

THE POPULATION AND COMMUNITY STRUCTURE OF HAWAIIAN FRINGING-REEF CRUSTOSE CORALLINACEAE (RHODOPHYTA, CRYPTONEMIALES)

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Abstract: Measurements of cover, relative density, and frequency are given for the major reef-builders on the Waikiki fringing reef. Crustose coralline algae cover 39 % of the reef surface and exceed all other organisms as the major builders and consolidators of reef materials. An unidentified coralline (melobesioid *C*) covers the greatest area (17 %), but *Hydrolithon reinboldii* (Weber-van Bosse & Foslie) Foslie (11 % cover) because of its thicker thalli and higher relative density (45 %) and frequency (68 %) values is the primary limestone former. Melobesioid *C* ranks second and *Sporolithon erythraeum* (Rothpletz) Kylin (6 % cover) third in relative importance. *Porolithon onkodes* (Heydrich) Foslie (3 % cover), although shown by its low density (4 %) and frequency (6 %) to have a comparatively restricted distribution, is more important than *P. gardineri* (Foslie) Foslie (2 % cover). *P. onkodes* maintains and provides the surf-resistant reef edge and is, therefore, of great ecological importance. Coelenterate corals cover less than 1 % of the total area and are relatively unimportant on the fringing reef. The hypothesis is developed that the high ratio (200 : 1) of crustose corallines to corals at Waikiki may be partly due to increases in eutrophication.

Experimental evidence shows that *P. onkodes* can withstand intense illumination and is thereby unique among Hawaiian crustose Corallinaceae. *Sporolithon erythraeum* is more typical of other crustose corallines since it is physiologically adapted to low-light habitats.

INTRODUCTION

Although many have recognized the abundance of tropical crustose corallines, information concerning their ecology consists mainly of rather subjective observations. This work was concerned with the quantitative ecology, biology, and rôle of Hawaiian reef-builders, with emphasis on causal environmental relationships. A review of the literature on crustose Corallinaceae has appeared (Littler, 1972) and that which is pertinent to the present study is discussed here.

It was Foslie (1907) who first pointed out that, although crustose corallines are the dominant components of tropical reefs, the number of species is small and each occurs in great abundance. It has been firmly established (Foslie, 1907) that in great areas of the Indian and Pacific Oceans, three or four species (*viz.*, *Neogoniolithon frutescens*, *Porolithon onkodes*, *P. craspedium*, and *P. gardineri*) are the important reef-builders in littoral and shallow sublittoral zones. Lemoine (1940) and Johnson (1954) indicated that *Porolithon* and *Goniolithon* (including *Neogoniolithon*) are essentially tropical genera. According to Johnson (1963), most of the recently described species of *Sporolithon* (as *Archaeolithothamnium*) occur in the tropical Pacific, Indian Ocean, Red Sea, and Mediterranean Sea. The notable lack of ecological data concerning the crustose Corallinaceae was stressed by Lee (1967) who noted that these algae are the major components of nearly all atoll reefs.

The first measurements of crustose-coralline cover were carried out by Pollock (1928) on fringing and fossil reefs of Oahu Island, Hawaii. Pollock's results showed that corals were subordinate to crustose-coralline algae in all of the living (2.9 % coral and 4.6 % coralline) and fossil (24 % corals and 44 % coralline) reefs examined. He found the reef edge of leeward Hawaiian fringing reefs to be characterized by both encrusting and compact, branching corallines. Other forms that develop as free nodules (*Hydrolithon reinboldii* almost certainly) were found in depressions, behind the outer reef front, where they are occasionally rolled about (Pollock, 1928).

Most information about the substrata on which tropical crustose corallines grow consists merely of collection records. Ladd (1950) observed that crustose-coralline algae, as well as other reef organisms, generally require a solid bottom for attachment. On the other hand, Johnson (1963) has suggested that broken fragments from some of the saxicolous species often continue to grow unattached. Many crustose-coralline species show no substratum preference, growing equally well on any solid material (Johnson, 1954).

There are no published reports of temperature as a causal factor in tropical crustose-coralline biology, other than at a phytogeographical level. Studies in the North Atlantic (Adey, 1964, 1966, 1968, 1970a) have demonstrated that temperature is one of the most important factors determining regional and local distributions of temperate crustose corallines. Detailed records of temperature were provided by Edmondson (1928) for the nearshore surface waters of the Waikiki fringing reef. He concluded that temperature was a relatively unimportant factor in respect to corals in this habitat because the annual extreme variation of the surface water only 30 m from shore was 10 °C and this became much less towards deeper water.

There are no studies of pollution effects on crustose-coralline algae, although Dawson (1958, 1959, 1965) has observed that species of such genera of articulated coralline algae as *Bossiella*, *Lithothrix*, and *Corallina* occurred in nearly pure stands within 25 to 50 ft of sewage outfalls in southern California. In habitats known to be little affected by sewage (Dawson, 1959, 1965), the articulated Corallinaceae were an inconspicuous component of the flora.

No one has studied the development of tropical crustose corallines with respect to light on more than a casual basis. That some crustose corallines are adapted to habitats of low light energies has been implied. The report of David, Halligan & Finckh (1904) of a thin crust living at depths of at least 400 m indicates crustose corallines can grow where light energy must be slight. The ability of red algae to grow under conditions of reduced light has been postulated as possibly due to the presence of phycoerythrin, which enables them to use blue light in photosynthesis (Strain, 1951); this interesting possibility has never been investigated in the crustose Corallinaceae.

In the present work new information has been collected in the field to improve a set of working hypotheses, and experiments have been made to test some of them.

The area selected for study is a section of reef from the War Memorial Natatorium

at Waikiki Beach, Oahu Island, outward for 280 m to just beyond the surf. At this site, the seasonal changes and productivity of the non-crustaceous algae have been extensively monitored (Doty, 1971) during 1967–68. This habitat is a fringing reef typical of populated, tropical high islands, and calcium carbonate deposition results mainly from abundant crustose-coralline growth.

METHODS

STANDING STOCK SAMPLING PROCEDURES

Because reliable techniques for measuring crustose-coralline standing stocks were lacking, special methods have been devised, including a photogrammetric technique used with a line-intercept procedure; this was used on the Waikiki fringing reef during the summer of 1968 (Littler, 1971): 121 stratified-random photo-samples were taken, along with 840 m of intercepts. These are shown in Fig. 1 of the paper by Littler (*loc. cit.*).

Some experimental work was done using variations in primary productivity as an index to the organisms' response to environmental factors, particularly light and temperature. Replicate measurements were made using O₂- and pH-electrode techniques to determine the productivity of the fringing-reef species. Duplicate samples of 3–5 small fragments of freshly collected crustose coralline were placed in specially constructed Plexiglas chambers containing Millipore-filtered (0.45 μ m pore size) sea water. The two chambers were placed in a water bath situated over identical, modified (*i.e.*, so as to run at lower temperatures) magnetic stirring motors in a Percival photoperiod incubator running under pre-determined light and temperature programs. The rate of stirring was set and the chambers were allowed to equilibrate for about one hour before beginning the experiments. All the sea water used was from a single batch that was collected just shoreward of the algal ridge and immediately filtered. The recording was begun at the same time each day so as to minimize the effects of possible periodicity. Dissolved oxygen and pH were monitored in the duplicate chambers for a 1 h dark period to measure respiration. At the end of the dark period, the lights were turned on and the above parameters were followed for 2 h. The area of the algal samples used was subsequently measured. The dissolved oxygen readings (parts/million) were converted to changes in carbon (mg/unit area/unit time) by standard methods (Strickland & Parsons, 1968), assuming a photosynthetic quotient of one (glucose metabolism). The method for conversion of pH changes to changes in carbon dioxide concentrations was that described by Beyers *et al.* (1963).

The experimental procedures, outlined above, were designed to test hypotheses derived empirically from observations of the algal-ridge corallines in nature. The effects of turbulence on productivity were determined by running magnetic stirrers as fast as possible without having the stirring bar jump out of phase with the motor's magnet and as slow as the stirring bars would run. The effect of temperature on

productivity was measured at 24° and 27 °C. Experiments to measure light intensities in relation to compensation and saturation points, photo-inhibition, and photo-oxidation were made at 450–12,000 ft-c; sunlight, fluorescent and incandescent lights, and layers of nylon neutral-density cloth all being used to vary the intensity over the ranges experienced by the algae in the field.

RESULTS

VARIATIONS IN COVER

Although a complete systematic analysis of the crustose Corallinaceae was not intended, considerable taxonomic work has been done. Five species of crustose corallines were identified as important reef-formers in the area studied and nine others were recognized taxonomically but are relatively unimportant as reef-builders.

The total % cover of the major calcium-carbonate producers on Waikiki reef is given in Fig. 1. Corallines constitute 38.9 % of the surface area, the rest of the bottom is mostly dead reef, sand, and rubble. On the fringing reef an unidentified form, designated here as melobesioid C, has the greatest cover (17.0 %) followed by *Hydrolithon reinboldii* (Weber-van Bosse & Foslie) Foslie (10.6 %), *Sporolithon erythraeum* (Rothpletz) Kylin (5.7 %), *Porolithon onkodes* (Heydrick) Foslie (3.0 %), and *P. gardineri* (Foslie) Foslie (1.8 %). Coelenterate corals cover less than .0.2 %.

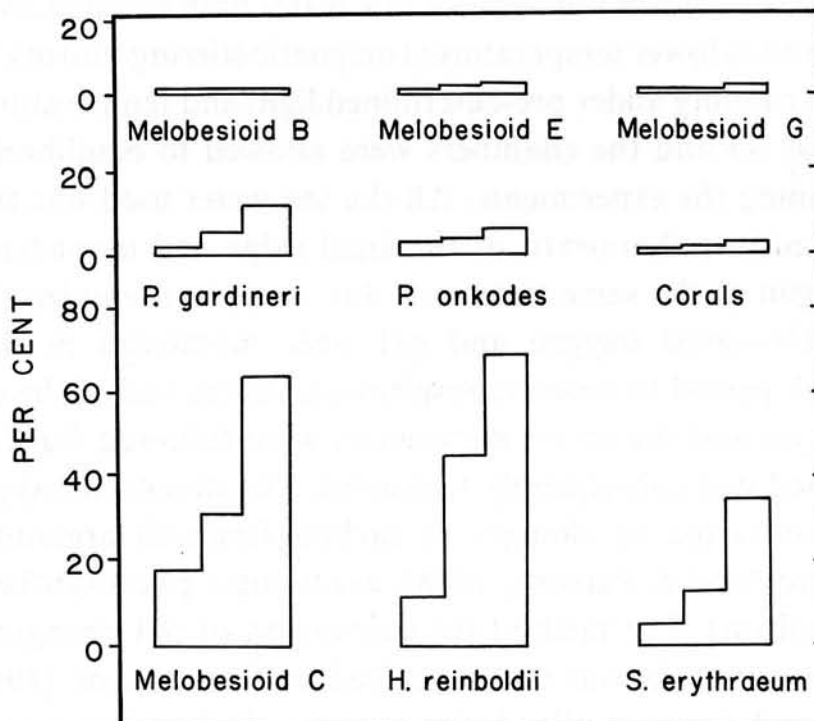


Fig. 1. The mean standing-stock of the major reef-builders over the whole Waikiki fringing-reef; in each histogram cover is given by the left column, relative density (% of total thalli sampled) by the middle column, and frequency (% of samples in which a given species was present) by the right column.

unidentified crustose corallines, designated here as melobesioids *B*, *E*, and *G*, were present but together covered $\approx 1\%$ of the total area.

Figs 2–6 show the distributional patterns of the crustose corallines, all plotted on the same scale. Melobesioid *C* (Fig. 2) is the most abundant coralline on the shallow reef flat, appearing as a very thin crust which penetrates the dead reef rock. This species disappears beyond the ridge as the depth increases from 7 m. *Hydrolithon reinboldii* grows either as a crust or as rounded nodules. It shows three coverage peaks on the reef flat (Fig. 3), reaches a maximum (23.0%) just before the crest of the ridge, and then decreases in abundance with depth, extending to a depth of 20 m. *Sporolithon erythraeum* (Fig. 4) shows cover maxima (up to 10.6%) on the shallow reef flat which coincide with dense stands of *Sargassum*. It develops best as a crust on the lower surfaces of reef slabs or in otherwise shaded spots. This species was not found growing in full sunlight, or below a depth of 7 m. The major species in the

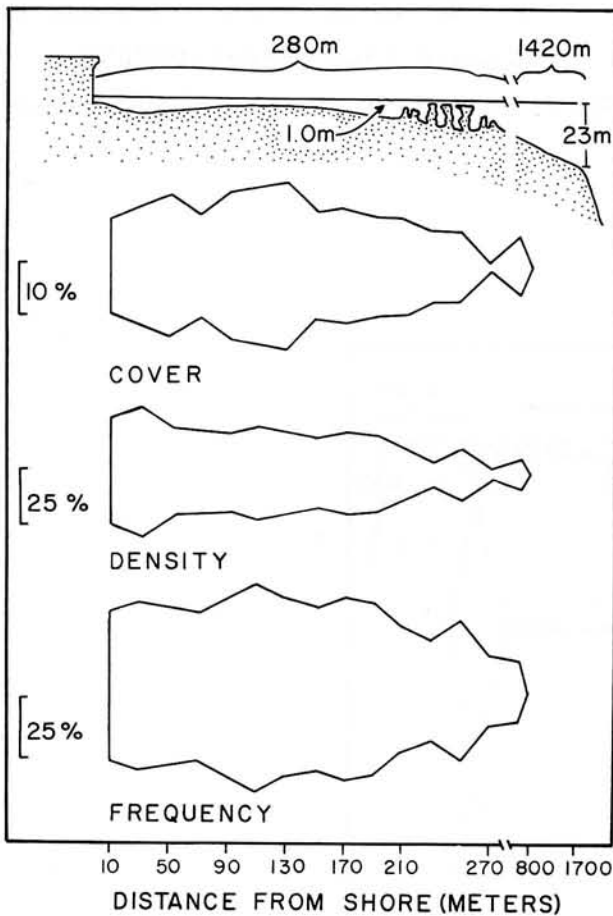


Fig. 2. Standing stock of melobesioid *C* in terms of cover, relative density, and frequency patterns extending across the fringing reef at Waikiki and offshore to a distance of 1.70 km: uppermost illustration is a bottom profile running from the Waikiki Natatorium 280 m across the shallow reef flat through the ridge: from here the scale changes and the last portion represents 1420 m, ending at a depth of 23 m.

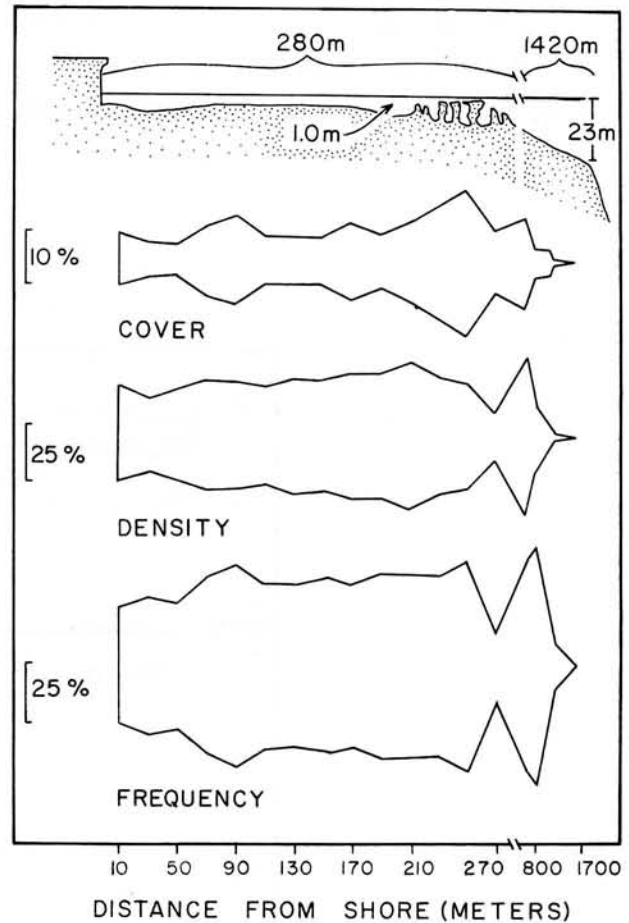


Fig. 3. Standing stock of *Hydrolithon reinboldii*; see Fig. 2 for details.

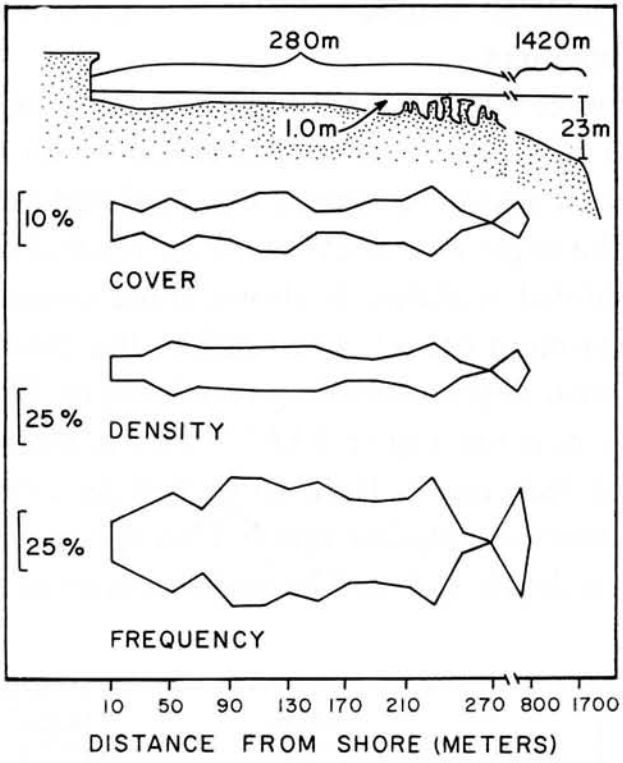


Fig. 4. Standing stock of *Sporolithon erythraeum*; see Fig. 2 for details.

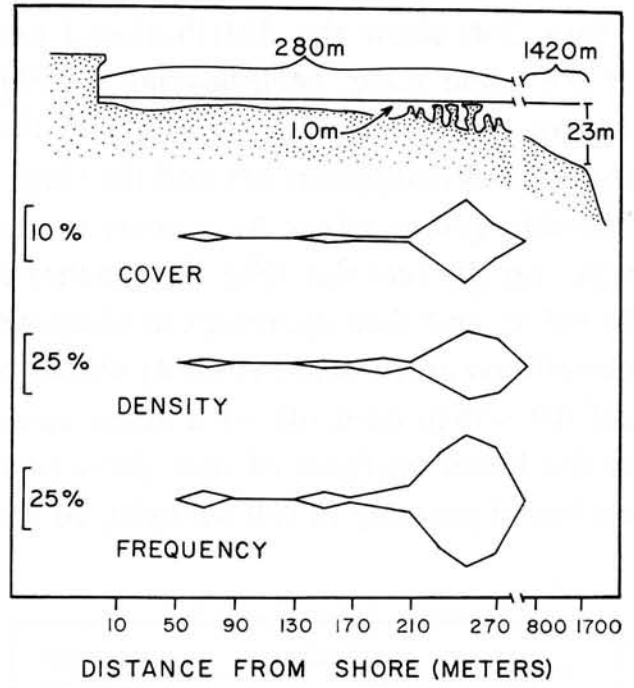


Fig. 5. Standing stock of *Porolithon gardineri*; see Fig. 2 for details.

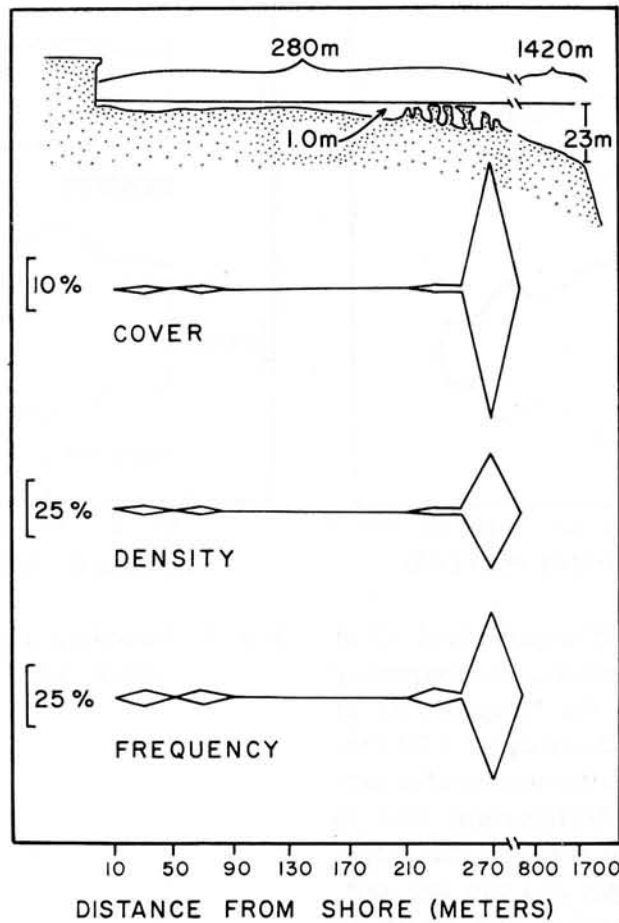


Fig. 6. Standing stock of *Porolithon onkodes*; see Fig. 2 for details.

crest portion of the algal ridge (Fig. 5) is *Porolithon gardineri*. This highly-branched alga is largely responsible for the heads and rugged aspect of the area of greatest surf action and seems to be restricted to habitats exposed to surf. *Porolithon onkodes* (Fig. 6) appears very abruptly as a thin crust (several mm thick) on the heavily-grazed seaward slope of the algal ridge. This species is quite massive (several cm thick) where the ridge extends above mean low water: it was not found below a depth of 5 m. The productivity and ecological relationships of both *P. gardineri* and *P. onkodes* are treated in detail by Littler & Doty (1973).

VARIATIONS IN RELATIVE DENSITY

The mean relative densities of the major reef builders are given in Fig. 1. Relative densities of individuals of each species were calculated for each zone from the average of the photo-samples (and intercepts) as a percentage of the total thalli sampled.

Hydrolithon reinboldii shows the highest mean relative density (44.7 %) followed by melobesioid *C* (30.9 %), *Sporolithon erythraeum* (13.7 %), *Porolithon gardineri* (5.4 %), and *P. onkodes* (3.7 %). Coelenterate corals have a mean relative density of 0.7 % and the unidentified melobesioids *B*, *E*, and *G*, while present, comprise less than 1 % of the total thalli sampled. The density distributions have been plotted (Figs 2–6). Melobesioid *C* (Fig. 2) occurs in greatest density (54.2 %) nearer the natatorium; the numbers of thalli decrease across the reef flat, increase slightly in the area of heavy surf, and then disappear 0.80 km offshore at a depth of 13 m. *Hydrolithon reinboldii* (Fig. 3) dominates the Waikiki shallow reef flat with consistently high values (44.7 % mean density). Thalli of this species decrease markedly in the algal-ridge zone and then attain a peak density (67.7 %) 0.60 km offshore at 7 m in depth. It decreases rapidly in relative density from a depth of 7 m and finally disappears at a depth of 23 m, 1.68 km offshore. The density pattern for *Sporolithon erythraeum* (Fig. 4) shows several fluctuations. There are relatively few thalli of this species next to the natatorium and in the zone just shoreward of the algal ridge, with a low density (6.2 %) in the crest of the algal ridge and just beyond. This species then increases in numbers of thalli at 0.60 km offshore (16.1 %) and disappears 0.80 km offshore at a depth of 13 m. The patterns for the relative density distributions of both *Porolithon gardineri* and *P. onkodes* (Figs. 5, 6) coincide closely with those of their coverage. It should be noted that the peak in density of *P. onkodes* (48.0 %) is not as high relative to that of *P. gardineri* (28.0 %) as is the peak for coverage.

VARIATIONS IN FREQUENCY

The mean frequencies of saxicolous organisms are shown in Fig. 1. The frequencies of the major species were determined by calculating the percentages of the samples in each zone in which a particular species occurred. 100 cm of intercepts were used per sample in the case of the line-transect data. *Hydrolithon reinboldii* was the most

frequent (68.5 %) in the fringing-reef samples (Fig. 1), followed closely by melobesioid *C* (63.6 %). Subordinate to this are *Sporolithon erythraeum* (35.5 %), *Porolithon gardineri* (11.4 %), and *P. onkodes* (6.4 %). Coelenterate corals occurred in 2.0 % of the samples and the unidentified melobesioids *B*, *E*, or *G* were present in only 1.4 % of the samples.

Frequency distributions have been plotted (Figs 2–6) for the abundant limestone producers on the fringing reef. Melobesioid *C* occurs very frequently (Fig. 2) in samples (63.6 %) and shows a tendency to decrease as a function of distance from shore. This species was absent in all of the samples taken from below 7 m and beyond 0.60 km offshore. *Hydrolithon reinboldii* (Fig. 3) was present in more samples (68.5 %) than any other species from the natatorium to the algal ridge. In the algal-ridge zone the % frequency of this species decreases markedly, followed by an increase at 0.60 and 0.80 km offshore. From the peak (100 % frequency) at 0.80 km, *H. reinboldii* decreases and then is absent from samples further than 1.67 km offshore and deeper than 21 m. The frequency of occurrence of *Sporolithon erythraeum* (Fig. 4) is fairly low (16.6 %) near the natatorium, increases up to a distance of 50 m offshore (41.4 %), then decreases at 70 m offshore (28.0 %). From this point it occurs more frequently (54.0 %) and then shows another decline (34.4 %) between 170 and 210 m from shore. A maximum (53.6 % frequency) is reached just shoreward of the algal ridge, followed by a rapid decrease to 270 m offshore where it was absent. The frequency of *S. erythraeum* reaches a final peak (50.0 %), 0.60 km offshore at 7 m depth. This species did not occur in samples below 7 m nor beyond a distance of 0.60 km offshore. The frequency distributions of *Porolithon gardineri* and *P. onkodes* (Figs 5, 6) coincide with their patterns of coverage and relative density. *P. gardineri* reaches a maximum frequency (55.8 %) 250 m from shore in the area of greatest surf, while *P. onkodes* reaches a peak (71.6 %) 20 m further seaward.

VARIATIONS IN COMMUNITY STRUCTURE

The term community as used here refers to those aggregations of large and conspicuous organisms that occurred together frequently in the samples. Some communities of crustose corallines, animals and frondose algae were easily discernible in the field and others were apparent only after distributional patterns of cover, relative density, and frequency had been analyzed. These communities are characterized by their predominant organisms and are described in the succeeding paragraphs.

Melobesioid C – Frondose algal community

A most prominent shallow-reef community is one which can be classified as the melobesioid *C*-frondose algal community. Here melobesioid *C* occurs as a layer 1 to 2 mm thick entirely within a calcium carbonate substratum on 17.0 % of the fringing-reef surface. This species is found (Fig. 2) on the reef flat wherever a stable

calcareous substratum is available and where it is not overgrown by other corallines or corals. Almost all of the common frondose algae were observed attached to this coralline and no harmful effects to either melobesioid *C* or its epiphytes were apparent.

Hydrolithon reinboldii–*Peyssonelia* spp. – *Rubble community*

Aggregates of *Hydrolithon reinboldii* are found in the many sand and rubble pockets on the reef flat, together with numerous patches of *Peyssonelia* on the rounded rubble fragments. Components of this community appear capable of growing while partially buried by sand, even under anaerobic conditions. Random storms and heavy surf were seen to exert strong controlling effects on the composition and abundance of these nodules or movable organisms so that this community underwent continuous re-ordering.

Sporolithon erythraeum–*Hydrolithon reinboldii*–*Sargassum* community

This is one of the most important of the fringing-reef communities. Both *Sporolithon* and *Hydrolithon* occur in alternate layers, one on top of the other, depending upon environmental conditions. They are usually abundant (Figs 3, 4) wherever dense stands of *Sargassum* are found.

Algal-ridge communities

The *Porolithon gardineri* part of the algal-ridge community (Fig. 5) is located in the subtidal area of greater and more constant water motion and there this species commonly forms extensive crusts; however, where it grows near a surge channel or crevice, it forms branched excrescences and takes the shape of hemispherical 'heads'. The seaward margin of the algal-ridge community is an area extensively covered by a layer several mm thick of *Porolithon onkodes* (Fig. 6), which often underlies a turf of *Jania*, *Gelidium*, and scattered thalli of *Turbinaria*. The bottom is heavily grazed by fishes (Scaridae, Acanthuridae) and sea urchins, and the larger frondose algae are absent. Where the algal ridge extends above the level of mean low water it is dominated by crusts of *Porolithon onkodes* up to several cm thick, which are usually riddled by mesogastropod limpets, sea urchins, vermetid mollusks, and boring annelids. Stunted forms of *Sargassum* and *Turbinaria* sometimes grow attached to the crusts of *Porolithon onkodes*. These frondose algae are typically covered by *Ulva fasciata*. The herbivorous cowry *Cypraea caputserpentis* is abundant in this area with smaller numbers of *Cypraea maculifera*.

Coral communities

Coelenterate corals, predominantly of the species *Porites pukoensis*, *P. compressa*, and *Pocillopora meandrina*, occur as widely scattered small colonies, which also may be regarded individually as communities.

EXPERIMENTAL STUDIES

An example of one experiment using *Porolithon onkodes* is presented in Fig. 7, in which the light intensity was decreased for a period of 45 min in the middle of a 4 h run at one temperature, one rate of water movement, and one set of water conditions. The return to the basic physiological behavior after the experimental exposure period

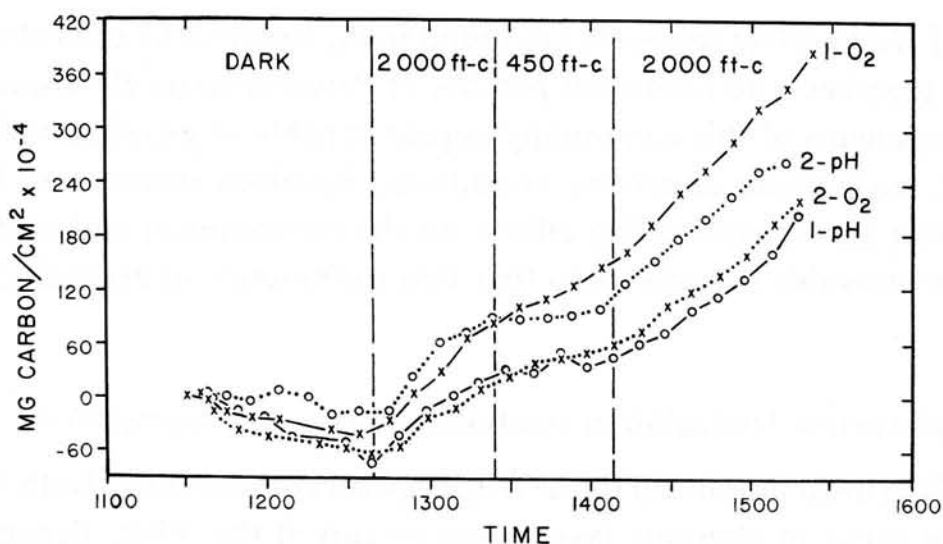


Fig. 7. The productivity of *Porolithon onkodes* at 24 °C as a function of light intensity. In Figs 7-10, 1, 2 chambers; O₂, pH, mode of measurement.

is to be noted. Such return is accepted as an indication that the stress on the alga was not too great and that the experimental conditions, including supply of materials, were not unnatural. A statistical analysis was made of each run. Every pH and oxygen set of results for the various light conditions was analyzed by correlation-regression statistics to evaluate differences in slope. The regression values were compared to determine whether there had been significant changes in productivity due to changes in light intensity.

No significant change from the initial control rates was observed for *Porolithon onkodes* following experimental periods at 450 ft-c (Fig. 7), 2000 ft-c (Figs 7, 8), and 12,000 ft-c (Figs 9, 10). The correlations of carbon fixed with time were significant at the $P < 0.01$ level during the control periods before and after the experimental light intensities (450 to 12,000 ft-c) in all of the above experiments. Above 2000 ft-c (Figs 9, 10) *P. onkodes* showed no increase in productivity.

Experiments similar to these for *P. onkodes* were run on *Sporolithon erythraeum* with very different results. All initial rates (Figs 7, 9, 10) were strongly correlated ($P < 0.01$) with time, but following experimental runs at more than 12,000 ft-c (Figs 9, 10) the correlation of carbon fixed with time was not significant ($P > 0.50$) for any of these same experiments. The correlations of carbon fixed on time were significant ($P < 0.01$) before and after an experimental period at 2000 ft-c. *S. erythraeum* showed no increase in productivity at light intensities above 1000 ft-c.

A few experiments were carried out to determine the effect of temperature and water movement on *Porolithon onkodes*. At 24 °C, *P. onkodes* showed a mean net

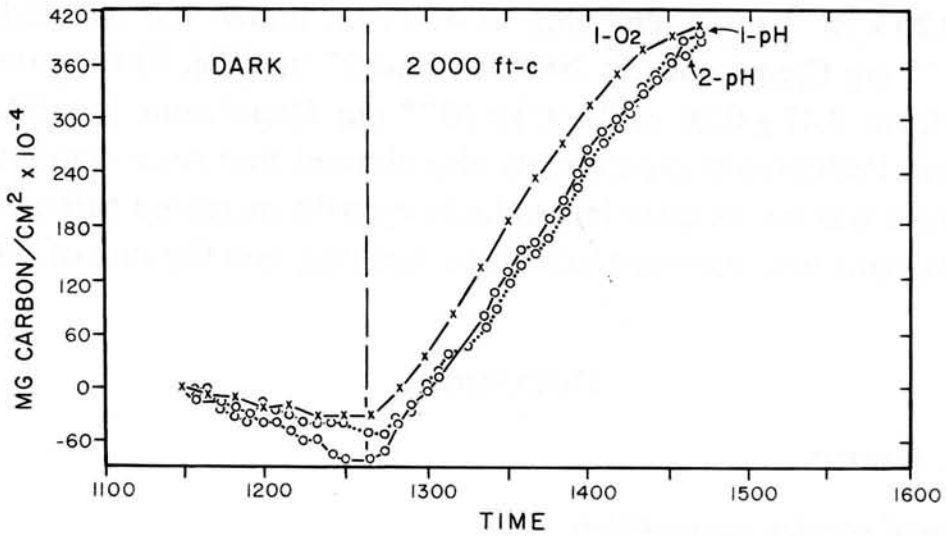


Fig. 8. The productivity of *Porolithon onkodes* at 27 °C and 2000 ft-c.

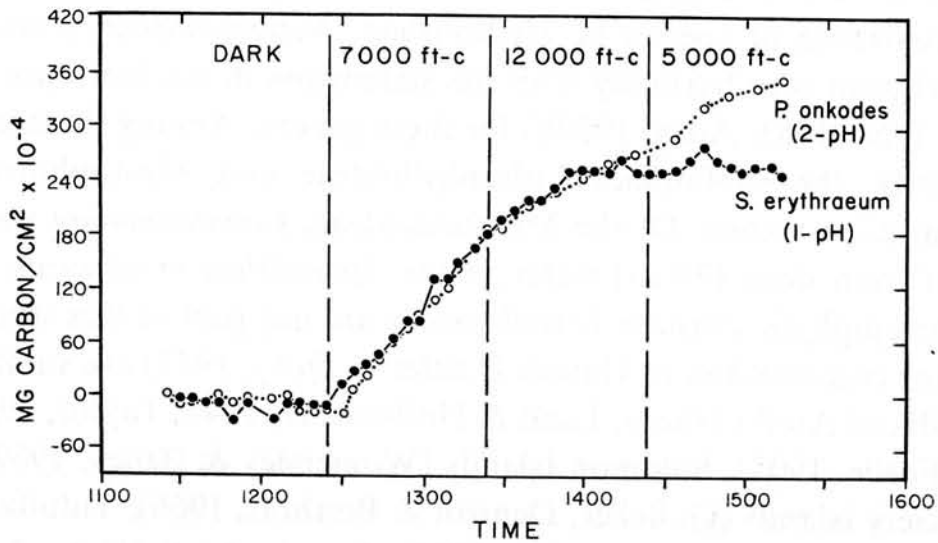


Fig. 9. Variations in the productivity of *Porolithon onkodes* and *Sporolithon erythraeum* as a function of light intensity.

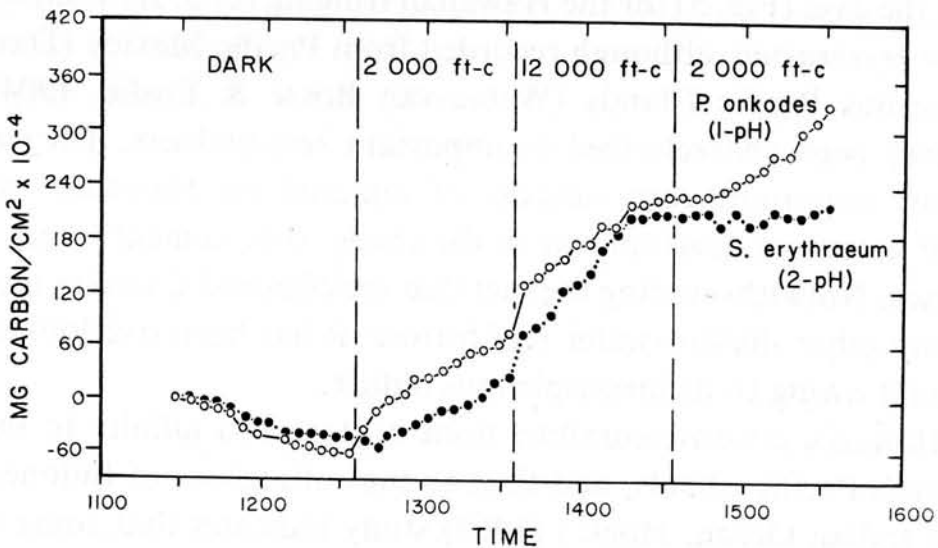


Fig. 10. Variations in the productivity of *Sporolithon erythraeum* and *Porolithon onkodes* as a function of light intensity.

rate of $1.03 \pm 0.20 \times 10^{-4}$ mg C/cm²/min at 450 ft-c; under 450 ft-c and at 27 °C, $0.96 \pm 0.43 \times 10^{-4}$ mg C/cm²/min; at 2000 ft-c and 27 °C (Fig. 8) the rate increased to 3.52 ± 0.51 (from 2.47 ± 0.26 at 24 °C) $\times 10^{-4}$ mg C/cm²/min (confidence limits at $P = 0.05$ level). Preliminary experiments also showed that once some stirring had been initiated there was no increase in productivity with increased turbulence; therefore, water movement was assumed not to be limiting and the rate of flow was not monitored.

DISCUSSION

DISTRIBUTIONAL ASPECTS

Aspects of the local species composition

The literature contains insufficient information to enable one to discuss the phytogeography of the Hawaiian crustose-coralline species in a comprehensive manner: the occurrence of species of *Hydrolithon*, *Neogoniolithon*, *Porolithon*, and *Sporolithon* in Hawaii is in harmony with the statements in the literature (Lemoine, 1940; Johnson, 1954, 1963; Adey, 1970b) for these genera. Among the non-epiphytic crustose corallines, the subfamilies Lithophylloideae and Mastophoroideae predominate in Hawaiian waters. Of the Melobesioideae, *Lithothamnium* was collected only rarely and from deep (30 m) water, while *Sporolithon erythraeum* was found abundantly. The epiphytic crustose Corallinaceae are not part of this study.

The algal-ridge communities in Hawaii (Littler & Doty, 1973) are similar to those reported from Bikini Atoll (Tracey, Ladd & Hoffmeister, 1948; Taylor, 1950), Indian Ocean Atolls (Foslie, 1907), Solomon Islands (Womersley & Bailey, 1969), Mopelia Atoll of the Society Islands (Guilcher, Denizot & Berthois, 1966), Tutuila and Tahiti (Setchell, 1926), Funafuti Atoll (Finckh, 1904), Raroia Atoll (Doty & Morrison, 1954), and Rongelap Atoll (Lee, 1967) where *Porolithon onkodes* is also the dominant organism. Most of these studies reported *P. gardineri* to be very important in the algal ridge as is the case (Fig. 5) for the Hawaiian fringing reefs. *Hydrolithon reinboldii* and *Sporolithon erythraeum*, although recorded from Pacific Mexico (Dawson, 1960) and from numerous Pacific Islands (Weber-van Bosse & Foslie, 1904; Lemoine, 1911), have never been characterized as important reef-builders. They are perhaps two of the most important consolidators of material on Hawaiian reefs where, because of their extensive development in the shade, they cement large, loose rocks to the reef surface. Notwithstanding the fact that melobesiod *C* covers more reef area (Fig. 2) than any other shallow-water reef former, it has been overlooked by earlier workers, no doubt owing to its inconspicuous nature.

In general, Hawaii's crustose-coralline flora is closest in affinity to that of other Central and South Pacific islands, and then to that of regions of Indonesia, but less like that of the Indian Ocean. Hoek's (1969) study indicates that some of the same genera, but different species from those in the Pacific, play comparable rôles in the Caribbean. The species diversity (14 taxa) on Hawaiian reefs appears to be consider-

ably greater than reported elsewhere although this is perhaps due to the intensity of this investigation.

Aspects related to standing stock

This study provides the first standing stock data for coralline algae (Figs 1–6) from measurements of cover, relative density, and frequency. Although quantitative measurements were made only on one fringing-reef area, numerous observations in the Hawaiian Islands indicate that similar abundances of the same species are to be expected where comparable environmental conditions prevail. For example, *Porolithon gardineri* and *P. onkodes* dominate the heavy-surf areas of any Hawaiian fringing reef with an algal ridge, so that these results can probably be extrapolated to most Hawaiian fringing reefs except for the geologically young areas and the patch reefs of Kaneohe Bay (a former coral-dominated area).

The communities described are clearly recognizable in the same regions at all times of the year, as evident from data collected over four years, which indicates that the fringing-reef crustose Corallinaceae are probably all perennials with their communities in a rather stable state. An estimate of the relative importance of the reef-builders may be made from the measurements of cover, relative density, and frequency, taken together. Fig. 1 illustrates the relative importance in these terms (*i.e.*, the areas within each histogram). Although melobesioid *C* (Figs 1, 2) covers more (17.0%), *Hydrolithon reinboldii* (Figs 1, 3), because of its thicker thalli and higher density (44.7%) and frequency distribution (68.5%), is the predominant builder on the fringing reef. *Sporolithon erythraeum* (Figs 1, 4) ranks third, behind *Hydrolithon reinboldii* and melobesioid *C*, in relative importance. *Porolithon onkodes* (Figs 1, 6) occurs in a comparatively restricted zone, shown by its low density (3.7%) and frequency (6.4%): nevertheless, it is more important than *P. gardineri* (Figs 1, 5) owing to its greater cover (3.0%). Its rôle in maintaining and providing the reef edge emphasizes the influence of *P. onkodes* in the ecology of tropical Pacific reefs. Crustose-coralline algae exceed (38.9% cover) all other organisms as important builders and consolidators of reef materials on the Waikiki fringing reef. Coelenterate corals and melobesioids *B*, *E*, and *G* (Fig. 1) are all relatively unimportant in the overall fringing-reef area.

While there are no previous reports of the effects of pollution on crustose-coralline algae, the photogrammetric sampling method revealed possible relationships, when the ratio of coralline to coral cover on the Waikiki fringing reef today (200 to 1) was compared with that reported by Pollock (2 to 1) in 1928. Pollock's estimates of crustose corallines were 'low' for the following reasons: first, his transects went only as deep as wading permitted; secondly, the algal-ridge organisms were inadequately sampled and; thirdly, according to his illustrations he overlooked the inconspicuous melobesioid *C* which is, therefore, not included in his estimates. The significant feature is the decrease in coelenterate coral cover on the reef flat from 4.6% in 1928 to less

than 0.2% today. Townsley (in Doty, 1968, 1969) found that some coelenterate corals (*e.g.*, *Porites compressa*) are extremely susceptible to increased phosphate concentrations, so that it seems highly probable that sewage effluent with both fecal and detergent phosphates would greatly reduce coral populations. Also pertinent in respect to the algae themselves, Dawson (1958, 1959, 1965) concluded that relative increase in cover by jointed corallines was related to increased sewage. In the photogrammetric samples at all of the sites studied, direct comparisons of the photographs, both before and after the removal of sand and silt, often show crustose corallines (*e.g.*, *Hydrolithon*) living beneath a layer of presumably bacterially-dominated, grey to black silt, which (also presumably) is rich in nutrients. Furthermore, other corallines (*e.g.*, melobesoid *E*) form a thick cover on, and near, the natatorium drain tubes where the water has long been declared unsafe for swimming because of high fecal-bacteria counts. Sewage effluents in 1941 were sufficient (Laevastu, Avery & Cox, 1964) to reach the Waikiki fringing reef. With the same sewage disposal system and the vastly increased population in Honolulu and Waikiki the effects of sewage pollution on the Waikiki biota must now be even greater. It is, therefore, suggested that the increased ratio of coralline to coral cover (200 to 1) at Waikiki, may be due in part to increases in sewage-derived phosphates.

Aspects of community structure

The interactions of Hawaiian crustose Corallinaceae and the layers formed above them by frondose algae in response to such conditions as grazing, wave action, and shading, seem more complex than those reported (Doty & Morrison, 1954; Chevalier *et al.*, 1968) from other tropical Pacific islands. This difference may only reflect variations in the scope or intensity of the investigations and may not be real. Definite patterns of zonation are evident (Figs 2-6) in the habitats studied. The present investigation shows that the zonation of branching, crustose, and nodular corallines described by Pollock (1928) still exists at Waikiki.

BIOLOGICAL AND ENVIRONMENTAL ASPECTS

Competition and grazing

Studies of sections of collected fragments frequently showed the alternate overlapping of corallines, corals, and encrusting bryozoa. From this and the standing-stock data, it seems logical that competition for space and light must be a critical factor influencing the distributions of many crustose Corallinaceae. In contrast to those forms encrusting solid bottoms, the loose nodule-forms of *Hydrolithon* and *Neogoniolithon* are moved about and typically come to rest in aggregate-filled depressions. These free nodules are doubtless capable of withstanding abrasive forces during periods of rough water and this feature enables them to exist in a habitat where other forms probably cannot compete effectively.

The crust forms of *Hydrolithon reinboldii* and *Sporolithon erythraeum* occur most abundantly in the shade and so often compete for the limited space, as was found by Weber-van Bosse & Foslie (1904) in their report on the Corallinaceae of the Siboga Expedition. Melobesioid *C* (Fig. 2) occurs principally in indirect light anywhere on the reef flat where a solid calcium-carbonate substratum is available, and where the thicker corallines (Figs 3–6) and corals are absent. This alga was never observed to grow thick enough to form crusts, so that other reef-building organisms can easily overgrow it. Its distribution is, therefore, considered to be influenced most by light, substratum, and interference from saxicolous organisms. The thalli of melobesioid *C* are so thin that it must be considered to be of little consequence as a consolidating organism.

Substratum

The substratum relationships of Hawaiian crustose corallines show *Porolithon onkodes*, *P. gardineri*, *Hydrolithon reinboldii*, and *Sporolithon erythraeum* to grow on virtually any reasonably solid substratum including glass, basalt, calcium carbonate, steel plates and pipes, concrete, and mollusc shells. Melobesioid *C* is apparently restricted to solid calcium carbonate substrata.

Temperature

There appears to be no correlation between the temperature and variations in standing stock other than with *Porolithon onkodes*. Of all the Hawaiian corallines, only this is subjected intertidally to extreme and rapid changes in temperature and it may be expected to be relatively insensitive to temperature stress. The productivity of *P. onkodes* increased slightly from 2.47 to 3.52×10^{-4} mg C/cm²/min between 24 and 27 °C. Because of the relatively small variations at Waikiki (Edmondson, 1928), temperature, except in this one case, is not considered to be a primary ecological factor on Hawaiian reefs.

Turbulence

The literature contains many statements to the effect that the abundance of crustose corallines often appears to coincide with the degree of water movement. In Hawaii the localization of *P. gardineri* (Fig. 5) and *P. onkodes* (Fig. 6) appears to be related to the proximity of surf. Pollock (1928) also found that some crustose corallines (probably the same *Porolithon* species as above) were associated with surf-battered areas. It appeared to Johnson (1954) and Lee (1967) that branching species represent adaptations to agitated water and that these species assume different growth forms in response to changes in current. Furthermore, according to Johnson, these branched forms do not occur in habitats where circulation is restricted. This is most certainly the case for *P. gardineri* in Hawaii. Nevertheless, it has been

found that other branched Hawaiian crustose Corallinaceae (*e.g.*, *Neogoniolithon frutescens* and *Hydrolithon breviclavium* Foslie (Foslie)) are not associated with highly-agitated water and assume no different growth forms as a result of greater turbulence. In Hawaiian crustose corallines, once there was some water movement there was no increase in carbon fixed with increased turbulence, and it may be assumed that water movement is not limiting under natural conditions.

Exposure to desiccation

The literature contains reports (Finckh, 1904; Adey, 1964) that intertidal crustose Corallinaceae require some means of keeping wet during periods of exposure to air. This agrees with observations on Hawaiian reefs where the intertidal *Porolithon onkodes* grows 10 to 30 cm higher on vertical rock faces during seasonal heavy surf than during the calmer periods, when it dies back, leaving bleached, white thalli as indicators of its former level of growth. Only *P. onkodes* of the crustose corallines appears able to withstand more than brief exposure to air.

Illumination

Illumination is implicated as an extremely important causal factor in the observed distributions of Hawaiian crustose Corallinaceae. The massive intertidal development of *P. onkodes* indicates that this species is capable of withstanding direct sunlight. The experimental data (Figs 7–10) show that the light saturation (2,000 ft-c) and compensation point (100 ft-c) of *P. onkodes* are relatively high and that photo-inhibition does not occur (Figs 9, 10) as a result of the highest intensities encountered (over 12,000 ft-c) in nature: Doty's & Morrison's (1954) statement regarding the special physiological nature of *P. onkodes* is, thereby, confirmed. That many crustose corallines are adapted to low light energy has been expected, particularly in the case of *Sporolithon erythraeum*. If light is a major controlling factor then *S. erythraeum* should be capable of photosynthesis in relatively dim light and be photo-inhibited by bright light. The experimental work indicates that *S. erythraeum* has a relatively low saturation (1000 ft-c) and compensation (50 ft-c) intensity. The lack of significant ($P > 0.50$) increase following experimental periods above 12,000 ft-c (Figs 9, 10) would seem to indicate that photo-inhibition or photo-destruction occurred, which is further borne out by numerous field observations where the dense cover of *Sargassum* was picked away from the underlying *S. erythraeum*; the *Sporolithon* rapidly changed from maroon to green to white, indicating death within three to four days following exposure to direct sunlight.

The results of this study indicate that Hawaiian crustose Corallinaceae are probably unsurpassed as consolidators and bulk producers and are important contributors to the overall fringing-reef primary productivity.

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