providing their own substrata, calcareous forms such as non-articulated corallines, articulated corallines with prostrate axes (Littler and Kauker, 1984) and *Halimeda* may themselves increase the stability and quality of their attachment sites.

Calcareous algal growth rates and accretion. The first growth measurements of reef-building algae were performed upon coralline crusts (possibly *Porolithon onkodes*) and *Halimeda* at Funafuti Atoll (Finckh 1904). Coralline crusts on the reef increased in diameter an average of 30 mm $\cdot$ yr^{-1} and one *Halimeda* thallus produced a cluster 55 mm high and 30 mm in diameter (weighing 14.4 g when dried) in 6 wks. Setchell (1926) recorded 0.3–0.5 mm $\cdot$ yr^{-1} increases in thickness of

P. onkodes on the barrier reef of Papeete, Tahiti. The branch extension rates of 7–20 $\mathrm{mm \cdot yr^{-1}}$ for *P. gardineri* on Hawaiian reef flats (Agegian 1982) are the highest reported for any non-articulated branched coralline. The more important colonizing non-articulated corallines extended their margins on artificial substrata from 10.8 to 27.6 $\mathrm{mm \cdot yr^{-1}}$, at St. Croix, U.S. Virgin Islands (Adey and Vassar 1975), with accretion rates of about 1.0 to 5.2 $\mathrm{mm \cdot yr^{-1}}$; rates that were considerably greater than for subarctic corallines. Bermuda rhodoliths on ships sunk in 1943 (Bosellini and Ginsburg 1971), increased in thickness an average of 0.4 $\mathrm{mm \cdot yr^{-1}}$. Thus, average-sized rhodoliths would have taken a minimum of 75 yrs to form. Continuously-growing deep-water rhodoliths 20–30 cm in diameter were estimated (Adey and Macintyre, 1973) to be as much as 500 to 800 yrs old. For *Lithophyllum congestum* (Fosl.) Fosl. at St. Croix, Steneck and Adey (1976) recorded protuberance elongations of up to 8 $\mathrm{mm \cdot yr^{-1}}$, increases in thicknesses up to 5.2 $\mathrm{mm \cdot yr^{-1}}$ and marginal extensions of at least 10.8 $\mathrm{mm \cdot yr^{-1}}$.

Abiotic factors. The calcareous Chlorophyta prefer calcareous sand or mud bottoms although some (e.g. *Halimeda opuntia*) grow attached to solid substrata. It would seem that many of the sediment forming Chlorophyta are adapted to produce their own attachment sites because they typically are observed growing in dead sand composed of calcified segments and particles of their own species' origin. Most of the frame-building algae (non-articulated Corallinaceae such as *Porolithon onkodes* and *P. gardineri*) prefer solid and stable substrata that they themselves have helped to stabilize, whereas some form only nodules or rhodoliths (Fig. 1c) that continue to grow unattached [e.g. *Neogoniolithon strictum, Sporolithon timorense* (Weber-van Bosse and Fosl.) Kylin]. Others grow on solid substrata but form rhodoliths when broken free [e.g. *Hydrolithon reinboldii* (Weber-van Bosse and Fosl.) Fosl., *S. erythraeum*]. Rounded free-living, branched and unbranched rhodoliths occur abundantly on continental shelves to depths of 200 m (Adey and Macintyre 1973). Branch fragments of non-articulated coralline algae sometimes form a gravel called maerl and also can grow to form rhodoliths (Bosellini and Ginsburg 1971; Bosence 1977).

Temperature effects, at least indirectly, are implicit in the fact that nearly all calcareous Chlorophyta and many corallines (*Porolithon, Neogoniolithon, Hydrolithon, Lithoporella, Sporolithon*) are essentially tropical reef species. Of the reef-formers, only the genus *Porolithon* [e.g. *P. onkodes, P. pachydermum* (Weber-van Bosse and Fosl.) Fosl., *P. sonorense* Daws.] is found in habitats having extreme and rapid changes in temperature (Littler 1973a; Adey and Vassar 1975; Littler and Littler 1981); it appears to be relatively insensitive to temperature stress. Because of relatively small variations, temperature, except in the case of the aerial exposure of *Porolithon* on algal ridges (Littler and Doty 1975), is not considered to be a primary ecological factor on tropical reefs.

Light is of major importance in controlling the distribution (Littler 1973a) and production rates (Littler 1973c) of reef-building coralline algae. The dominant tropical coralline genera are depth stratified to a large extent, even at the subfamily level (Adey *et al.* 1982). Such stratification is presumably in response to variations in light quantity and quality; however, the possibility of differential herbivory as a causal agent cannot yet be ruled out. Some non-articulated corallines (e.g. *Sporolithon erythraeum*) are adapted to habitats with low light energy. Most Corallinaceae, when growing in shaded situations, become more deeply pigmented by phycobilins (personal observations), which may enable them to use the relatively abundant shorter wavelengths more effectively in photosynthesis. Unfortunately, light acclimation has not been critically investigated in reef-building algae. That some non-articulated coralline algae are adapted to low light energies is implicit in our personal observations (from submersible) of two autotrophic species covering 10 per cent of the bedrock substratum at depths to 268 m in the Bahamas (midday light energies of $<0.02\ \mathrm{uE} \cdot \mathrm{m}^{-2} \cdot \mathrm{sec}^{-1}$ P.A.R.). Conversely, the massive intertidal development of *Porolithon onkodes, P. gardineri* and *Lithophyllum kotschyanum* on the intertidal algal ridges of Indo-Pacific reefs, and *P. pachydermum* and *L. congestum* on Caribbean reefs, indicates that these species are adapted to withstanding extremely bright light. This was experimentally shown to be the case for *P. onkodes* (Littler 1973a; see also Littler and Doty 1975).

The literature contains many statements that the distributions and abundances of reef-building algae often are related to turbulence. For example, the smaller rhodolith-forming corallines (Fig. 1c) and sediment-producing Chlorophyta tend to occur in relative calm waters, the latter usually with their thallus axes at right angles to prevailing surge and currents. Spherical coralline rhodoliths occur lined up in sand troughs nearly 100 m deep off the Canary Islands (McMaster and Conover 1966). There are three mechanisms postulated (Bosellini and Ginsburg 1971) for the remarkably symmetrical growth of such deep-water rhodoliths; (1) they could be periodically and regularly rolled by some unknown type of storm or internal waves to provide uniform illumination, (2) they developed when water levels were shallower at which time surface waves provided the movement; however, they no longer move and are biologically dormant and (3) rhodoliths are turned by the shifting of the sand nearby which requires less wave energy. Alternative explanations that might account for the usual round morphology of deep-water rhodoliths are that (a) metabolite translocation or (b) heterotrophy could be important in balancing growth under uneven illumination.

In Hawaii, the occurrences of *Porolithon onkodes, P. gardineri* and *Lithophyllum kotschyanum* appear to be related to the proximity of heavy surf, which reduces the feeding activity of the more powerful grazing fishes while periodically ripping away relatively delicate frondose algal epiphytes. Littler (1976) noted the presence of abundant gastropods (Fig. 9b and 9c) that may escape predation in this habitat and which also remove filamentous algae. It has been observed (Johnson 1954; Lee 1967; Littler 1973a) that branched forms of non-articulated corallines tend to become more compact in highly turbulent waters, and Steneck and Adey (1976) documented this phenomenon experimentally. Beyond the point of water movement sufficient to eliminate diffusion gradients, non-articulated Hawaiian corallines showed (Littler 1973a) no increase in photosynthesis or respiration with increased turbulence, therefore, circulation is not physiologically limiting to them under most reef conditions. However, the break-down of diffusion gradients within compact algal turfs could require considerable turbulence (Santelices 1978; Littler and Arnold 1980) to allow optimal gas exchange and nutrient uptake.

Reef-forming algae generally do not tolerate desiccation and intertidal forms usually require some means of keeping wet during periods of low tide. For example, where wave splash, rivulets, small pools or cover provided by moisture-retaining invertebrates and frondose algae are present, some shallow water corallines (particularly *Porolithon* on ridges, Fig. 9) may withstand emergence. One special example of the remarkable resiliency of calcified crustose algae following severe desiccation stress is illustrated in the account by Finckh (1904) on Funafuti Atoll. He observed that extremely calm water during the low springtide conditions resulted in aerial exposure and drying, causing the dominant pink crust to die and become white. After several days of re-immersion, pink growths reappeared, always starting from small depressions and spreading outward to meet similarly recovered expanses. Nearly complete restoration of living cover occurred within only two weeks.

Salinity effects on reef-building algae have not been quantitatively examined. No response of *Porolithon onkodes* to either rain or evaporation was observed (Littler and Doty 1975) on the intertidal crest of Hawaiian algal-ridges.

Biotic Factors. Until recently, quantitative data on competition as a factor important to the biology of reef algae have been lacking. Indirect evidence for the importance of interference competition is shown by numerous observations (Finckh 1904; Ladd 1950; Van den Hoek 1969a, 1969b; Hay *et al.* 1983) of alternate overgrowth of one encrusting organism (e.g. corals, corallines, frondose algae, bryozoans and sponges) by another. Recently, more direct evidence has suggested (Buss and Jackson 1979) the presence of competitive hierarchies in which non-articulated coralline algae play important roles. Several lines of evidence from transplant studies indicate (Hay 1981c) that sand-plain algae are competitively superior over the more grazer resistant reef-slope species. The predominance of *Porolithon onkodes* as a builder of algal ridges (Fig. 9) seems to be directly determined by interspecific competition under the indirect influences of wave force, grazing and shading. Transplant and ecophysiological experiments indicated (Littler 1973a; Littler and Doty 1975) that the dominance of algal ridges by *P. onkodes* is due to a combination of (1) its physiological tolerance and (2) its physical nature, the peculiar physiology of *P. onkodes* gives it competitive advantage over corals and other corallines intertidally in direct sunlight. Secondly, it would seem to be relatively insensitive to the ripping forces of waves, and grazing by echinoderms, gastropods and fishes which tend to remove the frondose algae and delicate corals that overgrow it under other circumstances.

The extremely pitted aspect of algal ridges caused by innumerable limpet (Fig. 9b), chiton (Fig. 9c) and sea urchin (Fig. 9d) populations, indicates that these grazers contribute significantly to reef destruction. If not for the hard calcite deposits of non-articulated corallines (Finckh 1904), reef platforms would undergo rapid diminution. The conclusion was reached in an early review by Duerden (1902) that penetrating or boring algae also play a critical part in the disintegration of reef masses. Penetrating algal filaments likewise were characterized (Gardiner 1931) as the chief boring organisms of reefs and of considerable importance in determining reef structure. Since that time, other workers have confirmed the destructive effect of such algae. 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. The commonest of these are certain Cyanophyta (see Nadson 1900; Purdy and Kornicker 1958) that attack skeletal materials differentially; the aragonitic coral skeletons being most susceptible, and the denser calcitic deposits of coralline algae being most resistant (Ginsburg 1957).

Several distributional surveys of rock-boring by microalgae (Green 1975; Perkins and Tsentas 1976; May *et al.* 1982) documented the importance of this group on Caribbean reef systems. A close association exists between endolithic algae and organic matrices within substrata, the latter were suggested (May *et al.* 1982) as being required nutrient sources. 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. The average living coral colony on Enewetak Atoll

Figure 9. Illustration (a) is a view of the *Porolithon—Lithophyllum* dominated algal ridge in Guam. Note the hemispherical heads of *Lithophyllum kotschyanum* on the leading edges of the ridge buttresses in areas of very heavy wave shock. (b) shows the large number of herbivorous limpets on the *P. onkodes* ridge at Guam. (c) is on the lower-intertidal seaward margin of a Caribbean *P. pachydermum* crest showing numerous chiton excavations. Water spouts (d) indicate the honeycombed nature of an Enewetak algal ridge.

contains three times as much plant as animal tissue (Odum and Odum 1955), of which only about six per cent is contributed by zooxanthellae, the remainder being composed of microfilamentous green algae within the skeletal structure. The green alga *Ostreobium* is interesting in that its filaments, after penetrating the reef rock, deposit skeletal magnesium calcite by means of two precipitative cements (Schroeder 1972). This occurs both intracellularly and on the surfaces of the filaments, but only following the death of the alga (Kobluk and Risk 1977). An undescribed species from Hawaii, 'melobesioid C' (Littler 1973a), may represent such a rock-borer among the Rhodophyta. The importance of endolithic microalgal filaments as paleontological indicators in the field of applied geology, including petroleum exploration, has been stressed by Golubic and Yun (1983).

Significant erosion of the algal ridge (Fig. 9) by the scraping and rasping actions of echinoderms, sipunculid worms, mesogastropod limpets and other organisms has been recorded at Raroia Atoll (Doty 1954; Doty and Morrison 1954; Newell 1954), St. Croix (Adey and Vassar 1975), Oahu Island (Littler 1973a) and Guam (Littler 1976). However, there may be more of a mutualistic relationship in this case than is readily apparent. Hypothetically, rasping and scraping organisms may be acting to prevent 'fouling' of the coralline crusts by removing softer organisms (Fig. 9b and 9c). For example, limpet grazing, by removing blue-green algal epiphytes and inhibitory epithallial cells (Adey 1973), is required for successful growth of the subarctic species *Clathromorphum circumscriptum* (Strom.) Fosl. Also, the tunneling action of chitons, limpets and sea urchins may provide wetting spouts (miniature blowholes) of water (Fig. 9d) to portions of the reef crest that might dry out and die otherwise. The appropriate field test of these hypotheses (i.e. a study of community development following the removal of invertebrates with suitable controls and replicates) could provide powerful predictive insights into the ecological forces directly structuring this extremely important reef habitat.

Tropical reef algae are subjected to relatively high grazing intensities by abundant and diverse assemblages of mobile fishes (Stephenson and Searles 1960; Randall 1961, 1965, 1974; Bakus 1964, 1966, 1967; John and Pople 1973; Littler and Doty 1975; Wanders 1977; Borowitzka 1981b; Hay 1981b, 1984; Littler *et al.* 1983b). Sea urchin grazing (Dart 1972; Ogden *et al.* 1973; Sammarco *et al.* 1974; Benayahu and Loya 1977; Carpenter 1981), especially by *Diadema antillarum* Philippi, also has a significant impact on the localized distributions and abundances of marine macroalgae throughout the world's tropical waters. The above studies have shown up to a 15-fold decrease in frondose algal standing stocks and a shift in community structure from diverse algal-turf assemblages towards dominance by relatively few larger species (see Mathieson *et al.* 1971; Sammarco *et al.* 1974) where grazing effects are large.

Several strategies hypothetically are available to seaweeds for reducing losses due to the severe grazing pressures encountered on most tropical reefs. More than one of these herbivore-resistance mechanisms is often expressed by a given species (Littler and Littler 1980) and include: (1) occupation of refuge habitats that are physically unfavorable or unavailable to herbivores (Dahl 1972; Earle 1972; Ogden *et al.* 1973; Adey and Vassar 1975; Parrish and Zimmermann 1977; Brock 1979; Menge and Lubchenco 1981; Hay 1981a; Hay *et al.* 1983b). (2) cryptic appearance or mimicry (Kraft 1972; Littler *et al.* 1983b). (3) unpredictable spatial and temporal distributions (Littler and Littler 1980; Lubchenco and Cubit 1980), (4) rapid growth involving the replacement of vegetative and reproductive tissues while simultaneously satiating the appetites of grazers (Littler and Littler 1980; Borowitzka 1981a), (5) close association with unpalatable organisms (Montgomery *et al.* 1980) carnivorous predators (Randall 1965; Ogden *et al.* 1973; Hay 1981c; Hay *et al.* 1983) or highly territorial animals (Brawley and Adey 1977; Montgomery 1980; Hixon and Brostoff 1982) and (6) allocation of materials and energy toward herbivore defenses. The last strategy has several non-mutually exclusive components that encompass: (a) toxins, digestion-inhibitors or unpalatable secondary metabolites (Fenical 1975; Wells and Barrow 1979; Norris and Fenical 1982; Paul and Fenical 1983), (b) reduced calorific contents (Paine and Vadas 1969; Littler *et al.* 1983a), (c) morphological shapes and sizes that minimize accessibility (Hay 1981a; Steneck and Watling 1982), (d) textures that inhibit the physical processes of herbivore manipulation and feeding (Nicotri 1980) and (e) structural materials (e.g. $CaCO_3$) that decrease palatability or nutritional value (Littler 1976).

The importance of aspects of the first (a) as well as the last four of these (b–e) to tropical algae recently has been shown by bioassays of chemicals (Norris and Fenical 1982; Paul and Fenical 1983) and functional-form experiments (Littler *et al.* 1983a, 1983b), respectively, on the Belizian barrier reef system. Forms that rely primarily on chemical defenses (e.g. *Dictyota cervicornis* Kützing. *Laurencia obtusa* (Hudson) Lamouroux, *Stypopodium zonale* (Lamouroux) Papenfuss are able to maintain high photosynthetic rates (each had the highest productivity of its respective group; Littler *et al.* 1983a), but remain susceptible to physical forces such as wave shear and sand scour. Contrastingly, the coarser and tougher species such as thick forms, calcareous and encrusting species resist both grazing and physical forces by means of relatively high proportions of structural materials (Littler *et al.* 1983a, 1983b), but at the cost of markedly lower photosynthetic and growth rates.

The role of fish grazing is relatively complex. Van den Hoek (1969a, 1969b) and Littler and Doty (1975) pointed out that fish act to maintain coralline and coral populations in habitats which would otherwise become overgrown by the softer non-building algae (e.g. clearly shown by the exclosure experiments of Randall 1961; McVey 1970; Mathieson *et al.* 1975; Wanders 1977). Succession of coralline algal populations (only) was followed (Adey and Vassar 1975) on polyvinylchloride plates within areas subjectively determined to be grazed to varying degrees. The effects of grazing by fishes on the relatively thin developing recruits was interpreted to be one of the major disruptive forces on reef-building processes. Adey and Vassar (1975) presumed that the reduction of grazing by fishes in high wave-shock situations is the primary causal mechanism permitting algal-ridge development. Destructive overgrazing of ridge-forming species certainly does occur. For example (Littler and Doty 1975), *Porolithon onkodes* crusts are considerably more massive on higher portions of algal ridges where limpets (as opposed to fish) are the main grazers (Fig. 9b). However, algal-ridge development stems from a combination of two critical factors: (1) reduced severity of grazing to moderate levels due to wave shock, plus (2) the ripping effect of large waves on frondose algal forms, preventing them from overgrowing the non-articulated coralline builders.

4. EUTROPHICATION MODEL FOR REEF BIOGENESIS

Though vital, descriptive studies have dominated previous research on reef dynamics. This is philosophically an important point, because the products of such studies are usually empirical correlations based on habitat- or organism-oriented descriptions that too often become repeated from one reef system to another. An hypothesis-testing approach that leads to predictive understandings of causal phenomena and processes has been lacking, although experiments on biological interactions (e.g. Hay 1981a, 1981c; Menge and Lubchenco 1981; Hay *et al.* 1983; Littler *et al.* 1983a, 1983b) are increasing rapidly. However, geological drillings, with some exceptions (e.g. Macintyre and Glynn 1976, Easton and Olson 1976), are still frequently conducted almost at random with the objective to describe reef histories at yet another single position.

A more powerful approach involves searching for convergent evolutionary patterns within reef ecosystems by indirect means, taking advantage of natural experiments, successional events or developmental sequences. Simpson (1949) suggested that this technique be designated 'postdiction', rather than prediction, since the focus is on attempting to decipher the events of the past leading to present results. However, this viewpoint does have the element of prediction, because hypotheses are generally of the form 'If selection has acted in the following way over evolutionary time, then we would expect nature to have the following structure.'

To illustrate the potential of the postdictive (versus purely descriptive) approach, we propose a testable 'eutrophication model' of reef development (Fig. 10) based upon observations of living reefs of different ages in the Hawaiian Archipelago. The reason for pursuing this theoretical tactic is to illustrate an area where field ecologists can interact productively with paleontologists and geologists in a more powerful approach that permits testing of causal mechanisms of reef biogenesis. One exemplary study of this nature is the collaborative research of Macintyre and Glynn (1976), involving core transects across a Caribbean (Panama) fringing reef.

These workers also felt that a broader perspective was needed in future geological studies of modern reef development.

In the geologically young and oligotrophic areas around the island of Hawaii (Figs 8 and 10), *Porites compressa* (Fig. 11a) as well as other corals occurs in abundance close to shore down to about 30 m. This broad distributional pattern, hypothetically, represents an early stage in Hawaiian reef development, whereby further consolidation might progress following entrapment of broken coral, other reef fragments and land materials by the highly open and three-dimensional morphology of *P. compressa,* which is alive mainly at the distal branch tips. Such fragments (Fig. 11b) are apparently cemented and consolidated (Fig. 11c) by the abundant corallines (e.g. *Lithophyllum pallescens, Sporolithon erythraeum* and *Hydrolithon breviclavium*) that grow on the lower dead portions of the *P. compressa.* As these coral-dominated bottoms build toward the surface and the habitat becomes richer in nutrients (presumably biological succession and soil development on the reef's terrestrial watershed would account for increased eutrophication with time), the *P. compressa* colonies would become gradually nutrient inhibited (Fig. 7), filled-in and overgrown due to increased growth responses of shallow-water forms of non-articulated coralline algae (Littler 1973a) along the shoreward portions of the reefs. This eutrophication process and the accumulation of fragments deeper [which would be consolidated by deep-water corallines (Littler 1973b; Adey *et al.* 1982)] would allow *P. compressa* to develop in an upward but mainly seaward-restricted direction until a pattern of zonation similar to that observed off Waikiki today is attained (Figs 8 and 10).

The interactions between the *Porites compressa—Lithophyllum pallescens—Hydrolithon breviclavium* rhodolith community appear to be instrumental in controlling the depth profile. The zone of *P. compressa* (Figs. 10 and 11a) acts as a barrier and accumulates large numbers of living *L. pallescens* and *H. breviclavium* rhodoliths along the upper shoreward margin (Fig. 11b), thereby concentrating a zone of encrusting nodule bulk favourable to consolidation. We predict that the underlying reef structure in this zone is dead *P. compressa* (Fig. 11), with both consolidated and unconsolidated reef materials completely filling spaces between its branches. Tests of this ecological model for Hawaiian reef biogenesis could be provided by drilling the appropriate reef zones, indicated in Figures 10 and 11, and comparing the relative percentages of *P. compressa* (hypothetically abundant) in the deeper strata of reefs off Oahu Island (Pollock 1928) to the predicted predominance of rhodolith-forming corallines (except for the geologically younger, low nutrient areas as indicated earlier) in the upper strata of living or raised fossil reefs (Littler 1973a, 1973b). Of course, differential losses due to boring organisms, re-solution and re-mineralization would have to be considered. Some support for the eutrophication model comes from transect corings in the 7,000 yr-old reef at Hanauma Bay, Oahu, Hawaii (Easton and Olson 1976), where corals are prevalent in older portions and calcareous algae are most abundant in the upper younger strata of the reef.

The upward reef growth from the observed 30 m-deep *Porites compressa* zone (Fig. 10) to the algal ridge slightly above sea level would take approximately $6\text{–}10 \times 10^3$ years at the average accretion rate of 3 to 5 $\mathrm{mm \cdot yr^{-1}}$ documented for several reef systems (Smith 1973; Adey and Vassar 1975; Smith and Kinsey 1976), and this could be accommodated by static, slowly rising or slowly falling sea-level rates during the same period. Considerable controversy exists regarding sea-level changes near Hawaii (see Stearns 1977; Easton 1977); however, the evidence from Hanauma Bay (Easton and Olson 1976) indicates a constant sea level from +7,000

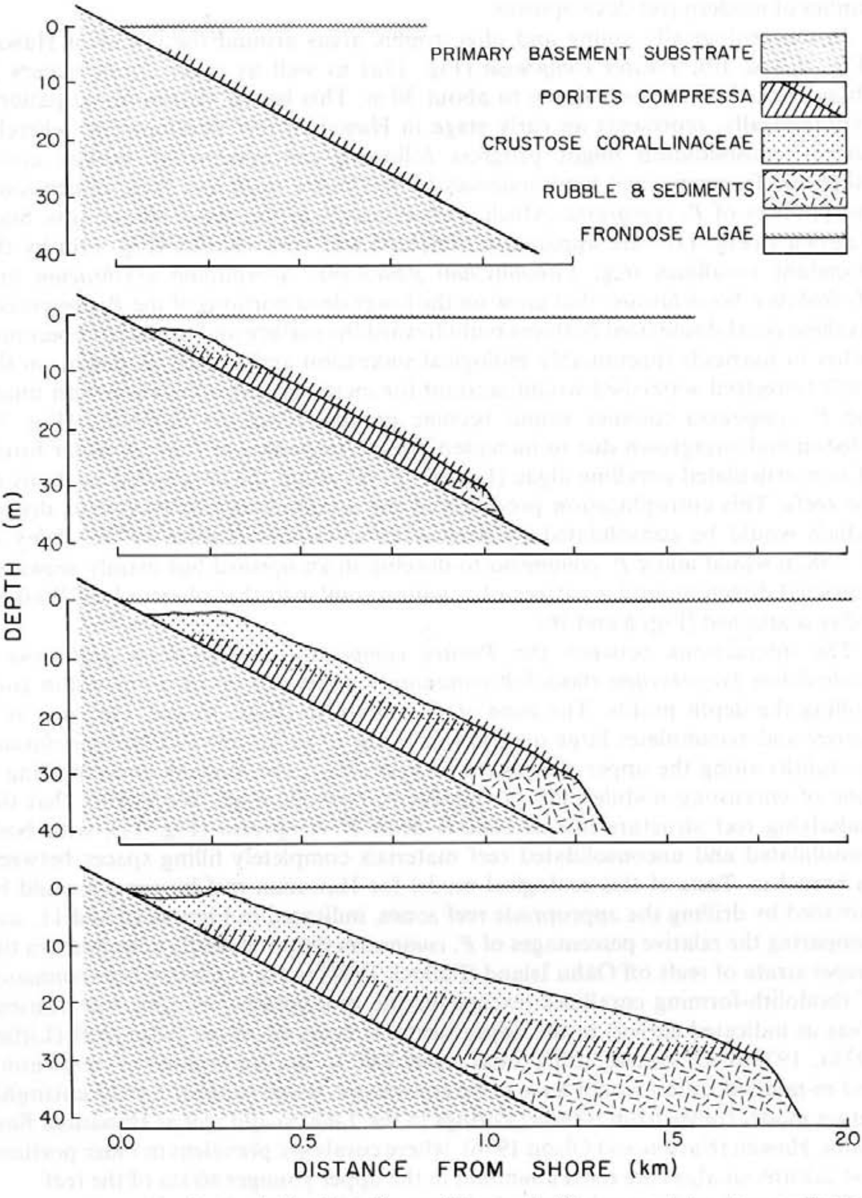

Figure 10. Eutrophication model for Hawaiian reef biogenesis. The youngest stage (upper diagram) is a simplified representation of the type of reef system in geologically young areas such as Kealakekua Bay (see Fig. 8). The oldest stage (lowermost) is surficially representative of the present Waikiki reef system (Fig. 8). For simplicity and clarity of presentation, the legends indicate only the predominant constituents, although all of these components normally occur intermingled in varying degrees of patchiness.

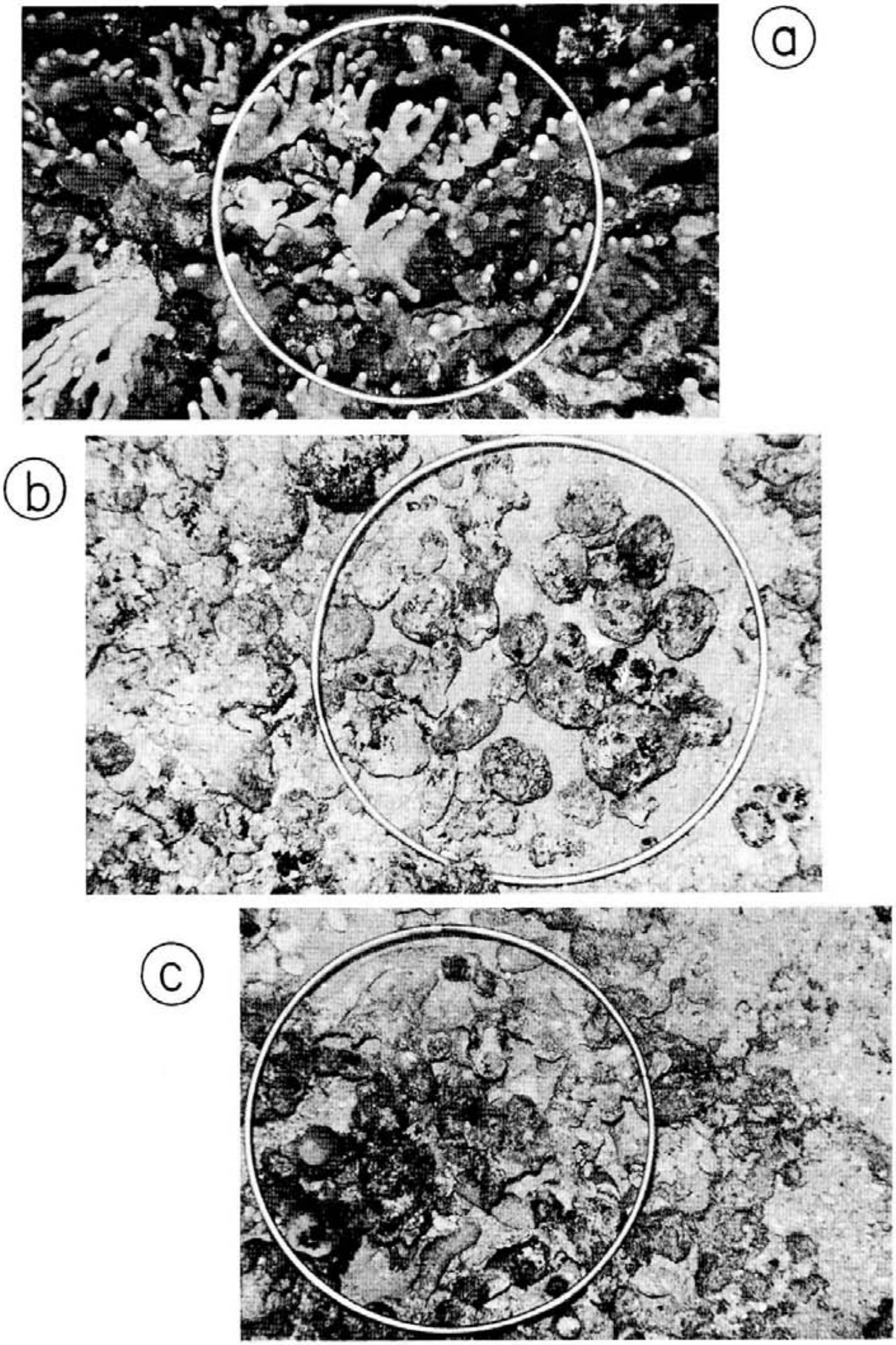

Figure 11. Illustration (a) is a photo-sample of a 30-cm diameter ring taken in the *Porites compressa* belt about 23 m deep and 1.7 km off Waikiki (Figs. 8 and 9). (b) was photographed adjacent to the shoreward margin of this same *P. compressa* zone, in the region of *Lithophyllum*/*Hydrolithon* rhodolith accumulation. (c) was also taken in the latter zone but all rhodoliths and sand were cleared away to reveal the underlying dead *P. compressa* framework with interstices of consolidated sediments and rhodoliths (the interconnected darker areas are dead *Porites* structure). The right sides of all three samples are toward the Waikiki shoreline.

to 5,800 yrs ago, a mean rise of 2.9 mm · yr^{-1} during 5,800 to 3,500 years before present, while sea level increases averaged 0.3 mm · yr^{-1} between 3,500 years ago and the present.

The evolution of non-articulated corallines appears (Adey *et al.* 1982) to have been very slow in the Indo-Pacific since the Miocene. Consequently, detailed paleoecological interpretations using the relative abundances of genera found in limestone cores and outcrops, is quite feasible (Adey *et al.* 1982). With regard to the postulated process of calcium carbonate build-up due to the *Lithophyllum*/*Hydrolithon* rhodolith community, a similar circumstance was described (Adey 1968) in the North Atlantic where fragments of *Lithothamnium* from shallow ledges continue to accumulate and grow just seaward below the area of ledges and boulders. The proposed accumulation and concentration of bulk and cementing organisms from broad source areas (Fig. 10) could result in disproportionately rapid upward development of specific reef zones and should be considered more widely in estimating vertical reef growth.

By considering the appropriate depths, the eutrophication model (Fig. 10) could be tested with a minimum of well-placed cores and paleontologists could be prepared for the appropriate organisms. The reefs in the northwestern Hawaiian Archipelago are limestone caps on older volcanic islands, produced as the Pacific plate migrated over a hot spot now located to the south of the island of Hawaii. Consequently, comparisons of reef biogenesis in a south to northwestern island series has potential to document major environmental changes biologically recorded while the fringing reefs developed. The model presented here, whether supported or falsified, would still serve as a useful intellectual frame of reference for interpreting the fossil remains.

We are at a stage where traditional empirical studies (i.e. observational/correlative) and mechanistic (i.e. experimental/causative) approaches must be combined, with increased emphasis on the latter, to accelerate our predictive understanding of algal roles in reef biogenesis. This is increasingly being done (e.g. Menge and Lubchenco 1981), 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). Because seaweeds are recognized by their external and internal morphology, it has proven instructive to relate morphological groups (Littler 1980a) with measurements of functional properties, relative to the environmental parameters normally experienced. A major assumption (Littler and Littler 1984) is that structure, at the lower levels of organization, ultimately governs all biological activities. Since morphological features can be measured quite accurately and easily, functional/morphological groups have proven to be extremely useful (Steneck and Watling 1982; Littler *et al.* 1983a, 1983b; Gaines and Lubchenco 1982; Littler and Littler 1984) for the interpretation of complex biotic reef ecosystems. A burgeoning awareness of the amenability and advantages of tropical marine plants as experimental systems for the elucidation of processes of reef ecology and biogenesis offers exciting prospects for the next decade.

5. CONCLUSIONS

Tropical reefs are remarkable for their development of massive structure and for their high primary production rates. Algae are responsible for much of the former and all of the latter, but have received disproportionately less study than the animal components, largely because of taxonomic and methodological problems that can now be overcome. The high productivity of biotic reefs is due, in large part, to: (1)

increased surface areas for metabolic activities, (2) continuous water movement across these surfaces, (3) abundant nitrogen-fixing blue-green algae and associated micro-organisms and (4) biological systems that recycle limiting nutrients and organic compounds. The photosynthetic organisms responsible are: (A) symbiotic zooxanthellae, (B) microalgal filaments, (C) corallines and (D) frondose macroalgae. A hypothetical relative-dominance model is proposed, and evaluated in view of present knowledge, that emphasizes shifting competitive hierarchies between these four producer groups under varying regimes of nutrients and herbivory.

In summarizing the ecological research on reef-building algae, the published data for the sediment-producing Chlorophyta indicate an assemblage adapted to calm, soft-bottom shallow habitats (which are unsuited for most other macroalgae) throughout the subtropical to tropical zones of the world ocean. There are extremely few quantitative studies 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), which often dominates deeper reef-slope habitats. For the frame-building Corallinaceae, the available information indicates an algal group able to grow at greater depths in weaker light than other primary producers. *Porolithon* and certain *Lithophyllum* species (e.g. *P. onkodes, P. pachydermum, L. kotschyanum, L. congestum*) are somewhat exceptional in that they can withstand considerable desiccation and exposure to the highest sunlight intensities. Some species of coralline algae tolerate or perhaps are favored by extremes of temperature such as are characteristic of high tropical tide pools on the one hand, whereas others characterize Arctic and Antarctic deeps on the other. Several reef-building seaweeds flourish intertidally in the most turbulent of natural waters, probably because of their mechanical resistance to ripping forces and their physiological nature.

Calcareous algae are considerably less vulnerable to herbivore grazing than is true of the softer algae and some may actually require herbivory to prevent inhibitory overgrowth. The low edibility (Littler *et al.* 1983b) of calcareous forms could be a result of reduced calorific contents (Littler and Murray 1978; Littler *et al.* 1983a) and increased mechanical resistances to scraping and biting mechanisms. However, it is now clear (Littler *et al.* 1983a) that this structural resistance to herbivory comes at the cost of dramatically lower photosynthetic and growth rates than is the case for most other reef algae.

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

Because problems of taxonomic identification in the field (Adey and Macintyre 1973) and high-resolution sampling (Littler 1971, 1980b; Stoddart and Johannes 1978) recently have been overcome, one can now expect the reef-building algae to be increasingly included in studies by reef biologists. Considerable progress in regard to aspects of tropical algal functional morphology is being made (Hay 1981a, 1981c; Littler and Littler 1981, 1984; Littler *et al.* 1983a, 1983b) that includes information concerning productivity ecology, biomechanics, edibility and allocation of resources from a costs/benefits perspective. The algal functional groups proposed by Littler (1980a) have been used, with minor variations (Littler and Arnold 1982; Steneck and Watling 1982; Gaines and Lubchenco 1982; Littler *et al.* 1983a; Littler and Littler 1984), as an effective means for interpreting complex community patterns, without having to tediously deal with each of the component species.

Calcifying mechanisms are understood only poorly at present and Littler (1973c) and Borowitzka (1979) indicated some of the complexities involved. There are, however, several areas where future research should prove especially rewarding. For example, further attempts should be made to partition pH changes into those due to calcite calcification and those due to photosynthesis (Sikes *et al.* 1980; Jacques and Pilson 1980), by precisely following pH and total alkalinity in controlled and well-defined systems, combined with the methodologies described by Borowitzka (1979). Open-flow ecosystem studies have proven instructive; however, it ultimately becomes necessary to examine specific features of algal communities on a 'contained' individual-species basis. It is mandatory that the floristic and faunistic composition, as well as environmental conditions, of any natural ecosystem monitored be provided to render the data interpretable and scientifically reproducible. The newer analytical techniques (Böhm 1978; Borowitzka 1979) should be utilized to test working models (Digby 1979) and to gain finer levels of precision in isotopic studies. Also, studies of periodicity and stress effects on calcite depositional rates should prove particularly rewarding. Perhaps organic and biochemical approaches (e.g. Böhm and Goreau 1973; Borowitzka 1979) in concert with specialized expertise from physical chemistry and geochemistry (e.g. Alexandersson 1974; Smith 1973, 1974) as well as environmental physiological-ecology (e.g. Littler 1973a; Smith and Marsh 1973) are needed to unravel the mechanisms of algal skeletal formation and the environmental control of reef-building processes.

We still know very little about the physiological ecology, population biology and community dynamics of algae that affect the nature of biotic reefs. Especially lacking have been taxonomic and biological studies of reef-boring microalgae. As pointed out by Littler (1972), and still true more than one decade later, areas of investigation concerning the role of bioenergetics, heterotrophy, allelopathy, inter-specific and intra-specific competition, recruitment, natality and mortality phenomena remain virtually untouched for most tropical algae. Until we begin to understand processes at these levels, it will remain difficult to make definitive statements concerning the role of algae, or other organisms, in the dynamics of reef biogenesis.

A eutrophication model of Hawaiian reef development is presented to illustrate an area where field ecologists, paleontologists and geologists might interact productively in a postdictive hypothesis testing approach to analyze causal mechanisms of reef biogenesis. The likelihood that carbonate fragments and cementing rhodoliths could become concentrated to produce exceptionally rapid upward development in specific zones, relative to the broader source areas, should be more widely considered in estimates of accretion rates on reefs. A general trend in emphasis from empirical-correlative viewpoints toward mechanistic-causative experimental approaches is underway and offers exciting prospects for rapid increases in knowledge with improved predictive capabilities. Recognition of the great importance of tropical algae as ecological research tools and in regard to their roles in reef biogenesis is long overdue.

ACKNOWLEDGEMENTS

We sincerely thank K. Bucher, R. Fosberg, S. Fredericq, M. Hay, B. Lapointe, I. Macintyre and J. Norris for reviewing the initial draft of this work. The ideas for this synopsis were catalyzed during our participation in the International Symposium on Coral Reef Biogenesis, organized by M. Gilmartin, and cordially hosted by the Australian Institute of Marine Science, Townsville, Australia (1975).

REFERENCES

Adey, W. H. (1968). The distribution of crustose corallines on the Icelandic coast. *Sci. Isl. Anniv., 1968*, 16–25.

Adey, W. H. (1970). A revision of the Foslie crustose coralline herbarium. *K. Nor. Vidensk. Selsk. Skr., 1970* **(1),** 1–46.

Adey, W. H. (1973). Temperature control of reproduction and productivity in a subarctic coralline alga. *Phycologia,* **12,** 111–118.

Adey, W. H. (1978a). Coral reef morphogenesis: a multidimensional model. *Science,* **202,** 831–837.

Adey, W. H. (1978b). Algal ridges of the Caribbean sea and West Indies. *Phycologia,* **17,** 361–367.

Adey, W. H., Adey, P. J., Burke, R. and Kaufman, L. (1977). The Holocene reef systems of eastern Martinique, French West Indies. *Atoll. Res. Bull.,* **218,** 1–40.

Adey, W. H. and Macintyre, I. G. (1973). Crustose coralline algae: a re-evaluation in the geological sciences. *Geol. Soc. Am. Bull.,* **84,** 883–904.

Adey, W. H., Townsend, R. A. and Boykins, W. T. (1982). The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. *Smithsonian Contributions to the Marine Sciences,* No. **15,** 1–74.

Adey, W. H. and Vassar, J. M. (1975). Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). *Phycologia,* **14,** 55–69.

Agegian, C. R. (1982). Growth of the branched coralline alga, *Porolithon gardineri* (Foslie) in the Hawaiian Archipelago. *Proc. 4th Int. Coral Reef Symp.,* **2,** 419–423.

Alexandersson, T. (1974). Carbonate cementation in coralline algal nodules in the Skagerrak, North Sea: biochemical precipitation in undersaturated waters. *J. Sed. Petrology,* **44,** 7–26.

Alexandersson, T. (1977). Carbonate cementation in recent coralline algal constructions. In: *Fossil algae* (Flügel, E. ed.), pp. 261–269, Springer-Verlag, Berlin.

Antonius, A. (1982). Coral reef pathology: a review. *Proc. 4th Int. Coral Reef Symp.,* **2,** 3–6.

Arnott, H. J. and Pautard, F. G. E. (1970). Calcification in plants. In: *Biological Calcification: Cellular and Molecular Aspects* (Schraer, H. ed.), pp. 357–445, Appleton-Century-Crofts, New York.

Atkinson, M. (1982). Phosphate exchange between reef communities and the water column. *Proc. 4th Int. Coral Reef Symp.,* **1,** 417–418.

Bach, S. D. (1979). Standing crop, growth and production of calcareous Siphonales (Chlorophyta) in a south Florida lagoon. *Bull. Mar. Sci.,* **29,** 191–201.

Bailey, A. and Bisalputra, T. (1970). A preliminary account of the application of thin-sectioning, freeze-etching, and scanning electron microscopy to the study of coralline algae. *Phycologia,* **9,** 83–101.

Bakus, G. J. (1964). The effects of fish-grazing on invertebrate evolution in shallow tropical waters. *Allan Hancock Foundation Publication, Occasional Paper,* **27,** 1–29.

Bakus, G. J. (1966). Some relationships of fishes to benthic organisms on coral reefs. *Nature,* **210,** 280–284.

Bakus, G. J. (1967). The feeding habits of fishes and primary production at Eniwetok, Marshall Islands. *Micronesica,* **3,** 135–149.

Banner, A. H. (1974). Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. *Proc. 2nd Int. Coral Reef Symp.,* **2,** 685–702.

Barnes, D. J. and Crossland, C. J. (1977). Coral calcification: sources of error in radioisotope techniques. *Mar. Biol.,* **42,** 119–129.

Benayahu, Y. and Loya, Y. (1977). Seasonal occurrence of benthic-algae communities and grazing regulation by sea urchins at the coral reefs of Eilat, Red Sea. *Proc. 3rd Int. Coral Reef Symp.,* **1,** 383–389.

Birkeland, C. (1977). The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proc. 3rd Int. Coral Reef Symp.,* **1,** 15–21.

Böhm, E. L. (1978). Application of the ^{45}Ca tracer method for determination of calcification rates in calcareous algae: effect of calcium exchange and differential saturation of algal calcium pools. *Mar. Biol.*, **47**, 9–14.

Böhm, E. L. and Goreau, T. F. (1973). Rates of turnover and net accretion of calcium and the role of calcium binding polysaccharides during calcification in the calcareous alga *Halimeda opuntia* (L.). *Int. Rev. Ges. Hydrobiol.*, **58**, 723–740.

Böhm, E. L., Fütterer, D. and Kaminski, E. (1978). Algal calcification in some Codiaceae (Chlorophyta): ultrastructure and location of skeletal deposits. *J. Phycol.*, **14**, 486–493.

Borowitzka, M. A. (1977). Algal calcification. *Oceanogr. Mar. Biol. Ann. Rev.*, **15**, 189–223.

Borowitzka, M. A. (1979). Calcium exchange and the measurement of calcification rates in the calcareous coralline red alga *Amphiroa foliacea*. *Mar. Biol.*, **50**, 339–347.

Borowitzka, M. A. (1981a). Algae and grazing in coral reef ecosystems. *Endeavour*, **5**, 99–106.

Borowitzka, M. A. (1981b). Calcification and silicification. In *Marine Botany: An Australasian Perspective* (Clayton, M. N. and King, R. T. eds.), pp. 349–354, Longman Cheshire, Melbourne.

Borowitzka, M. A. (1982a). Mechanisms in algal calcification. In *Progress in Phycological Research, Vol. 1*. (Round, F. E. and Chapman, D. J., eds.). pp. 137–177, Elsevier Biomedical Press, Amsterdam.

Borowitzka, M. A. (1982b). Morphological and cytological aspects of algal calcification. *Int. Rev. Cytol.*, **74**, 127–162.

Borowitzka, M. A. and Larkum, A. W. D. (1976a). Calcification in the green alga *Halimeda*. II. The exchange of Ca^{2+} and the occurrence of age gradients in calcification and photosynthesis. *J. Exp. Bot.*, **27**, 864–878.

Borowitzka, M. A. and Larkum, A. W. D. (1976b). Calcification in the green alga *Halimeda*. III. The sources of inorganic carbon for photosynthesis and calcification and a model of the mechanism of calcification. *J. Exp. Bot.*, **27**, 879–893.

Borowitzka, M. A. and Larkum, A. W. D. (1976c). Calcification in the green alga *Halimeda*. IV. The action of metabolic inhibitors on photosynthesis and calcification. *J. Exp. Bot.*, **27**, 894–907.

Borowitzka, M. A. and Larkum, A. W. D. (1977). Calcification in the green alga *Halimeda*. I. An ultrastructure study of thallus development. *J. Phycol.*, **13**, 6–16.

Borowitzka, M. A., Larkum, A. W. D. and Nockolds, C. E. (1974). A scanning electron microscope study of the structure and organization of the calcium carbonate deposits of algae. *Phycologia*, **13**, 195–203.

Bosellini, A. and Ginsburg, R. N. (1971). Form and internal structure of recent algal nodules (rhodolites) from Bermuda. *J. Geol.*, **79**, 669–682.

Bosence, D. (1977). Ecological studies on two carbonate sediment-producing algae. In: *Fossil Algae* (Flügel, E. ed.), pp. 270–278, Springer-Verlag, Berlin.

Brawley, S. H. and Adey, W. H. (1977). Territorial behaviour of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. *Envir. Biol. Fish.*, **2**, 45–51.

Brock, R. E. (1979). An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Mar. Biol.*, **51**, 381–388.

Brown, V., Ducker, S. C. and Rowan, K. S. (1977). The effect of orthophosphate concentration on the growth of articulated coralline algae (Rhodophyta). *Phycologia*, **16**, 125–131.

Bunt, J. S. (1975). Primary productivity of marine ecosystems. In *Primary Productivity of the Biosphere. Ecological Studies*. Vol. **14** (Lieth, H. and Whittaker, R. H., eds.). pp. 169–183, Springer-Verlag, Berlin.

Burris, R. H. (1976). Nitrogen fixation by blue-green algae of the Lizard Island area of the Great Barrier Reef. *Aust. J. Plant Physiol.*, **3**, 41–51.

Buss, L. W. and Jackson, J. B. C. (1979). Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Nat.*, **113**, 223–234.

Capone, D. G. (1977). N_2 (C_2H_2) fixation by macroalgal epiphytes, *Proc. 3rd Int. Coral Reef Symp.*, **1**, 337–342.

Capone, D. G., Taylor, D. L. and Taylor, B. F. (1977). Nitrogen fixation (acetylene reduction) associated with macroalgae in a coral-reef community in the Bahamas. *Mar. Biol.*, **40**, 29–32.

Carpenter, R. C. (1981). Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. *J. Mar. Res.*, **39**, 749–765.

Chapman, F. and Mawson, D. (1906). On the importance of *Halimeda* as a reef-forming organism: with a description of the *Halimeda*-limestones of the New Hebrides. *J. Geol. Soc. Lond.*, **62,** 702–711.

Chu, H. and Wu, B. T. (1983). Studies on the lime-boring algae from China. I. The lime-boring algae collected from the Xisha Islands. *XIth Int. Seaweed Symp.*, Qingdao, China. p. 46. (Abstract only).

Cloud, P. E. (1965). Carbonate precipitation and dissolution in the marine environment. In *Chemical Oceanography, Vol. II.* (Riley, J. P. and Skirrow, F. eds.), pp. 127–158, Academic Press, London.

Connor, J. L. and Adey, W. H., (1977). The benthic algal composition, standing crop, and productivity of a Caribbean algal ridge. *Atoll. Res. Bull.*, **211,** 1–15.

Cribb, A. B. (1973). The algae of the Great Barrier Reefs. In: *Biology and Geology of Coral Reefs* (Jones, O. A. and Endean, R. eds.). pp. 47–75, Academic Press, New York.

Crossland, C. J. (1939). Further notes on the Tahitian barrier reef and lagoons. *J. Linn. Soc. Lond., Zool.*, **40,** 459–474.

Crossland, C. J. and Barnes, D. J. (1976). Acetylene reduction by corals. *Limnol. Oceanogr.*, **21,** 153–155.

Dahl, A. L. (1972). Ecology and community structure of some tropical reef algae in Samoa. *Proceedings of the Seventh International Seaweed Symposium* (Nisizawa, K., ed.), pp. 36–39, University of Tokyo Press, Tokyo, Japan.

Dahl, A. L. (1973). Surface area in ecological analysis: quantification of benthic coral-reef algae. *Mar. Biol.*, **23,** 239–249.

Dahl, A. L. (1976). Generation of photosynthetic surface area by coral reef algae. *Micronesica*, **12,** 43–47.

Dart, J. K. G. (1972). Echinoids, algal lawn and coral recolonization. *Nature*, **239,** 50–51.

David, T. W. E., Halligan, G. H. and Finckh, A. E. (1904). Report on dredging at Funafuti, Section VII. In: *The Atoll of Funafuti*, pp. 151–159, Report of the Coral Reef Committee, Royal Society, London.

Dawes, C. J. (1969). A study of the ultrastructure of a green alga, *Apjohnia laetevirens* Harvey with emphasis on cell wall structure. *Phycologia*, **8,** 77–84.

Digby, P. S. B. (1977a). Growth and calcification in the coralline algae, *Clathromorphum circumscriptum* and *Corallina officinalis*, and the significance of pH in relation to precipitation. *J. Mar. Biol. Assoc., U.K.*, **57,** 1095–1109.

Digby, P. S. B. (1977b). Photosynthesis and respiration in the coralline algae, *Clathromorphum circumscriptum* and *Corallina officinalis* and the metabolic basis of calcification. *J. Mar. Biol. Assoc., U.K.*, **57,** 1111–1124.

Digby, P. S. B. (1979). Reducing activity and the formation of base in the coralline algae: an electrochemical model. *J. Mar. Biol. Assoc., U.K.*, **59,** 455–477.

Doty, M. S. (1954). Floristic and ecological notes on Raroia, Part I. *Atoll Res. Bull.*, **33,** 1–54.

Doty, M. S. (1968). *Biological and physical features of Kealakekua Bay, Hawaii*, 210 pp., Hawaii Botanical Science Paper No. 8, University of Hawaii.

Doty, M. S. (1969). *The ecology of Honaunau Bay, Hawaii*, 221 pp., Hawaii Botanical Science Paper No. 14, University of Hawaii.

Doty, M. S. (1971). Physical factors in the production of tropical benthic marine algae. In *Fertility of the Sea, Vol. I.* (J. D. Costlow, Jr., ed.), pp. 99–121, Gordon and Breach, New York.

Doty, M. S. (1974). Coral reef roles played by free-living algae, *Proc. 2nd Int. Coral Reef Symp.*, **1,** 27–33.

Doty, M. S. and Morrison, J. P. E. (1954). Interrelationships of the organisms on Raroia aside from man. *Atoll Res. Bull.*, **35,** 1–70.

Dravis, J. J. (1983). Hardened subtidal stromatolites, Bahamas. *Science*, **219,** 385–386.

Duerden, J. E. (1902). Boring algae as agents in the disintegration of corals. *Bull. Am. Mus. Nat. His.*, **16,** 323–332.

Earle, S. A. (1972). The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. In *Results of the Tektite Program: Ecology of Coral Reef Fishes* (Collette, B. B. and Earle, S. A., eds.), pp. 17–44, Science Bulletin 14, Los Angeles County Natural History Museum, Los Angeles, California.

Easton, W. H. (1977). Radiocarbon profile of Hanauma Reef, Oahu, Hawaii: reply. *Geol. Soc. Am. Bull.*, **88**, 1535–1536.

Easton, W. H. and Olson, E. A. (1976). Radiocarbon profile of Hanauma Reef, Oahu, Hawaii. *Geol. Soc. Am. Bull.*, **87**, 711–719.

Ekman, S. (1953). *Zoogeography of the Sea* (translated from Swedish by E. Palmer), 417 pp., Sidgwick and Jackson, London.

Emery, K. O., Tracey, J. I., Jr. and Ladd, H. S. (1949). Submarine geology and topography in the northern Marshalls. *Trans. Am. Geophys. Union*, **30**, 55–58.

Entsch, B., Boto, K. G., Sim, R. G. and Wellington, J. T. (1983). Phosphorous and nitrogen in coral reef sediments. *Limnol. Oceanogr.*, **28**, 465–476.

Fenical, W. H. (1975). Halogenation in the Rhodophyta: a review. *J. Phycol.*, **11**, 245–259.

Fenical, W. H. (1980). Distributional and taxonomic features of toxin-producing marine algae. In *Pacific Seaweed Aquaculture* (Abbott, I. A., Foster, M. S. and Eklund, L. F. eds.). pp. 144–151, California Sea Grant Program. La Jolla.

Finckh, A. E. (1904). Biology of the reef-forming organisms at Funafuti Atoll, Section VI. In *The Atoll of Funafuti*, pp. 125–150, Report of the Coral Reef Committee, Royal Society, London.

Foslie, M. H. (1895). The Norwegian forms of *Lithothamnion. K. Norske Vidensk. Selsk. Skr., 1894*, 1–80.

Franzisket, L. (1968). Zur ökologie der Fadenalgen in Skelett lebender Riffkorallen. *Zool. Jb. Physiol., Bd.* **74**, 246–253.

Friedmann, E. I., Roth, W. C., Turner, J. B. and McEwen, R. S. (1972). Calcium oxalate crystals in the aragonite producing green alga *Penicillus* and related genera. *Science*, **177**, 891–893.

Gaines, S. D. and Lubchenco, J. (1982). A unified approach to marine plant-herbivore interactions. II. Biogeography. *Ann. Rev. Ecol. Syst.*, **13**, 111–138.

Gardiner, J. S. (1931). Photosynthesis and solution in formation of coral reefs. *Proc. Linn. Soc. London*, **143**, 65–71.

Gebelein, C. D. (1969). Distribution, morphology, and accretion rate of recent subtidal algal stromatolites, Bermuda. *J. Sed. Petrology*, **39**, 49–69.

Ginsburg, R. N. (1956). Environmental relationships of grain size and constituent particles in some south Florida carbonate sediments. *Bull. Am. Assoc. Petrol. Geol.*, **40**, 2384–2427.

Ginsburg, R. N. (1957). Early diagenesis and lithification of shallow-water carbonate sediments in South Florida. *Soc. Econ. Paleontol. Mineral., Spec. Publ.*, **5**, 80–100.

Glynn, P. W. (1973). Aspects of the ecology of coral reefs in the western Atlantic region. In *Biology and Geology of Coral Reefs* (Jones, O. A. and Endean, R., eds.), pp. 271–324, Academic Press, New York.

Glynn, P. W., Wellington, G. M. and Birkeland, C. (1979). Coral reef growth in the Galapagos: limitation by sea urchins. *Science*, **203**, 47–49.

Golikov, A. N., Krasnov, E. V., Moskalev, L. I. and Naumov, D. V. (1973). The comparative-ecological analysis of some biocoenoses in the upper parts of the island shelves in the western tropical Pacific. *Okeanologia*, **13**, 158–172.

Golubic, S. and Yun, Z. (1983). Phycological expertise in geological applications. *XIth Int. Seaweed Symp.*, Qingdao, China. p. 79. (Abstract only).

Goreau, T. F. (1963). Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef-builders. *Ann. N.Y. Acad. Sci.*, **109**, 127–167.

Green, M. A. (1975). Survey of Endolithic Organisms from the Northeast Bering Sea, Jamaica, and Florida Bay. M.S. Thesis, Duke University, Durham, North Carolina.

Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. 222 pp., John Wiley & Sons, New York.

Gross, M. G., Milliman, J. D., Tracey, J. I., Jr. and Ladd, H. S. (1969). Marine geology of Kure and Midway Atolls, Hawaii: a preliminary report. *Pac. Sci.*, **23**, 17–25.

Halldal, P. (1968). Photosynthetic capacities and photosynthetic action spectra of endozoic algae of the massive coral *Favia. Biol. Bull.*, **134**, 411–424.

Hatcher, B. G. (1982). The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. *Proc. 4th Int. Coral Reef Symp.*, **2**, 515–524.

Hatcher, B. G. and Larkum, A. W. D. (1983). An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *J. Exp. Mar. Biol. Ecol.*, **69,** 61–84.

Hay, M. E. (1981a). The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology*, **62,** 739–750.

Hay, M. E. (1981b). Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat. Bot.*, **11,** 97–109.

Hay, M. E. (1981c). Herbivory, algal distribution, and the maintenance of between habitat diversity on a tropical fringing reef. *Am. Nat.*, **118,** 520–540.

Hay, M. E. (1984). Patterns of fish and urchin grazing on Caribbean barrier reefs: are previous results typical? *Ecology*, **65,** 446–454.

Hay, M. E., Colburn, T. and Downing, D. (1983). Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia*, **58,** 299–308.

Hillis-Colinvaux, L. (1977). *Halimeda* and *Tydemania:* distribution, diversity and productivity at Enewetak. *Proc. 3rd Int. Coral Reef Symp.* **1,** 365–370.

Hillis-Colinvaux, L. (1980). Ecology and taxonomy of *Halimeda*: primary producer of coral reefs. *Adv. Mar. Biol.*, **17,** 1–327.

Hillis-Colinvaux, L. (1982). Submersible study of the calcareous green algae of Enewetak Atoll, Marshall Islands. *21st Northeast Algal Symposium*, Woods Hole, Mass. p. 9. (Abstract only).

Hixon, M. A. and Brostoff, W. N. (1982). Differential fish grazing and benthic community structure on Hawaiian reefs. In: *Fish Food Habit Studies, Proc. 3rd Pacific Workshop*. (Cailliet, G. M. and Simenstad, C. A. eds.), pp. 249–257, Washington Sea Grant Program, Seattle.

Howe, M. A. (1912). The building of 'coral' reefs. *Science*, **35,** 837–842.

Ikemori, M. (1970). Relation of calcium uptake to photosynthetic activity as a factor controlling calcification in marine algae. *Bot. Mag. Tokyo*, **83,** 152–162.

Jacques, T. G. and Pilson, M. E. Q. (1980). Experimental ecology of the temperate scleractinian coral *Astrangia danae* I. Partition of respiration, photosynthesis and calcification between host and symbionts. *Mar. Biol.*, **60,** 167–178.

John, D. M. and Pople, W. (1973). The fish grazing of rocky shore algae in the Gulf of Guinea. *J. Exp. Mar. Biol. Ecol.*, **11,** 81–90.

Johnson, J. H. (1954). An introduction to the study of rock building algae and algal limestones. *Colo. Sch. Mines Q.*, **49,** 1–117.

Kanwisher, J. W. and Wainwright, S. A. (1967). Oxygen balance in some reef corals. *Biol. Bull.*, **133,** 378–390.

Kaufman, L. (1977). The three spot damselfish: effects on benthic biota of Caribbean coral reefs. *Proc. 3rd Int. Coral Reef Symp.*, **1,** 559–564.

Kinsey, D. W. and Davies, P. J. (1979). Effects of elevated nitrogen and phosphorus on coral reef growth. *Limnol. Oceanogr.*, **24,** 935–940.

Kinsey, D. W. and Domm, A. (1974). Effects of fertilization on a coral reef environment primary production studies. *Proc. 2nd Int. Coral Reef Symp.*, **1,** 49–66.

Kjellman, F. R. (1883). The algae of the Arctic Sea. *K. Svenska Vetensk.-Akad. Handl.*, **20,** 1–335.

Kobluk, D. R. and Risk, M. J. (1977). Calcification of exposed filaments of endolithic algae, micrite envelope formation and sediment production. *J. Sed. Petrology*, **47,** 517–528.

Kraft, G. T. (1972). Preliminary studies of Philippine *Eucheuma* species (Rhodophyta). Part 1. taxonomy and ecology of *Eucheuma arnoldii* Weber-van Bosse. *Pac. Sci.*, **26,** 318–334.

Ladd, H. S. (1950). Recent reefs. *Bull. Am. Assoc. Petrol. Geol.*, **34,** 203–214.

Ladd, H. S., Ingerson, E., Townsend, R. C., Russell, M. and Stephenson, H. K. (1953). Drilling on Eniwetok Atoll, Marshall Islands. *Bull. Am. Assoc. Petrol. Geol.*, **37,** 2257–2280.

Ladd, H. S., Tracey, J. I., Jr. and Gross, M. G. (1967). Drilling on Midway Atoll, Hawaii. *Science*, **156,** 1088–1094.

Ladd, H. S., Tracey, J. I., Jr. and Gross, M. G. (1970). Deep drilling on Midway Atoll. *U.S. Geol. Surv. Prof. Pap.* **608-A,** 1–22.

Laevastu, T., Avery, D. E. and Cox, D. C. (1964). *Coastal Currents and Sewage Disposal in the Hawaiian Islands,* 101 pp., Hawaii Institute of Geophysics, HIG-64-1.

Land, L. S. (1970). Carbonate mud: production by epibiont growth on *Thalassia testudinum*. *J. Sed. Petrology*, **40,** 1361–1363.

Lapointe, B. E. (1983). Nutrient limited seaweed growth in nearshore waters of the Florida Keys: nitrogen and phosphorus. *EOS, Trans. Am. Geophys. Union,* **64:** 1056. (Abstract only).

Larkum, A. W. D. (1981). Marine Primary productivity. In. *Marine Botany, an Australasian Perspective* (Clayton, M. N. and King, R. J., eds.), pp. 370–385, Longman Cheshire, Melbourne.

LaVelle, J. M. (1979). The vertical distribution of attached marine algae in Malta. *Mar. Biol.,* **55,** 37–44.

Lebednik, P. A. (1977). The Corallinaceae of northwestern North America. I. *Clathromorphum* Foslie emend. Adey. *Syesis,* **9,** 59–112.

Lee, R. K. S. (1967). Taxonomy and distribution of the melobesioid algae on Rongelap Atoll, Marshall Islands. *Can. J. Bot.,* **45,** 985–1001.

Lewin, J. C. (1962). Calcification. In: *Physiology and Biochemistry of Algae* (Lewin, R. A., ed.), pp. 457–465, Academic Press, London.

Lewis, J. B. (1977). Processes of organic production on coral reefs. *Biol. Rev.,* **52,** 305–347.

Lighty, R. G. (1982). Fleshy algal domination of a modern Bahamian Barrier reef: example of an alternate climax reef community. *Proc. 4th Int. Coral Reef Symp.,* **1,** p. 722 (Abstract only).

Littler, M. M. (1971). Standing stock measurements of crustose coralline algae (Rhodophyta) and other saxicolous organisms. *J. Exp. Mar. Biol. Ecol.,* **6,** 91–99.

Littler, M. M. (1972). The crustose Corallinaceae. *Oceanogr. Mar. Biol. Ann. Rev.,* **10,** 311–347.

Littler, M. M. (1973a). The population and community structure of Hawaiian fringing-reef crustose Corallinaceae (Rhodophyta, Cryptonemiales). *J. Exp. Mar. Biol. Ecol.,* **11,** 103–120.

Littler, M. M. (1973b). The distribution, abundance, and communities of deepwater Hawaiian crustose Corallinaceae (Rhodophyta, Cryptonemiales). *Pac. Sci.,* **27,** 281–289.

Littler, M. M. (1973c). The productivity of Hawaiian fringing-reef crustose Corallinaceae and an experimental evaluation of production methodology. *Limnol. Oceanogr.,* **18,** 946–952.

Littler, M. M. (1976). Calcification and its role among the macroalgae. *Micronesica,* **12,** 27–41.

Littler, M. M. (1980a). Morphological form and photosynthetic performances of marine macroalgae: tests of a functional/form hypothesis. *Bot. Mar.,* **22,** 161–165.

Littler, M. M. (1980b). Southern California rocky intertidal ecosystems: methods, community structure and variability. In: *The Shore Environment, Vol. 2: Ecosystems* (Price, J. H., Irvine, D. E. G. and Farnham, W. F., eds.), pp. 565–608, Systematics Association Special Volume No. 17(b), Academic Press, London.

Littler, M. M. and Arnold, K. E. (1980). Sources of variability in macroalgal primary productivity: sampling and interpretative problems. *Aquat. Bot.,* **8,** 141–156.

Littler, M. M. and Arnold, K. E. (1982). Primary productivity of marine macroalgal functional-form groups from southwestern North America. *J. Phycol.,* **18,** 307–311.

Littler, M. M. and Doty, M. S. (1975). Ecological components structuring the seaward edges of tropical Pacific reefs: the distribution, communities and productivity of *Porolithon, J. Ecol.,* **63,** 117–129.

Littler, M. M. and Kauker, B. J. (1984). Heterotrichy and survival strategies in the red alga *Corallina officinalis* L. *Bot. Mar.,* **27,** 37–44.

Littler, M. M. and Littler, D. S. (1980). The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am. Nat.,* **116,** 25–44.

Littler, M. M. and Littler, D. S. (1981). Intertidal macrophyte communities from Pacific Baja California and the upper Gulf of California: relatively constant vs. environmentally fluctuating systems. *Mar. Ecol. Prog. Ser.,* **4,** 145–158.

Littler, M. M. and Littler, D. S. (1984). Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. *J. Exp. Mar. Biol. Ecol.,* **74,** 13–34.

Littler, M. M. and Murray, S. N. (1978). Influences of domestic wastes on energetic pathways in rocky intertidal communities. *J. Appl. Ecol.,* **15,** 583–595.

Littler, M. M., Littler, D. S. and Taylor, P. R. (1983a). Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. *J. Phycol.,* **19,** 229–237.

Littler, M. M., Taylor, P. R. and Littler, D. S. (1983b). Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs,* **2,** 111–118.

Lowenstam, H. A. and Margulis, L. (1980). Evolutionary prerequisites for early Phanerozoic calcareous skeletons. *BioSystems,* **12,** 27–41.

Lubchenco, J. and Cubit, J. (1980). Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology,* **61,** 676–687.

Lubchenco, J. and Gaines, S. D. (1981). A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Ann. Rev. Ecol. Syst.,* **12,** 405–437.

Lucas, W. C. and Smith, F. A. (1973). The formation of alkaline and acid regions at the surface of *Chara corallina* cells. *J. Exp. Bot.,* **24,** 1–14.

Macintyre, I. G. (1984). Extensive submarine lithification in a cave in the Belize barrier reef platform. *J. Sed. Petrology,* **54,** 11–25.

Macintyre, I. G. and Glynn, P. W. (1976). Evolution of modern Caribbean fringing reef, Galeta Point, Panama. *Am. Assoc. Petrol. Geol. Bull.,* **60,** 1054–1972.

Mague, T. H. and Holm-Hansen, O. (1975). Nitrogen fixation on a coral reef. *Phycologia,* **14,** 87–92.

Marsh, J. A., Jr. (1970). Primary productivity of reef-building calcareous red algae. *Ecology,* **51,** 255–263.

Marsh, J. A., Jr. (1974). Preliminary observations on the productivity of a Guam reef flat community. *Proc. 2nd Int. Coral Reef Symp.,* **1,** 139–145.

Marsh, J. A., Jr. (1976). Energetic role of algae in reef ecosystems. *Micronesica,* **12,** 13–21.

Marszalek, D. S. (1971). Skeletal ultrastructure of sediment producing green algae. In *Scanning Electron Microscopy, Part I.* (Johari, O. and Corvin, T., eds.), pp. 273–280, I.I.T. Research Institute, Chicago.

Mathieson, A. C., Fralick, R. A., Burns, R. and Flashive, W. (1971). Comparative studies of subtidal vegetation in the Virgin Islands and the New England coastlines. In *Scientists in the Sea, Vol. I* (Miller, J. W., Van Derwalker, J. G. and Waller, R. A., eds.), pp. 106–131, U.S. Department of the Interior, Washington, D.C.

Mathieson, A. C., Fralick, R. A., Burns, R. and Flashive, W. (1975). Phycological studies during Tektite II, at St. John, U.S. V.I. In *Results of the Tektite Program: Coral Reef Invertebrates and Plants* (Earle, S. A. and Lavenberg, R. J. eds.), pp. 77–103, Sci. Bull. 20., Nat. Hist. Mus. Los Angeles, Los Angeles.

May, J. A., Macintyre, I. G. and Perkins, R. D. (1982). Distribution of microborers within planted substrates along a barrier reef transect, Carrie Bow Cay, Belize. In *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I. Structure and Communities* (Rützler, K. and Macintyre, I. G., eds.), pp. 93–107, Smithsonian Contributions to the Marine Sciences, No. 12., Smithsonian Institution Press, Washington, D.C.

McMaster, R. L. and Conover, J. T. (1966). Recent algal stromatolites from the Canary Islands. *J. Geol.,* **74,** 647–652.

McRoy, C. P. and McMillan, C. (1977). Production ecology and physiology of seagrasses. In *Seagrass Ecosystems. A Scientific Perspective* (McRoy C. P. and Helfferich, C. eds.), pp. 53–81, Marcel Dekker, New York.

McVey, J. P. (1970). Fishery Ecology of the Pokai Artificial Reef, Ph.D. Dissertation, University of Hawaii, Honolulu.

Menge, B. A. and Lubchenco, J. (1981). Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol. Monogr.,* **51,** 429–450.

Milliman, J. D. (1973). Caribbean coral reefs. In *Biology and Geology of Coral Reefs* (Jones, O. A. and Endean, R. eds.), pp. 1–50. Academic press, New York.

Moberly, R., Jr. (1968). Composition of magnesian calcites of algae and pelecypods by electron microprobe analysis. *Sedimentology,* **11,** 61–82.

Montgomery, W. L. (1980). The impact of non-selective grazing by the giant blue damselfish, *Microspathodon dorsalis,* on algal communities in the Gulf of California, Mexico. *Bull. Mar. Sci.,* **30,** 290–303.

Montgomery, W. L., Gerrodette, T. and Marshall, L. D. (1980). Effects of grazing by the yellowtail surgeonfish, *Prionurus punctatus,* on algal communities in the Gulf of California, Mexico, *Bull. Mar. Sci.,* **30,** 901–908.

Nadson, G. (1900). Die perforierenden (kalkbohrenden) Algen und ihre Bedeutung in der Natur. *Botanica Scripta*, **18,** 1–40.

Neudecker, S. (1977). Transplant experiments to test the effect of fish grazing on coral distribution. *Proc. 3rd Int. Coral Reef Symp.*, **1,** 317–323.

Neumann, A. C. and Land, L. S. (1969). Algal production and lime mud deposition in the Bight of Abaco: a budget. *Geol. Soc. Am. Special Pap.*, **121,** 219.

Neumann, A. C. and Land, L. S. (1975). Lime mud deposition and calcareous algae in the Bight of Abaco, Bahamas: a budget. *J. Sed. Petrology*, **45,** 763–786.

Newell, N. D. (1954). Reefs and sedimentary processes of Raroia. *Atoll Res. Bull.*, **36,** 1–35.

Nicotri, M. E. (1980). Factors involved in herbivore food preference. *J. Exp. Mar. Biol. Ecol.*, **42,** 13–26.

Norris, J. N. and Fenical, W. (1982). Chemical defense in tropical marine algae. In *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I. Structure and Communities* (Rützler, K. and Macintyre, I. G. eds.), pp. 417–431, Smithsonian Contributions to the Marine Sciences, No. 12. Smithsonian Institution Press, Washington, D.C.

Odum, H. T. and Odum, E. P. (1955). Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.*, **25,** 291–320.

Ogden, J. C., Brown, R. A. and Salesky, N. (1973). Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. *Science*, **182,** 715–717.

Okazaki, M., Ikawa, T., Furuya, K., Nisizawa, K. and Miwa, T. (1970). Studies on calcium carbonate deposition of a calcareous red alga *Serraticardia maxima*. *Bot. Mag., Tokyo*, **83,** 193–201.

Paine, R. T. and Vadas, R. L. (1969). Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. *Mar. Biol.*, **4,** 79–86.

Parrish, J. D. and Zimmerman, R. J. (1977). Utilization by fishes of space and food resources on an offshore Puerto Rican coral reef and its surroundings. *Proc. 3rd Int. Coral Reef Symp.*, **1,** 297–303.

Paul, V. J. and Fenical, W. (1983). Isolation of halimedatrial: chemical defense adaptation in the calcareous reef-building alga *Halimeda*. *Science*, **221,** 747–749.

Pearse, V. B. (1972). Radioisotopic study of calcification in the articulated coralline alga *Bossiella orbigniana*. *J. Phycol.*, **8,** 88–97.

Pentecost, A. (1978). Calcification and photosynthesis in *Corallina officinalis* L. using the $^{14}CO_2$ method. *Br. Phycol. J.*, **13,** 383–390.

Perkins, R. D. and Tsentas, C. I. (1976). Microbial infestation of carbonate substrates planted on the St. Croix shelf, West Indies. *Geol. Soc. Am. Bull.*, **87,** 1615–1628.

Pilson, M. E. Q. and Betzer, S. B. (1973). Phosphorus flux across a coral reef. *Ecology*, **54,** 581–588.

Pollock, J. B. (1928). Fringing and fossil coral reefs of Oahu. *Bull. Bernice P. Bishop Mus.*, **55,** 1–56.

Potts, D. C. (1977). Suppression of coral populations by filamentous algae within damselfish territories. *J. Exp. Mar. Biol. Ecol.*, **28,** 207–216.

Purdy, E. G. and Kornicker, L. S. (1958). Algal disintegration of Bahamian limestone coasts. *J. Geol.*, **66,** 97–99.

Randall, J. E. (1961). Overgrazing of algae by herbivorous marine fishes. *Ecology*, **42,** 812.

Randall, J. E. (1965). Grazing effect on seagrasses by herbivorous reef fishes in the West Indies. *Ecology*, **46,** 255–260.

Randall, J. E. (1974). The effect of fishes on coral reefs. *Proc. 2nd Int. Coral Reef Symp.*, **1,** 159–166.

Rogers, C. S. and Salesky, N. H. (1981). Productivity of *Acropora palmata* (Lamarck), macroscopic algae, and algal turf from Tague Bay Reef, St. Croix, U.S. Virgin Islands. *J. Exp. Mar. Biol. Ecol.*, **49,** 179–187.

Rützler, R. and Macintyre, I. G., eds. (1982). *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I. Structure and Communities.* 539 pp., Smithsonian Contributions to the Marine Sciences, No. 12. Smithsonian Institution Press, Washington, D.C.

Sammarco, P. W., Levinton, J. S. and Ogden, J. C. (1974). Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea): a preliminary study. *J. Mar. Res.*, **32,** 47–53.

Santelices, B. (1978). The morphological variation of *Pterocladia caerulescens* (Gelidiales, Rhodophyta) in Hawaii. *Phycologia,* **17,** 53–59.

Schroeder, J. H. (1972). Calcified filaments of an endolithic alga in Recent Bermuda reefs. *Neues Jb. Geol. Paläont. Mh.,* **1,** 16–33.

Setchell, W. A. (1926). Nullipore versus coral in reef-formation *Proc. Am. Philos. Soc.,* **65,** 136–140.

Setchell, W. A. (1928). Coral reefs as zonational plant formations. *Science,* **68,** 119–121.

Sikes, C. S., Roer, R. D. and Wilbur, K. M. (1980). Photosynthesis and coccolith formation: inorganic carbon sources and net inorganic reaction of deposition. *Limnol. Oceanogr.,* **25,** 248–261.

Silva, P. C. and Johansen, H. W. (1982). Reappraisal of the order Corallinales (Rhodophyceae). *First International Phycological Congress,* St. John's, Newfoundland. p. a46. (Abstract only).

Simkiss, K. (1964). Phosphates as crystal poisons of calcification. *Biol. Rev.,* **39,** 487–505.

Simpson, G. G. (1949). *The Meaning of Evolution,* Yale University Press, New Haven, Connecticut.

Smith, A. D. and Roth, A. A. (1979). Effect of carbon dioxide concentration on calcification in the red coralline alga *Bossiella orbigniana. Mar. Biol.,* **52,** 217–225.

Smith, S. V. (1973). Carbon dioxide dynamics: a record of organic carbon production, respiration, and calcification in the Eniwetok reef flat community. *Limnol. Oceanogr.,* **18,** 106–120.

Smith, S. V. (1974). Coral reef carbon dioxide flux. *Proc. 2nd Int. Coral Reef Symp.,* **1,** 77–85.

Smith, S. V. and Kinsey, D. W. (1976). Calcium carbonate production, coral reef growth, and sea level change. *Science,* **194,** 937–939.

Smith, S. V. and Marsh, J. A., Jr. (1973). Organic carbon production on the windward reef flat of Eniwetok Atoll. *Limnol. Oceanogr.,* **18,** 953–961.

Smith, S. V., Jokiel, P. C., Key, G. S. and Guinther, E. B. (1979). *Metabolic Responses of Shallow Tropical Microcosm Communities to Perturbation,* 57 pp., U.S. Environmental Protection Agency Report, EPA-600/3-79-061.

Smith, S. V., Kimmerer, W. J., Laws, E. A., Brock, R. E. and Walsh, T. W. (1981). Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pac. Sci.,* **35,** 279–397.

Sournia, A. (1976). Oxygen metabolism of a fringing reef in French Polynesia. *Helgoländer wiss. Meeresunters.,* **28,** 401–410.

Stark, L. M., Almodovar, L. and Krauss, R. W. (1969). Factors affecting the rate of calcification in *Halimeda opuntia* (L.) Lamouroux and *Halimeda discoidea* Decaisne. *J. Phycol.,* **5,** 305–312.

Stearn, C. W., Scoffin, T. P. and Martindale, W. (1977). Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part I—Zonation and productivity. *Bull. Mar. Sci.,* **27,** 479–510.

Stearns, H. T. (1977). Radiocarbon profile of Hanauma Reef, Oahu, Hawaii: discussion. *Geol. Soc. Am. Bull.,* **88,** 1535–1536.

Steneck, R. S. (1983). Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology,* **9,** 44–61.

Steneck, R. S. and Adey, W. H. (1976). The role of environment in control of morphology in *Lithophyllum congestum,* a Caribbean algal ridge builder, *Bot. Mar.,* **19,** 197–215.

Steneck, R. S. and Watling, L. (1982). Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar. Biol.,* **68,** 299–319.

Stephenson, W. and Searles, R. B. (1960). Experimental studies on the ecology of intertidal environments at Heron Island. *Aust. J. Mar. Freshwater Res.,* **11,** 241–267.

Stockman, K. W., Ginsburg, R. N. and Shinn, E. A. (1967). The production of lime mud by algae in south Florida. *J. Sed. Petrology,* **37,** 633–648.

Stoddart, D. R. (1969). Ecology and morphology of recent coral reefs. *Biol. Rev.,* **44,** 433–498.

Stoddart, D. R. and Johannes, R. E., eds. (1978). *Coral Reefs: Research Methods,* 581 pp., UNESCO, Paris.

Stoddart, D. R. and Yonge, M., eds. (1971). *Regional Variation in Indian Ocean Coral Reefs,* 584 pp., Zool. Soc. London Symp. No. 28.

Van den Hoek, C. (1969a). Algal vegetation-types along the open coasts of Curacao, Netherlands Antilles I. *Proc. K. Ned. Akad. Wet. Ser. C Biol. Med. Sci.,* **72,** 537–558.

Van den Hoek, C. (1969b). Algal vegetation-types along the open coasts of Curacao, Netherlands Antilles II. *Proc. K. Ned. Akad. Wet. Ser. C Biol. Med. Sci.,* **72,** 559–577.

Van den Hoek, C., Breeman, A. M., Bak, R. P. M. and Van Buurt, G. (1978). The distribution of algae, corals and gorgonians in relation to depth, light attenuation, water movement and grazing pressure in the fringing coral reef of Curacao, Netherlands Antilles. *Aquat. Bot.*, **5**, 1–46.

Van den Hoek, C., Cortel-Breeman, A. M. and Wanders, J. B. W. (1975). Algal zonation in the fringing coral reef of Curacao, Netherlands Antilles, in relation to zonation of corals and gorgonians. *Aquat. Bot.*, **1**, 269–308.

Vine, P. J. (1974). Effects of algal grazing and aggressive behaviour of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. *Mar. Biol.*, **24**, 131–136.

Wanders, J. B. W. (1976). The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles). I: primary production in the coral reef. *Aquat. Bot.*, **2**, 235–270.

Wanders, J. B. W. (1977). The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) III: the significance of grazing. *Aquat. Bot.* **3**, 357–390.

Wanders, J. B. W. and Wanders-Faber, A. (1974). Primary productivity of the S.W. coast shallow reef and the N.E. coast brown algae of Curacao. *Br. Phycol. J.*, **9**, 223–224.

Webb, K. L. and Wiebe, W. J. (1978). The kinetics and possible significance of nitrate uptake by several algal-invertebrate symbioses. *Mar. Biol.*, **47**, 21–27.

Webb, K. L., DuPaul, W. D., Wiebe, W., Sottile, W. and Johannes, R. E. (1975). Enewetak (Eniwetok) Atoll; aspects of the nitrogen cycle on a coral reef. *Limnol. Oceanogr.*, **20**, 198–210.

Weber, J. N. and Kaufman, J. W. (1965). Brucite in the calcareous alga *Goniolithon. Science*, **149**, 996–997.

Weber-van Bosse, A. (1932). Algues. *Mem. Mus. R. Hist. Natur. Belg.*, **6**, 1–27.

Wells, J. W. (1957). Coral Reefs. In *Treatise on Marine Ecology and Paleoecology. Vol. 1. Ecology* (Hedgpeth, J. W. ed.), *Geol. Soc. Am., Memoir* **67**, 609–631.

Wells, R. J. and Barrow, K. D. (1979). Acyclic diterpenes containing 3 enol acetate groups from the green alga *Chlorodesmis fastigiata. Experimentia*, **35**, 1544–1545.

Westlake, D. F. (1963). Comparisons of plant productivity. *Biol. Rev.*, **38**, 385–425.

Wiebe, W. J., Johannes, R. E. and Webb, K. L. (1975). Nitrogen fixation in a coral reef community. *Science*, **188**, 257–259.

Wilbur, K. M., Colinvaux, L. H. and Watabe, N. (1969). Electron microscope study of calcification in the alga *Halimeda* (order Siphonales). *Phycologia*, **8**, 27–35.

Wollaston, E. M. (1968). Morphology and taxonomy of southern Australian genera of Crouanieae Schmitz (Ceramiaceae, Rhodophyta). *Aust. J. Bot.*, **16**, 217–417.

Womersley, H. B. S. and Bailey, A. (1970). Marine algae of the Solomon Islands. *Phil. Trans. Roy. Soc., Ser. B*, **259**, 257–352.

Wray, J. L. (1971). Algae in reefs through time. *Proc. N. Am. Paleontol. Soc. Convention, Chicago. 1969(1)*. 1358–1373.

Wray, J. L. (1977). *Calcareous Algae*, 185 pp., Elsevier, Amsterdam.