

Calcification and its Role among the Macroalgae¹

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Introduction

Calcareous algae are important components of the limestone deposits of antiquity. Such deposits are often associated with petroleum reserves and, for this reason, calcareous algae have attracted attention from a broad spectrum of workers that includes geologists, phycologists and paleontologists. While nearly all have agreed that calcifying algae of modern depositional habitats are abundant, diverse and ecologically important, critical quantitative information is scarce and these organisms are in nearly every respect poorly known. Most of our knowledge of biological calcification comes from studies of bone and shell producing animals. Much of the present information on calcareous macroalgae concerns the location, appearance and degree of calcification, but the mechanisms and ultrastructural features are only beginning to be explored (see for examples Marszalek, 1971; Borowitzka, Larkum and Nockolds, 1974). Reasons for this lack of research are varied, but the naive presumption that calcium deposits in plants are fortuitous or by-products of photosynthesis and other metabolic reactions has contributed heavily.

In this presentation, calcification is characterized as the accumulation of calcium carbonate in all physical states within or upon the thallus, including crystalline and non-crystalline aggregates and amorphous impregnations. The first portion of this paper surveys the calcium-depositing habit. Secondly, an overview of recent work on the distribution and ecology of calcareous macrophytes is developed. The last part considers the scant information on physiological mechanisms including the importance and possible functional roles of calcification. In this connection, certain aspects of my own research on calcium-carbonate production rates and ratios in calcareous algae are reviewed with suggestions of areas where future work is needed.

Aspects of the Calcareous Habit

Five principal aspects of the calcareous habit to be considered are: 1) the distinction between physical and physiological forms of calcification, 2) the sites of deposition, 3) the mineral forms deposited, 4) the extent of occurrence of calcifica-

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tion among macroalgae, and 5) the morphological structure of calcareous macroalgae.

PHYSICAL VERSUS PHYSIOLOGICAL CALCIFICATION

Physical deposits of calcium salts may be produced through processes of mechanical accretion by filamentous blue-green algae. For example (see Gebelein, 1969), the Bermuda algal stromatolite accretions are produced by the activities of two blue-green species. During the daylight growth period, the mucilaginous upright filaments of *Schizothrix calcicola* trap particulate matter and at night, the horizontal growth of *Oscillatoria* firmly binds these trapped grains.

However, most calcareous macroalgae deposit material physiologically in intimate association with the cells or thallus surface. The two proposed mechanisms of skeletal deposition are: (1) cellular metabolic processes (which have yet to be elucidated) and (2) removal of carbon dioxide and bicarbonate during photosynthesis, thereby raising the carbonate ion concentration to levels where precipitation occurs. There are several empirical discrepancies with this latter proposal. One is the fact that calcified and non-calcified algal species live side-by-side in nature. In this regard, Lewin (1962) has pointed out that an alternative to questions as to why certain forms calcify and others do not, is the unanswered question: Why don't all marine algae calcify? Secondly, the presence of uncalcified but photosynthetic areas, as joints or flex-points in some of the erect and heavily-calcified algae, is difficult to explain if photosynthetic precipitation is the sole mechanism invoked. A third point is that calcification in the absence of light has been shown (Goreau, 1963; Stark, Almodovar and Krauss, 1969) for several species of macroalgae.

SITES OF PHYSIOLOGICAL ACCUMULATION

The possible zones of deposition (Fig. 1) vary greatly among algae belonging to different taxonomic groups (see Table 1). Only the coccolithophorids (primarily

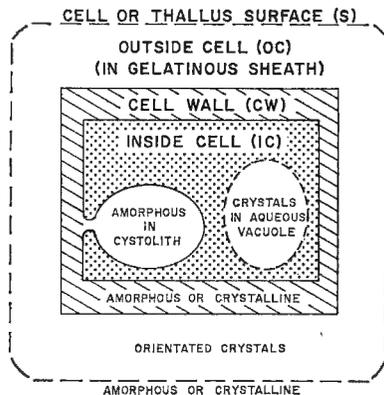


Fig. 1. Diagrammatic view of the four regions (IC, CW, OC, S) of calcium carbonate deposition in algae. (modified from Arnott and Pautard, 1970)

phytoplankters) show deposition inside the cell proper. Nostocales and Cryptonemiales (mostly coralline algae) are the only groups having deposition associated with the cell wall or its organic sheath. Caulerpales, Dasycladales, Charales, Nemaliales, Nostocales and Cryptonemiales deposit calcium carbonate both intercellularly and on the thallus surface. The Gigartinales and Dictyotales that calcify do so only in the latter position.

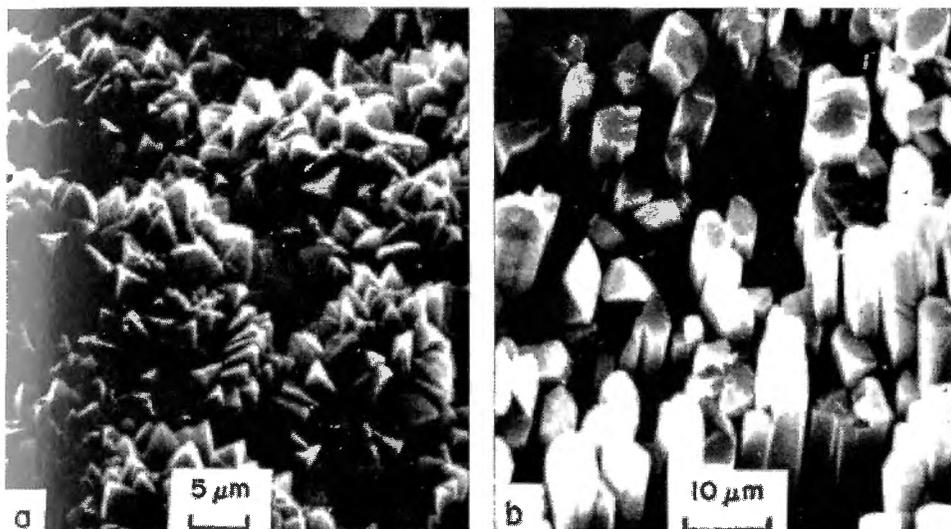


Fig. 2. Scanning electron micrograph of calcite crystals (a) and aragonite needles (b) from reef rock. (from Ginsberg and Schroeder, 1973; photograph by J. H. Schroeder)

Table 1. Calcium carbonate mineralogy and distribution among living algae.

Divisions and Orders	Generic Examples	Mineralogy	Depositional Site*
CHRYSOPHYTA (Golden browns)		Calcite and Aragonite	IC
Coccolithophoridales	<i>Coccolithus</i>		
CYANOPHYTA (Blue greens)		Calcite and Aragonite (?)	OC & S
Nostocales	<i>Oscillatoria, Schizothrix</i>		
CHLOROPHYTA (Greens)			
Caulerpales	<i>Halimeda, Penicillus</i>	Aragonite	S
Dasycladales	<i>Neomeris, Acetabularia</i>	Aragonite	S
CHAROPHYTA (Charophytes)			
Charales	<i>Chara, Nitella</i>	Calcite	S
RHODOPHYTA (Reds)			
Nemaliales	<i>Liagora, Galaxaura</i>	Aragonite	S
Gigartinales	<i>Titanophora</i>	Aragonite	S
Cryptonemiales	<i>Corallina, Porolithon</i>	Calcite	CW & S
PHAEOPHYTA (Browns)			
Dictyotales	<i>Padina</i>	Aragonite	S

* See Fig. 1 for symbols.

MINERAL FORMS DEPOSITED

In algae, crystalline calcium carbonate (Fig. 2) 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 (magnesianite) is often incorporated (7 to 50 percent of the skeleton by weight) into algal calcite (Moberly, 1968), while magnesium hydroxide (brucite) has been reported for *Goniolithon* (4-5 percent) by Weber and Kaufman (1965). The faster the growth rate of the alga (Moberly, 1968), the greater the percentage of magnesium. Strontium carbonate (strontianite) is incorporated to a relatively greater extent in aragonite (up to about 3 percent).

Table 1 gives the distribution of mineral forms among the taxonomic groups. Most calcareous species (*i.e.*, Cryptonemiales) deposit only calcite while Rhodophyta other than Cryptonemiales, all Chlorophyta and Phaeophyta deposit only aragonite. Although not well established, it appears that most members of the Cyanophyta and Chrysophyta deposit calcite while some may deposit aragonite. Cloud (1965) has pointed out that in freshwater supersaturated with calcium carbonate, calcite is physically the most likely form to be precipitated, while in seawater aragonite is more likely to precipitate. As noted by Borowitzka *et al.* (1974), the occurrence of mineral forms among those algae with only surficial deposition (Table 1) accords with those predictions. In the exceptional groups, that is the marine algae that deposit calcite (Coccolithophoridales and Cryptonemiales), it is likely (Borowitzka *et al.*, 1974) that the organic matrices at the sites of deposition (Table 1) control the specific precipitation of calcite.

EXTENT OF CALCIFICATION AMONG MACROALGAL TAXA

By far, the majority and the most heavily calcified of the calcareous species (Table 2) belong to the family Corallinaceae (order Cryptonemiales) of the red algae. The green algae rank next in number of calcifying species, while the brown algae contain only one genus (*Padina*) with calcification.

Table 2. The approximate numbers of genera and species of calcareous marine macroalgae and their distribution among major taxonomic groups (modified from Dawson, 1966).

Major Groups	Approximate No. of genera	Approximate No. of species	Mostly Tropical (X) or Temperate (O)	Mostly Heavily (H) or Lightly (L) Calcified
CHLOROPHYTA				
Caulerpaceae	5	46	X	L
Dasycladales	6	43	X	L
RHODOPHYTA				
Nemaliales	7	142	X	L
Cryptonemiales	35	443*	X-O	H
Gigartinales	1	6	X	L
PHAEOPHYTA				
Dictyotales	1	25	X	L

* over 400 of these are coralline algae.

It should be mentioned that a number of marine algae act to destroy the skeletal calcium carbonate deposited by calcifying forms (Table 2). The commonest of these are certain blue-green algae (see Nadson, 1900; Purdy and Kornicker, 1958). Schroeder (1972) recently described the boring activities of the green alga *Ostreobium* in Bermuda. This organism is interesting in that its filaments, after penetrating the reef rock, deposit skeletal magnesium calcite by means of two precipitative cements. An unidentified alga from Hawaii, melobesioid C (Littler, 1973a), may represent such a rock borer among the Rhodophyta.

MORPHOLOGICAL STRUCTURE OF CALCAREOUS MACROALGAE

There are three basic growth habits (Fig. 3) among macroalgae that calcify (*i.e.*, crustose, erect and filamentous). The crustose epilithic habit is restricted to the red algae, primarily the Peyssonneliaceae (formerly Squamariaceae) and Corallinaceae of the Cryptonemiales. There are three crustose forms (Fig. 3): those developing branched excrescences, forms with unbranched excrescences (knob-like) and those lacking excrescences altogether.

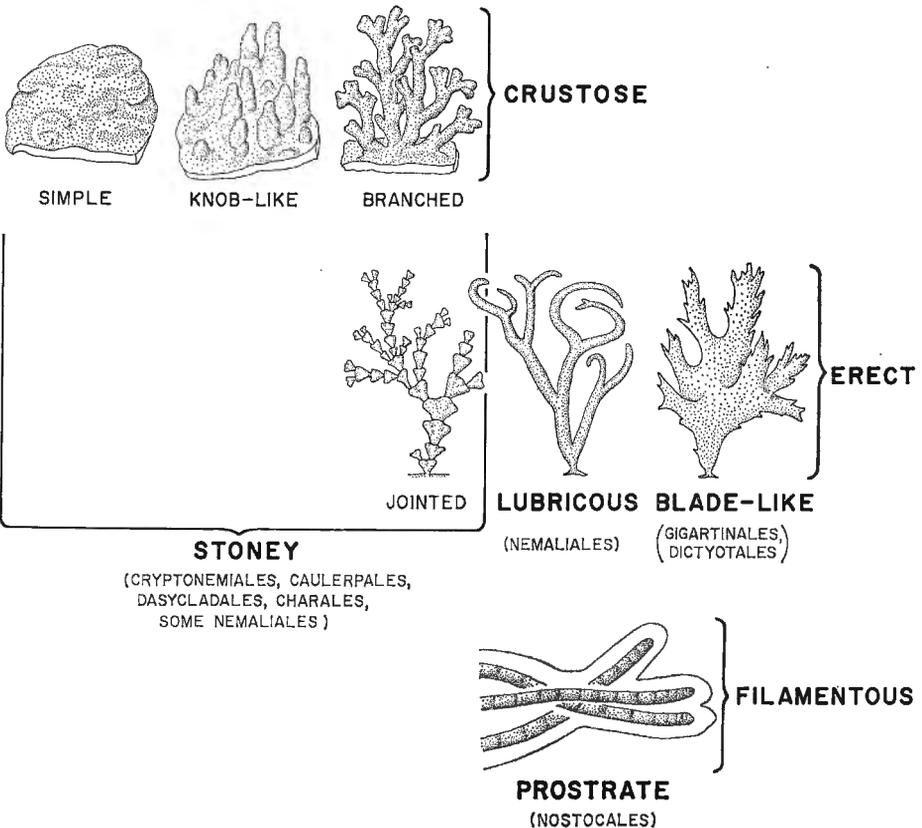


Fig. 3. The growth habits characteristic of calcifying macroalgae.

The erect habit (Fig. 3) includes both rigid (stoney) and non-rigid forms. If rigid, then jointed segments typically are present, as in the cases of *Corallina* (Rhodophyta), *Halimeda* (Chlorophyta) and *Chara* (Charophyta). If non-rigid, the thalli tend to be soft and lubricous, as in *Trichogloea* (Rhodophyta), or bladelike, as in *Titanophora* (Rhodophyta).

The filamentous habit occurs only in the calcified Cyanophyta. None of the living marine blue-green algae are known to possess physiological mechanisms of calcification (Wray, 1971), but numerous freshwater forms, particularly thermophilic species, characteristically show physiological accumulation of calcium salts.

Distribution and Ecology of Calcareous Macrophytes

GLOBAL DISTRIBUTIONAL PATTERNS

The abundance of calcareous algae is correlated to some extent with the concentration of dissolved calcium carbonate in seawater. Calcareous organisms, in general, are most abundant in tropical waters (Table 2), which are supersaturated with calcium carbonate. This saturation decreases towards the poles due to lower temperatures and a higher partial pressure of carbon dioxide. An exception to the above distributional rule is the occurrence (Foslie, 1895; Kjellman, 1883) of massive calcareous banks of crustose coralline algae in very cold sub-polar waters. It is also noteworthy (Golikov *et al.*, 1973) that the relative dominance of calcareous macroalgae over reef-building corals in the western tropical Pacific increases from the equator toward the subtropics and in the west-to-east direction, perhaps as a function of temperature.

HABITATS OF MAJOR GROUPS

The predominant habitats of the tropical marine groups of calcareous macroalgae are diagrammatically represented in Figure 4. The coccolithophorids are mainly open ocean micro-phytoplankters of tropical and sub-tropical warm waters.

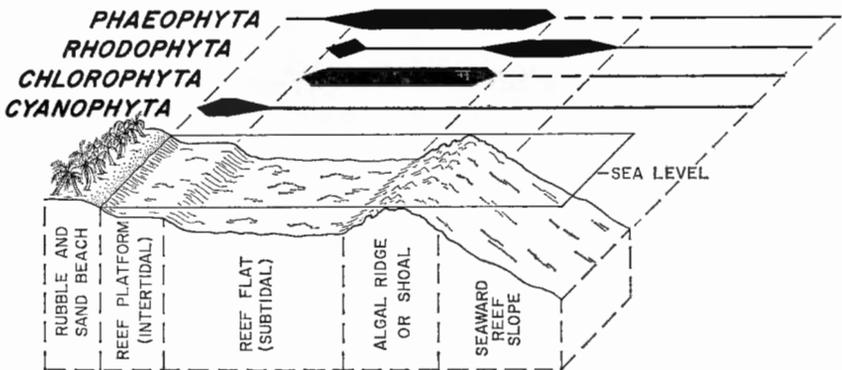


Fig. 4. The predominant habitats of the tropical marine divisions of calcareous macroalgae.

The calcareous Rhodophyta (Fig. 4) occur intertidally and subtidally down to at least a hundred meters (commonly in turbulent areas on rocky substrates) in sub-polar to tropical waters. The calcifying marine Chlorophyta predominate mainly in the tropics in protected shallow areas on soft bottoms. Blue greens (Cyanophyta) are most important on upper intertidal and tidal-flat habitats in tropical and temperate seas, while *Padina* (Phaeophyta) is principally a tropical to sub-tropical reef-flat genus that extends subtidally to moderate depths.

ECOLOGICAL RELATIONSHIPS

There are very few detailed surveys (see review by Littler, 1972) dealing with the ecological roles of calcareous algae and only several assessments that have tested environmental cause and effect relationships. Reasons for this scarcity (Littler, 1972) would seem to be taxonomic problems and a lack of applicable high-resolution field techniques. Consequently, our ability to utilize the extensive fossil record has been severely limited. Of the modern studies, the most numerous are the distributional assessments in the tropical Atlantic (see for examples, Stockman, Ginsberg and Shinn, 1967; Land, 1970) dealing with the abundances of sediment-producing macroalgae. Dr. W. H. Adey and others currently are mapping the locations of algal ridges in the Caribbean and Hoek (1969) has included calcareous algae in his phyto-sociological surveys of Curaçao, Netherlands Antilles. Crustose coralline algae and the green alga, *Halimeda*, have been noted (Ginsberg, 1956) as major elements of tropical Atlantic reefs. The coralline algae are not as impressively conspicuous on Atlantic reefs as they are in the Pacific and a well-developed algal ridge, with some exceptions, is lacking. *Halimeda* is the single most abundant component of Atlantic reef sands and dominates the back reef and nearshore algal banks.

The work of Adey (*e.g.*, 1966, 1968, 1970) on Northern Atlantic crustose coralline algae has resulted in important contributions. Adey and MacIntyre (1973)

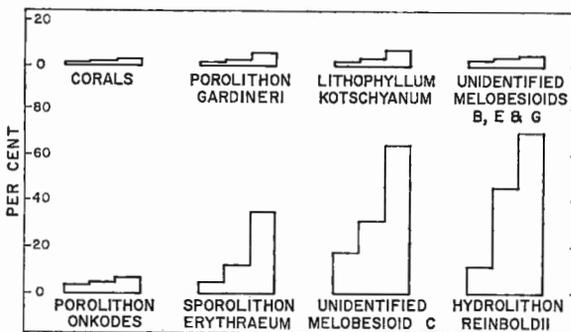


Fig. 5. The mean standing stocks of the major reef builders over the entire Waikiki, Hawaii, fringing reef study area. In each histogram cover is given in the left column, relative density (percent of total thalli sampled) by the middle column, and frequency (percent of samples in which a given species was present) by the right column. (modified from Littler, 1973a)

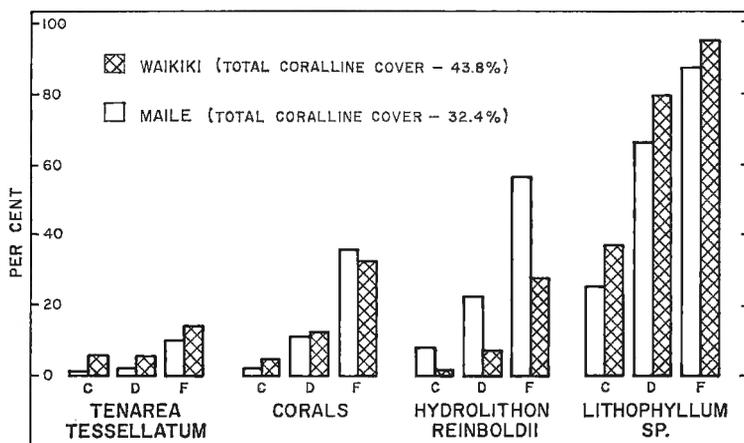


Fig. 6. The mean standing stocks, in terms of cover (C), density (D), and frequency (F), of the major deep (8–28 m) reef builders over the entire study areas at Waikiki and at Maile, Hawaii. (modified from Littler, 1973b)

observed that light and temperature were primary factors controlling the distributions of north-temperate crustose corallines. Work in Hawaii (Littler, 1971, 1973a, 1973b, 1973c) on the distributions, communities and productivity-ecology of reef-building organisms has revealed a predominance of crustose coralline algae on both fringing reef (Fig. 5) and deep-water reef (Fig. 6) habitats. It has been documented (Littler and Doty, 1975) that biotic factors (such as competition and grazing) as well as abiotic factors (for instance light and wave shock) are instrumental in controlling the development and structure of fringing reef systems.

Roles and Physiology of Calcification

The adaptive significance of skeletal carbonate in algae is not well understood. Obvious hypothetical functions include:

- (1) Mechanical support—Upright forms might be favored in competition for light and nutrients.
- (2) Persistence under abrasive stress—For example, Southern California coralline algae persist and predominate (Nicholson and Cimberg, 1971) in intertidal areas where human trampling is high.
- (3) Resistance to wave shock and grazing—Littler and Doty (1975) presented experimental evidence that herbivore grazing and the shearing forces of waves, by removing frondose algal competitors, are critical in maintaining *Porolithon onkodes* and *Lithophyllum kotschyianum* as dominants (Fig. 7) on the seaward margins of fringing reefs.
- (4) Protection against fouling epiphytes—There are published electronmicrographs (Bailey and Bisalputra, 1970) that clearly show rapid erosion and sloughing-off of the calcified outer layers of *Corallina officinalis*, *Corallina*

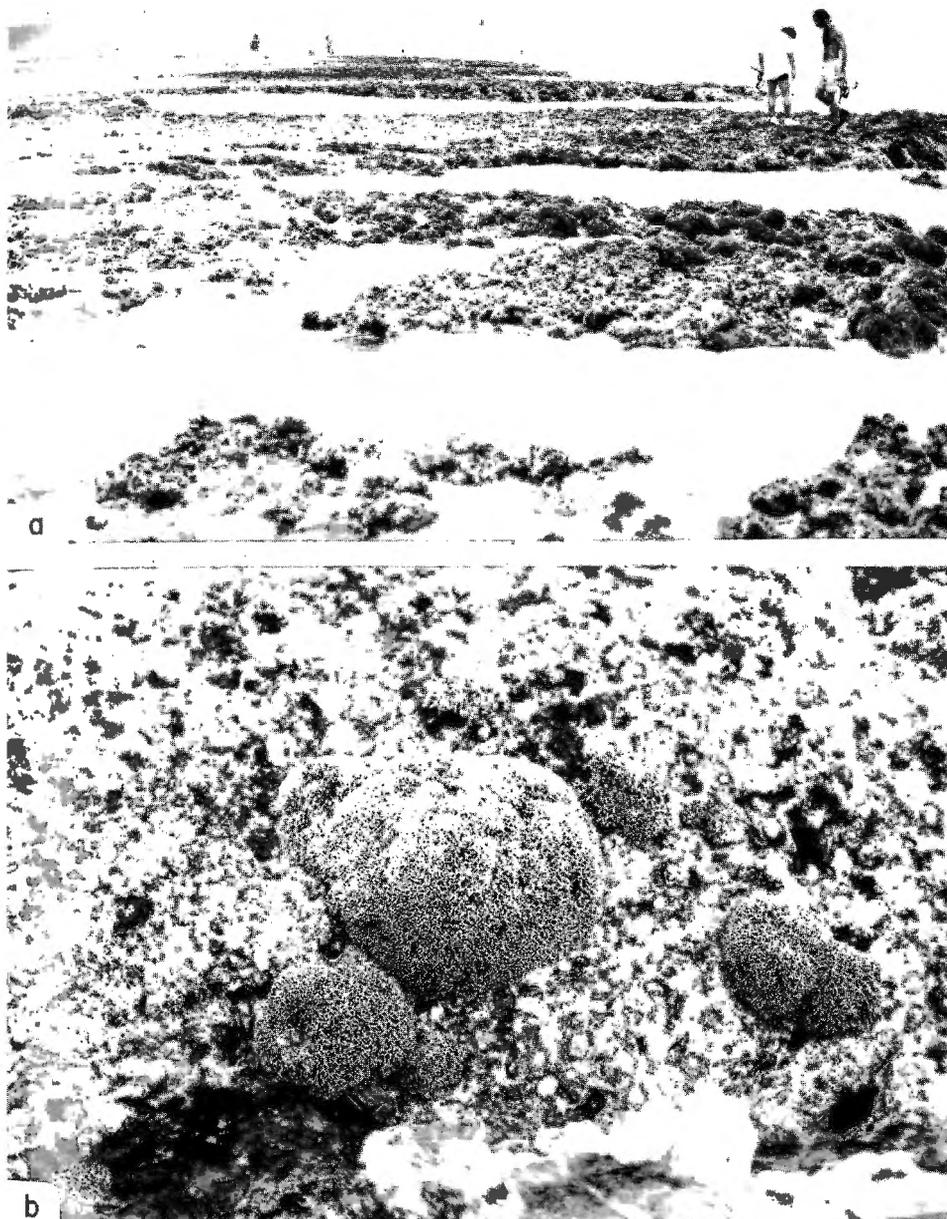


Fig. 7. Illustration (a) is a view of the *Porolithon*—*Lithophyllum* dominated algal ridge in Guam. Note the hemispherical heads of *Lithophyllum* on the leading edges of the ridge buttresses in areas of very high wave shock. Illustration (b) shows a closer view of several *Lithophyllum* heads surrounded by *Porolithon onkodes*. Note the large numbers of herbivorous limpets on the *Porolithon*.

vancouveriensis, *Bossiella dichotoma* and *Calliarthron tuberculosum* that may function much in the manner of some antifouling paints used on boat hulls.

- (5) Protection against intense light—The genus *Porolithon*, among Hawaiian crustose coralline algae, is unique in being able to withstand light intensities above 12,000 ft-c without photo-destruction (Littler, 1973a). However, interpretation of the calcareous matrix as a protective light screen is speculative because a similarly heavily-calcified coralline, *Sporolithon erythraeum*, was shown to be shade adapted.

The physiological mechanism(s) of calcification remain a major problem in tropical reef biology. The current thinking is that calcification and photosynthesis are often interrelated, but that the idea of carbon dioxide uptake causing calcium carbonate precipitation is inadequate to explain the relationship. In *Chara coralina*, Lucas and Smith (1973) demonstrated that segments of the internodal cells extrude hydroxide ions in the presence of light and it is on these alkaline regions of the cell wall that calcium carbonate deposition occurs. The coccolithophorids have been examined in greatest detail and show involvement of the Golgi apparatus and very high light/dark ratios in calcification rates. Some Rhodophyta and Chlorophyta exhibit twice 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, Almodovar and Krauss, 1969; Ikemori, 1970; Böhm and Goreau, 1973). It would seem, at least in *Bossiella* (Pearse, 1972), that the rate of calcification might be stimulated by translocated photosynthetic products which serve as structural components or energy sources rather than simply by the ionic changes surrounding ongoing photosynthesis. Böhm and Goreau (1973) concluded that calcification in *Halimeda opuntia* results from two opposing processes; both calcium uptake and calcium release were shown to be biological processes and part of the alga's metabolism.

There has been a longstanding debate (*e.g.*, Howe, 1912; Crossland, 1938; Setchell, 1926) concerning the relative importance of the various groups of calcareous organisms to tropical reef ecosystems. Biologists have stressed the importance of biotic standing stocks (usually in subjective terms) and geologists have emphasized data gathered from sediment and drilling measurements. By using both approaches, the scientists (Finckh, 1904; David, Halligan and Finckh, 1904) of the Funafuti Atoll expeditions helped to elucidate the relative roles of the various builders. The order of importance of reef-forming organisms in contributing to reef bulk at Funafuti was as follows (Finckh, 1904): crustose coralline algae, *Halimeda*, foraminifera and corals. Numerous deep drillings into reefs, subsequent to those at Funafuti [*e.g.*, Bikini Atoll (Emery, Tracey and Ladd, 1949); Eniwetok Atoll (Ladd *et al.*, 1953); Midway Atoll (Ladd, Tracey and Gross, 1967)], have substantiated clearly the importance of calcareous algae as bulk producers and builders of biotic reefs.

Most reef ecologists have not directed their efforts towards determining the functional roles of the organisms present. Particularly lacking is a calcification-

rate parameter, and as a result, little correlation has been noted between standing stock analyses and the remaining skeletal deposits after grazing, export and resolution have occurred. To date, the only studies on calcification rates in macroalgae have been the works of Goreau (1963), Doty (1960), Ikemori (1970), Smith (1973), Pearse (1972) and Littler (1973c) on coralline algae; and several studies (e.g., Stark *et al.*, 1969; Böhm and Goreau, 1973) on *Halimeda*. Until recently, only Goreau (1963) and Ikemori (1970) used radioactive tracers to measure primary production and calcification simultaneously; however, because of their particular experimental designs the data are not easily relatable to either standing stock or sedimentological studies.

Littler (1973c) attempted to determine the total carbon and calcium budgets (Table 3) for four crustose coralline algae and one unidentified rockboring rhodophyte (*i.e.*, Melobesiod "C") that may or may not prove to be referable to the Corallinaceae. A number of methods were used simultaneously on the same thalli which included Winkler oxygen titrations, dissolved oxygen electrodes and pH electrodes—to measure total organic carbon production, ^{14}C —to measure particulate organic and inorganic carbon production and ^{45}Ca —to measure calcification. The pH and oxygen data (Table 3) yielded virtually identical results and, although the ^{14}C data for total carbon were somewhat higher, all of the methods indicated the same serial order from highest to lowest producer.

There was a notable discrepancy between the expected weight ratio of calcium to inorganic carbon ($\text{CaCO}_3=3.3$ to 1.0) and that measured during experimental fixation (an average of about 1.0 to 1.7). Several untested alternatives that might partially explain the variance are: (a) the possibility of an uptake mechanism that allows the deposition of carbonate in some form other than calcium carbonate, (b) a daily or seasonal uptake periodicity independent of photosynthesis or (c) a

Table 3. The mean gross productivity (above light saturation) of four important corallines and an unidentified rhodophyte on the Waikiki fringing reef in mg Ca or C cm^{-2} (of thallus) $\text{min}^{-1} \times 10^{-4}$; determined by the ^{14}C , ^{45}Ca , O_2 and pH-electrode techniques simultaneously. Confidence limits are given at the $P=0.05$ level and the number of experiments is in parentheses (from Littler, 1973c).

	^{14}C			^{45}Ca	pH	O_2
	Inorg. C	Org. C	Total C			
Melobesiod "C"	(2) 1.10±1.21	(2) 0.43±0.38	(2) 1.52±0.59	—	(2) 1.76±3.88	(2) 1.57±2.54
<i>Sporolithon</i> <i>erythraeum</i>	(4) 1.48±0.41	(4) 0.97±0.35	(4) 2.45±0.42	(4) 1.40±1.01	(10) 2.72±0.38	(9) 2.25±0.39
<i>Hydrolithon</i> <i>reinboldii</i>	(8) 2.22±0.33	(8) 1.64±0.33	(8) 3.86±0.51	(8) 0.93±0.50	—	—
<i>Porolithon</i> <i>onkodes</i>	(12) 3.22±0.64	(12) 0.70±0.17	(12) 3.92±0.62	(12) 1.86±0.90	(15) 3.28±0.36	(12) 3.23±0.47
<i>Porolithon</i> <i>gardineri</i>	(2) 4.56±0.44	(2) 1.60±0.19	(2) 6.15±0.64	(2) 1.89±1.65	(2) 4.90±0.95	(2) 3.75±1.37

large internal exchange of inorganic and organic carbon. Relevant to the first point (a) is the finding (Moberly, 1968) that as much as 50 percent substitution of magnesium carbonate for calcium carbonate can occur during periods of rapid growth in coralline algae. This changes the expected ratio to 1.7: 1.0, an improvement but still different from the measured values. Perhaps bearing on the problem are observations by Dr. P. S. Dixon (personal communication) as well as by myself that some coralline algae, while growing well in laboratory cultures saturated with calcium carbonate, take on a non-calcified texture.

Another issue concerns the use of pH to estimate organic production in calcifying systems. The pH in seawater exposed to calcifying algae changes in response to calcification/solution reactions as well as in response to photosynthesis/respiration reactions, while oxygen changes reflect only the latter. Because coralline algae contain about as much inorganic as organic carbon, it would seem likely that inorganic carbon should represent a large portion of the total fixed. However, the close agreement between pH and oxygen data (Table 3) suggests that most of the carbon dioxide changes were due to photosynthesis rather than calcification. Aside from the possibility of a strange periodicity in calcium deposition, we are left with the suggestion of a considerable exchange between the inorganic and organic carbon within the algal thalli. Related to this is the finding (Böhm and Goreau, 1973) that in *Halimeda opuntia* calcium is simultaneously deposited and remobilized in the skeleton by opposing metabolic processes. Thus, there is a flux involving large quantities of calcium returned to the seawater from the skeleton; carbon might also follow a comparable pattern of flux. The possibility of internal exchange is brought out further by manipulating the data in Table 3, as suggested by Dr. S. V. Smith (personal communication). If the columns for total carbon, ^{45}Ca and oxygen productivity (Table 3) are converted to their appropriate molar values, we can then generate a "calculated" data set for organic carbon production by taking total carbon uptake (^{14}C) minus that due to ^{45}Ca -calcification (assuming calcium to be about 80 percent of the total inorganic cation). Comparing these molar values of calculated organic carbon to the measured oxygen-derived organic carbon values, we obtain ratios of 0.9 for *Sporolithon erythraeum*, 1.0 for *Porolithon onkodes* and 1.6 for *P. gardineri*. A similar comparison of the molar values of measured total carbon (^{14}C) to oxygen-determined organic carbon yields ratios of 1.1 for *S. erythraeum*, 1.2 for *P. onkodes* and 1.6 for *P. gardineri*. The closeness of these ratios (*i.e.*, measured total ^{14}C carbon/ O_2 organic carbon and calculated organic carbon/ O_2 organic carbon) supports, or at least reemphasizes, the hypothesis of a large exchange between the internal organic and inorganic carbon pools.

Calcifying systems are only poorly known at present and our findings indicate some of the complexities involved. There are, however, several areas where future research might prove especially rewarding. For example, further attempts (*e.g.*, Smith, 1973) should be made to partition the pH changes observed into those due to calcification and those due to photosynthesis by chemically following changes in the total alkalinity of the system in conjunction with the kinds of methodology

described above (Littler, 1973c). The utilization of new analytical techniques (Böhm and Goreau, 1974) will undoubtedly result in considerable advances in precision. Also, studies of periodicity and stress effects on deposition rates should be encouraged. Perhaps biochemical approaches (e.g., Böhm and Goreau, 1973) in concert with specialized expertise from geochemistry and environmental physiological-ecology are needed to unravel the mechanisms of biological skeletal chemistry and the environmental control of reef-building processes. Until we begin to understand processes at all of these levels, it will remain difficult to make definitive statements concerning the role of macroalgae in the production of calcium carbonate.

Acknowledgments

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