ECOLOGICAL COMPONENTS STRUCTURING THE SEAWARD EDGES OF TROPICAL PACIFIC REEFS: THE DISTRIBUTION, COMMUNITIES AND PRODUCTIVITY OF *POROLITHON*

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INTRODUCTION

The genus *Porolithon*, because of its critical role in providing an actively growing, and therefore self-renewable, reef rim, is one of the most important, land-forming tropical algae. Nearly all investigators (e.g. Gardiner 1903; Setchell 1926; Taylor 1950; Doty 1954; Doty & Morrison 1954; Guilcher, Denizot & Berthois 1966; Lee 1967; Womersley & Bailey 1969, 1970) of Indo-Pacific reefs have commented on the ecological importance of the crustose-coralline outer ridge. The efficiency of the crustose-coralline outer edge has been discussed (Tracey, Ladd & Hoffmeister 1948) insofar as its role in absorbing great amounts of wave energy is concerned.

Various environmental factors have been associated with the observed distributions of the coralline components of algal ridges. Many of these studies (e.g. Doty 1954; Johnson 1954; Lee 1967; Marsh 1970) have emphasized the extensive development of *P. onkodes* (Heydrich) Foslie on intertidal algal ridges. Doty & Morrison (1954) suggested that this species differs physiologically from other reef builders in its tolerance to heating, desiccation and sunlight in explaining the possible causes of the observed spatial dominance. Unbranched species of algal ridge corallines seem to be adapted to bright light (Doty & Morrison 1954), but Johnson (1954) believed that they could not tolerate prolonged heating or desiccation.

Distributional studies (Littler 1973a) on the reef at Waikiki revealed *Sporolithon erythraeum* (Rothpletz) Kylin and *Hydrolithon reinboldii* (Weber-van Bosse & Foslie) Foslie dominant inshore of the algal ridge and deep within it; other species dominate to the seaward (Littler 1973b). However, few studies have provided quantitative or experimental data on either the biotic or abiotic components of this zone largely because of taxonomic uncertainties, extremely rigorous surf conditions and a lack of practical measurement techniques.

The responses of *Porolithon* and *Sporolithon* in respect to light are known to vary from experiments undertaken to determine their physiological ecology. These experiments showed (Littler 1973a) that the light saturation at 1000 lm/ft^2 and compensation intensity at 50 lm/ft^2 for the reef-flat species (e.g. *S. erythraeum*) were very much lower than the values reported here for *Porolithon onkodes*. Also, for experimental runs at more than 10 000 lm/ft^2 in the case of *Sporolithon erythraeum*, there was no significant ($P > 0.05$)

linear regression between carbon fixed and time (Littler 1973a), indicating that photo-synthesis had been deactivated (presumably due either to photo-oxidation or photo-destruction).

Biological factors appear to influence the occurrence and abundance of crustose Corallinaceae. The crustose corallines at Funafuti Atoll (Finckh 1904) and elsewhere (Ranson 1955a, b) often overgrow and, as a consequence, kill coral colonies; Finckh believed this process to be essential for size increases of the reef. In agreement, Hoek (1969) reported that *Porolithon pachydermum* (Weber-van Bosse & Foslie) Foslie at Curaçao often encroaches upon corals and kills them. Further implication of direct spatial competition between encrusting coralline algae and corals was observed (Ladd 1950) from cross sections of reef that revealed an alternate overlapping of these two kinds of reef builders.

Frondose algae in Hawaiian waters, although represented by many species, are con-tinuously removed mainly by grazing fish and sea urchins. Beyond the reef flat, fish and sea urchin grazing was shown (Randall 1961; McVey 1970) to be responsible for keeping the frondose algal standing stock small. The coralline algae are also grazed, including *Porolithon* as shown by scars on its surface (Doty & Morrison 1954), but their growth exceeds the grazing losses on the reef margin. Grazing activities of sea urchins near Marseille were experimentally demonstrated (Kempf 1962) to favour the development of *Lithophyllum incrustans* Foslie although the urchins grazed on it as well. Where the *Porolithon*–coral formation is dominant on the south-west coast of Curaçao, Hoek (1969) suggested that grazing kept it a stable ecosystem, and he further supposed that under-grazing could lead to its gradual degradation. Consequently, Hoek believed the ratio of frondose algal to *Porolithon*–coral cover had potential as an indicator of fishing pressure on the herbivorous fishes.

The abundance of crustose coralline algae on the seaward edge of Rongelap Atoll led Sargent & Austin (1954) to presume that the area might have a high productivity. Their three productivity measurements of a single *Porolithon* thallus yielded rates comparable to those of corals based on weight. The first published measurements (Goreau 1963) of the rates of carbon fixation and calcium carbonate deposition for crustose corallines revealed their productivity to be less than that of other algae measured. Goreau's measure-ments were generally made using algae and other organisms brought from SCUBA depths to near the sea surface and incubated motionless in glass bottles. Recently, Marsh (1970) measured the net productivity of unidentified crustose corallines (held in aquaria several days prior to his experiments) from Eniwetok Atoll and from Kaneohe Bay, Oahu Island, Hawaii as 0.66 g C/m^2 per day. Marsh noted that among the photosynthetic reef organisms, crustose Corallinaceae, while within the same order of magnitude, had the lowest productivity of all. However, these last two authors were using techniques that may have strained the homeostatic capacities of the corallines which they studied.

Clearly, quantitative and experimental studies of the above phenomena and use of the resulting information in testing the various concepts presented is desirable if know-ledge of reef formation is to advance beyond the hypothetical stage. Therefore, the present study was undertaken: to determine quantitatively (1) the distribution and sig-nificance of *Porolithon*, (2) the possibility of *Porolithon* having a unique physiology or stress resistance in comparison to other species; to look more closely at (3) the biological interactions structuring the seaward edges of reefs and, in doing so, (4) reappraise the productivity of such reef margins.

METHODS

The distribution of *Porolithon* and the other related organisms was determined by a photographimetric technique used in conjunction with a line-intercept procedure. These field methods and their precision are fully described by Littler (1971). The work was done near the War Memorial Natatorium during the summer of 1968 in Honolulu, Hawaii. Water motion was measured with $CaSO_4$ clodcards (Doty 1971) over the same section of fringing reef.

Physiological and stress-resistance experimentation was carried out in the laboratory using special plastic chambers placed in open-topped controlled-environment incubators. A complete description of the chambers and details of the experimental design have been published elsewhere (see Littler 1973c). Light was provided by fluorescent and incandescent lights or direct sky or sunlight with and without nylon neutral-density screens for varying the illuminance over the appropriate ranges of observed field intensities. Measurements of photosynthetic and respirational rates were made using replicated oxygen and pH electrode techniques (Littler 1973a). The algae were collected immediately before use and great care was taken to introduce a minimum of variations in their environment other than those experimentally controlled. Experiments between 450 and 12 000 lm/ft^2 were made to measure light intensities in relation to compensation, saturation, photo-inhibition and photo-oxidation. Temperatures were varied with the environmental chambers, while water motion was controlled by means of teflon stirring bars activated within the plastic boxes by magnetic mixers. Light was measured by a Weston meter up to its limits, with a 50-junction Eppley pyrenometer being used to record intensity in the field.

Biological interactions were studied by recording populational changes as a function of time and other factors. Areas on the reef were cleared of their natural populations to assess the competitive interference-interactions during stages of succession. In doing so, two plots of approximately 1 m^2 each were cleared on the inshore slope of the ridge by scraping and chipping to remove all visible evidence of living materials. Two adjacent square metre plots were not cleared and served as controls. Additionally, populations were followed on eleven plate-glass panels, 13 mm thick and of about 0·25–0·50 m^2 area which were manipulated experimentally. These were initially lodged in crevices in the reef ridge for four weeks; during this time they became almost entirely encrusted on their bottom surfaces with *P. onkodes* and *Peyssonellia* spp., while their upper surfaces remained relatively free of frondose algae and other organisms. This growth was considered 'old' growth. Four 7·5-cm-wide strips of the encrusting organisms were scraped away across each panel; then the panels were placed with this strip-cleared algal side down as follows. Four were placed 1 m deep in the dense stand of frondose algae on the reef flat approximately 30 m shoreward of the ridge crest, three others were placed similarly 10 m seaward of the crest on the outer slope of the ridge, and the remaining four panels were returned to the original ridge area as controls. After approximately twelve weeks, the glass panels were re-examined and photographed for subsequent measurements of new cover on the cleared strips. Those from the reef flat had developed considerable populations of frondose algae. These reef-flat panels were then placed on the outer reef slope. Comparisons were made between the new growth and old growth in all cases after twelve weeks to verify that none of the panels had been subjected to unexpected or unusual circumstances.

The contributions of *Porolithon* to overall reef production were calculated from the physiological information obtained during the laboratory experiments.

RESULTS AND DISCUSSION

Distribution and significance of Porolithon

Over the fringing reef as a whole, from the intertidal shore to beyond the seaward margin (5 m depth), *Porolithon onkodes* and *P. gardineri* (Foslie) Foslie were found to cover, respectively, 3·0 and 0·8% of the total Waikiki reef area (Fig. 1). Dr W. H. Adey
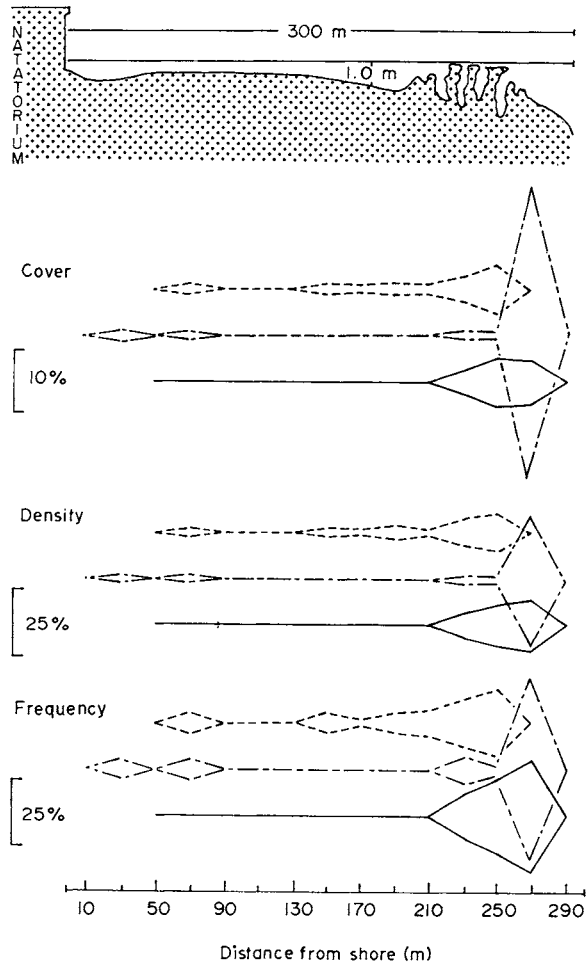

Fɪɢ. 1. The standing stocks of *Porolithon gardineri* (– – –), *P. onkodes* (— – – —) and *Lithophyllum kotschyanum* (———). The upper illustration is a bottom profile that runs from the Waikiki Natatorium 300 m across the shallow reef flat through the ridge. The cover, relative density (percentage of total thalli sampled) and frequency (percentage of samples in which a given species was present) are shown for 20-m-wide zones in relation to this profile with the scale given at the lower left.

has recently examined voucher specimens of our material and provided new taxonomic information. In two previous papers (Littler 1971, 1973a), *Lithophyllum kotschyanum* Unger and *Porolithon gardineri*, which co-occur (Fig. 1) as hemispherical heads of branched excrescences, had been included together as *P. gardineri*. Subsequent re-analysis of collections and photo-samples revealed *Lithophyllum kotschyanum* to comprise about

1·0% of the total cover of the Waikiki reef that had previously been attributed (see Littler 1971, 1973a) to *Porolithon gardineri*. *P. onkodes* and *P. gardineri*, in association with *Lithophyllum kotschyanum*, dominate the seaward margin of the reef where it is raised (Fig. 1) into a ridge of irregular columns or knees. This ridge is treated as being divisible into (a) inshore or inner slope, (b) crest and (c) seaward (or front or outer slope) portions. During the lowest tides on unusually calm days the uppermost parts of this ridge are continuously out of water for a period of minutes to perhaps an hour, but rarely more.

The two species of *Porolithon* have different distributional patterns in respect to cover, relative density and frequency. Subtidally in the crest portion (Fig. 1) of the algal ridge, *P. gardineri* (6% cover) is an important species; however, *Lithophyllum kotschyanum* is dominant. These highly-branched forms are largely responsible for the heads and rugged aspect of the area of greatest water motion (Fig. 2) and appear to be closely associated
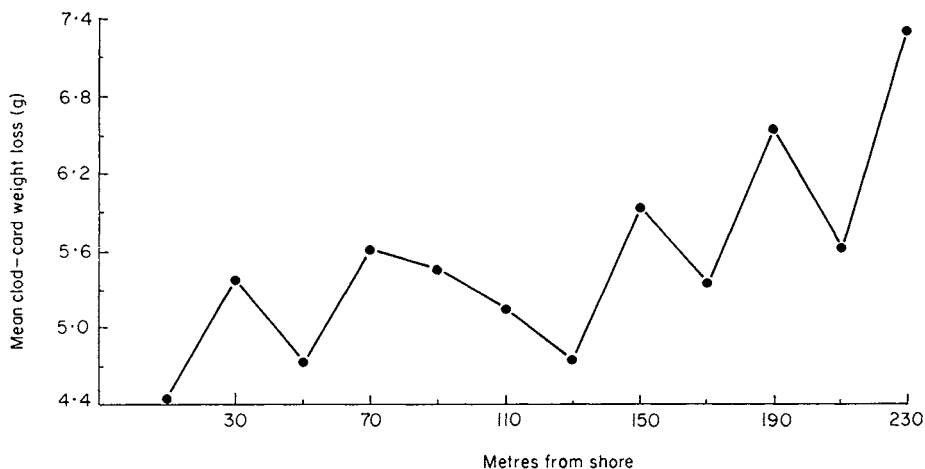

FIG. 2. The mean distribution of turbulence at Waikiki determined by $CaSO_4$ clod weight losses in grammes over 24 h during 21–22, 22–23, 28–29 and 29–30 December 1967. For 10 degrees of freedom the $P = 0·05$ confidence level for correlation (r) is 0·576; for $P = 0·01$, $r = 0·708$. Intense surf prevented the use of this technique beyond 230 m from shore.

with habitats exposed to the strongest surf action and turbulence. Measurement of water motion has not been made on this crest portion of the algal ridge but in deeper water, still further seaward, wave force and total motion on the bottom are less.

Intertidally on the crest and seaward slope of the algal ridge *P. onkodes* dominates (i.e. it has primacy in cover), with the upper portion of the columns 100% covered and its crust-like growth several centimetres thick in the area of greatest wave shock. Downward the *P. onkodes* pavement (41% cover) thins to a crust several millimetres thick and ends at about the 10 m level. At its lower edges, *P. onkodes* often underlies stunted forms of *Sargassum*; sometimes attached to the crusts are patchy turfs of *Jania*, *Gelidium* or scattered thalli of *Turbinaria*.

Commonly *Porolithon onkodes* is more widely spread over the reef than *P. gardineri*. The relative density patterns of both *P. gardineri* and *P. onkodes* (Fig. 1) coincide closely with their patterns of cover. The peak density of *P. onkodes* (48%) is not as high relative to that of *P. gardineri* (14%) as is the peak for cover. The frequency distributions of

P. gardineri and *P. onkodes* (Fig. 1) agree with their patterns of cover and relative density. *P. gardineri* reaches a maximum frequency (28%) 250 m from the shore in the area of greatest surf; while *P. onkodes* reaches a maximum (72%) 20 m farther seaward.

From the above and related standing stock data, it is possible to characterize an algal-ridge community. The *Lithophyllum kotschyanum–Porolithon gardineri* portion (Fig. 1) is exposed to direct sunlight in the subtidal area of greater and more constant water motion (Fig. 2). At similar and lower levels, patches of *Sporolithon erythraeum* and *Hydrolithon reinboldii* grow in the more densely shaded areas (see Littler 1973a), particularly under ledges or in the shade of *Sargassum*; however, *Hydrolithon reinboldii* was also found growing in direct sunlight elsewhere on the reef flat.

Because of its higher cover (3·0 %), density (3·7%) and frequency (6·4%) values, for the whole reef transect area, *Porolithon onkodes* is more important than either *Lithophyllum kotschyanum* or *Porolithon gardineri*. Its role in building and maintaining the reef edge places *P. onkodes* among the most ecologically important of the tropical crustose coralline algae.

Physiology relative to stress resistance

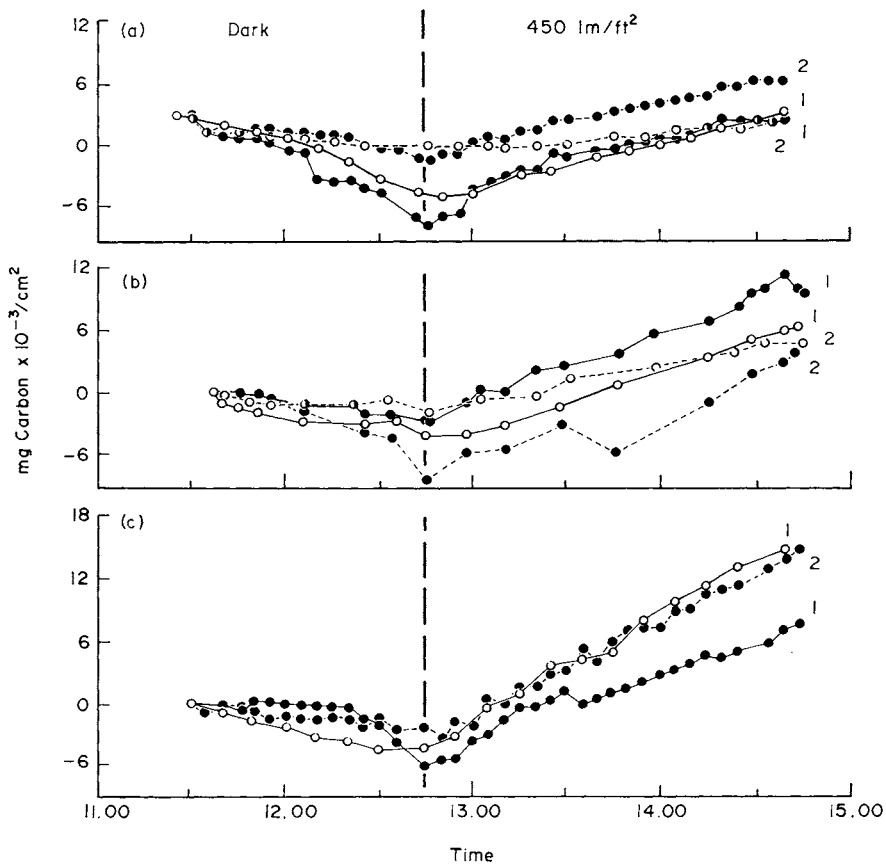The massive intertidal development of *P. onkodes* indicates that this species dominates

Fig. 3. The productivity of *Porolithon onkodes* at 450 lm/ft² (a) under 24·0° C and strong current; (b) under 24·0° C and low current; (c) under 27·0° C and strong current. 1 and 2, chamber numbers; mode of measurement: oxygen electrode, ○; pH electrode, ●.

under stress from temperature, water motion, wave force, salinity and direct sunlight. Serially these are taken up below insofar as relevant data were obtained by field observation or experimentation.

Several of the experiments done in the laboratory provided insight into the effects of temperature and water movement (e.g. Fig. 2) on the physiology of *P. onkodes*. Productivity was used as an index to the organism's response to stress and all rates given are in mg $C \times 10^{-4}/cm^2$ per min with confidence limits at the $P = 0.05$ level. At 24.0° C and strong water movement (Fig. 3a), *P. onkodes* showed a mean net rate of 1.03 ± 0.20 under 450 lm/ft². Exposed to the same light and temperature, but at the least movement controllable with the magnetic stirrers used, *P. onkodes* showed (Fig. 3b) a mean net rate of 0.96 ± 0.52. Under conditions of strong motion and 450 lm/ft², but where the temperature was increased to 27.0° C (Fig. 3c), *P. onkodes* fixed 0.96 ± 0.43. At 2000 lm/ft² and

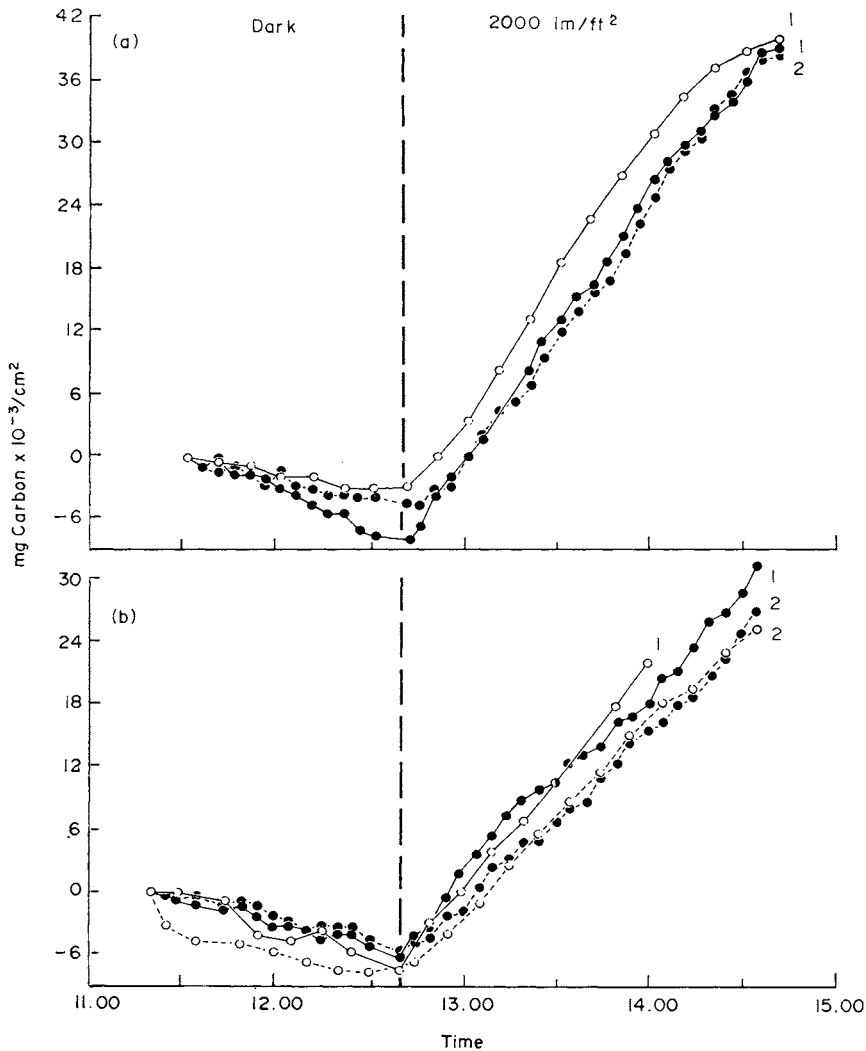FIG. 4. The productivity of *Porolithon onkodes* at 2000 lm/ft² under strong current (a) at 27.0° C; (b) at 24.0° C. Symbols are as in Fig. 3.

27·0° C (Fig. 4a) the rate increased to 3·52±0·51, from 2·47±0·26 at 24·0° C (Fig. 4b). These and other preliminary experiments showed that beyond the point of no water movement there is no increase in productivity with increased turbulence. Therefore, water movement was assumed not limiting and the rate of flow was not measured.

No evidence was seen that *Porolithon* or the other coralline crusts were inhibited by wave force. A large part of the considerable increase in turbulence near the algal ridge (Fig. 2) is due to the increasing frictional drag between wave force and the bottom. Certainly some of the loss of frondose algae on the glass panels was due to this shearing force. In support of this contention, Doty (1971) found that the larger frondose algal standing stocks were controlled on the reef flat, shoreward of the ridge studied here, as much by the turbulence produced by storms as by any of the regular seasonal factors.

The temperature ranges used are similar to those experienced in nature. While temperature was explored only in a very preliminary manner, it appeared that the warmer sun and colder evaporative cooling on intertidally exposed ridge surfaces would not inhibit the growth of *P. onkodes* seriously, although, in the results cited, a somewhat higher productivity was found when the temperature was higher.

Salinity effects were not studied *per se*, but rain and evaporation on the algal ridge crest were observed. No response on the part of either *Porolithon* species was seen in the field that could be correlated with salinity.

Study of the relationships of *Porolithon* to strong light has been most rewarding. The experimental data revealed that *P. onkodes* is light saturated at 2000 lm/ft^2, and at 100 lm/ft^2-it is above the compensation point. These levels are relatively high and it appears that photo-destruction does not occur (Fig. 5) as a result of the highest intensities en-
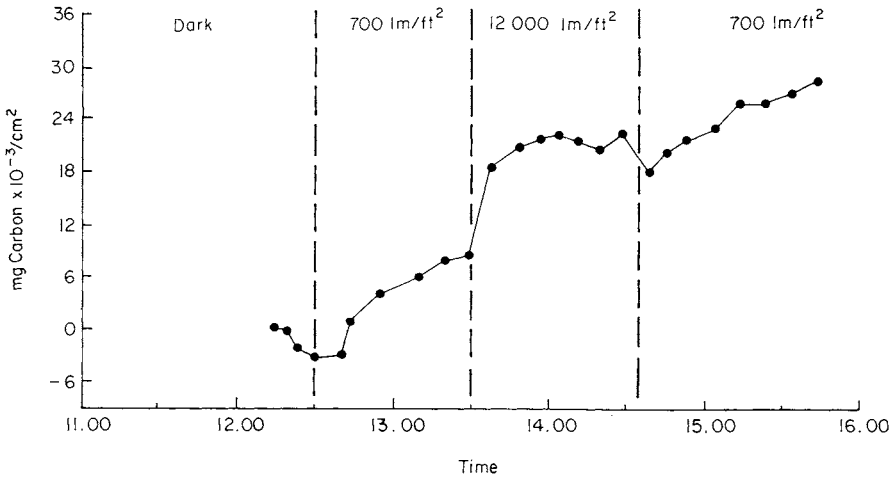

FIG. 5. An example of the productivity of *Porolithon onkodes* at 24·0° C and strong current as a function of an experimental light intensity at 12 000 lm/ft^2. Mode of measurement: pH electrode.

countered (over 12 000 lm/ft^2) in nature. *Sporolithon erythraeum*, with its lower values for these points and photo-inhibition (Littler 1973a), grows in the shadier areas and develops particularly well beneath the frondose algae shoreward where it reaches maximum abundance. Therefore, *Porolithon onkodes* is especially well suited to the algal-ridge habitat. Its responses are characteristic of an organism adapted to surviving intense

illumination and it is insensitive to the variations of the other factors measured, although the physical force of wave action may favour *P. onkodes* on intertidal portions of the algal ridge by removing or preventing establishment of the frondose algae. In this respect, the hypothesis of Doty & Morrison (1954) regarding the special physiological nature of *P. onkodes* is substantiated.

Biological interactions

The dominance of *Porolithon* on the algal ridge seems determined mainly by the effects of wave force, grazing and shading on competition between species. This was shown by various different observations and experiments in the field.

The interference component of competition between algal species is documented in the clearing experiments. *Calothrix crustacea* Bornet & Flahault was the first alga to appear in the cleared areas. In time, the *Calothrix* became covered by a thin, pink layer of *Porolithon onkodes*. *P. onkodes* showed no such development on the nearby uncleared control plots. The *P. onkodes* then thickened and embedded the *Calothrix* which remained alive. On some of this area, *Sargassum echinocarpum* J. Agardh and *S. obtusifolium* J. Agardh developed during the winter of 1969 and overgrew the *Porolithon*. Only where the *Sargassum* holdfasts encroached upon the new *Porolithon onkodes* did the coralline die. In this chain of events, it appears that light controlled the growth rates (in the case of primary substrate), with the overgrowth of other forms (secondary substrate) a major cause of the succession seen.

The most independent relationships in competition were revealed (Table 1) by the glass-panel manipulative experiment. The cleared strips became extensively repopulated after twelve weeks by *Peyssonellia* spp. (1·5% new cover) and *Porolithon onkodes* (16·2% new cover), but otherwise the four control panel populations remaining in the algal ridge area showed little change.

The four panels on the shallow reef-flat became nearly 100% covered on their upper surfaces primarily by species of *Jania, Sphacelaria* and *Padina*. The measured reduction in light intensity transmitted through this cover averaged 90%. On the lower surfaces of the panels the formerly abundant *Porolithon onkodes* clearly was reduced in cover. The patches of *P. onkodes* were mostly dead and the cleared strips showed only 4·3% new cover (Table 1). This was a steady development process. Here, inshore of the algal ridge crest, grazing was seldom noticed and shading appeared to cause the reduction of *P. onkodes* cover.

The seaward slope appears to be a most active region. Though the surface of a given ridge column or knee has a generally smooth covering of *Porolithon*, as at Raroia (Doty & Morrison 1954) and elsewhere, it may be riddled by mesogastropod limpets, sea

Table 1. *The percentage cover of new crustose growth on cleared sections of glass panels placed within different habitats (but within 40 m of each other) on the Waikiki fringing reef for twelve weeks; the mean new cover is given with confidence limits at the* P = 0·05 *level*

Organism	Algal ridge		Seaward		Shoreward reef-flat	
	Mean	Confidence limits	Mean	Confidence limits	Mean	Confidence limits
Porolithon onkodes	16·2	2·1	10·4	2·9	4·3	2·0
Dead *P. onkodes*	0·6	0·6	2·3	2·0	0·7	0·8
Peyssonellia	1·5	1·1	2·3	1·6	2·2	1·9
Glass	6·6	3·7	9·4	3·9	17·8	6·3

urchins, vermetid molluscs, boring annelids and other animals. The herbivorous *Cypraea caputserpentis* Linnaeus and *C. maculifera* Schilder, the latter of these cowries in smaller numbers, occur in this area. The bottom is heavily grazed during the day by fishes (Scaridae and Acanthuridae) and during the night by sea urchins.

When the glass test-panels were placed on the outer subtidal slope, both longer-term seral and immediate grazing processes were noted. The three panel populations placed on the outer slope for twelve weeks were like those of the control panels left in the crest area except that *Peyssonellia* (2·3% new cover) and *Porolithon onkodes* (10·4% new cover) were less deeply pigmented. When the four test-panels after twelve weeks on the inshore reef-flat were subsequently placed on the outer slope, numbers of the fishes mentioned began feeding on the frondose genera immediately; within one day nearly all algae had been removed from the exposed upper, but not the lower and much less accessible surfaces. These results demonstrate (Table 1) the tenability of the hypothesis that grazing excludes frondose algal competitors for space and, thus, light.

Obviously the absence of shade obtained initially by grazing and maintained by it, led to dominance by *Peyssonellia* and *Porolithon onkodes*. *Peyssonellia* leaves no skeletal material; thus the only lasting effect is that left by the calcareous *Porolithon onkodes* on the subtidal brightly-lit reef front. Were it not for the continuous removal of frondose algae by grazing, in agreement with Randall (1961) and McVey (1970), there is little question but that the crustose forms would be overgrown in these deeper waters. Where grazing is intense, as on the reef-flat panels moved to the outer slope of the algal ridge, the role of surf action in removing the frondose algae is relatively reduced. Nevertheless, the action of surf, especially on the intertidal crest of the ridge, and grazing on the seaward slope are accepted as major ecological components resulting in little but crustose algae on the bottom. In view of the comparability of these relationships to those noted by Hoek (1969) at Curaçao, it is likewise suggested here that a ratio of the cover by fleshy algae to that by the crustose algae, on the seaward slopes of reef ridges, might be a useful index to the status of the herbivore populations.

Contrasts between seral stages and mature communities are relevant in the interpretation of the dynamic interactions of the algal-ridge ecosystem. In general, as the populations at a site approach being in equilibrium with the environment (i.e. approach the mature or climax condition) there are more species present. Removal of the mature populations results in a simpler community of fewer species as the sere leading to the climax resumes. The results of both the succession and clearing experiments support this idea. Like the seral events on newly appearing lava shores (Doty 1967), both showed the quick-growing pioneer species, such as *Calothrix* on the algal ridge as in this case and *Enteromorpha* or *Ulva* almost ubiquitously elsewhere in intertidal situations, to be replaced by crustose forms at least intertidally inshore of the algal-ridge crest. Here *Sargassum* appears to be a later stage causing the demise of such crustose forms where wave force is reduced. One may presume that, following the successful establishment of the *Sargassum* overstorey, the community would develop further spatial heterogeneity by the addition of stratified or multilayered canopies.

In the present study, wave shock on the algal-ridge crest (Fig. 2) and grazing on the outer slope appeared to result both in suppression of the frondose algae, such as *Sargassum*, and in communities with fewer species than where these factors had less effect. Thus, the ridge crest and front community can be thought of as arriving through seral events and, due to wave forces and grazing, being held in a subclimax condition. The interpretation advanced is that on the experimental panels, as in the case of the physical

damage reported by Fahey (1953) and Dayton (1971), a subclimax condition was maintained through disclimatic events. The disclimatic factors leave the hardy, more resistant species and on the reef ridge *Porolithon* species are among those that dominate. If the disclimatic factors persist, subclimax conditions result and the biologically dominant organisms may change the environment at a site over the years as happens in the algal ridge.

Production rates

The production rates for an average section of algal ridge were calculated from the percentage cover and the net primary productivity per square metre of each species on that piece of ridge. The mean net organic production rates measured under experimental conditions designed to approximate those found in nature were $3\cdot0 \times 10^{-4}$ mg C/cm^2 per min for *P. onkodes* and $3\cdot4 \times 10^{-4}$ mg C/cm^2 per min for *P. gardineri*. The estimates of the maximum contribution to the entire fringing reef ecosystem were $0\cdot5$ g C/m^2 of reef per day for *P. onkodes* and $0\cdot2$ g C/m^2 per day for *P. gardineri*.

The net productivity of the two crustose corallines ($2\cdot2$ g C/m^2 of thallus per day for *P. onkodes* and $2\cdot4$ for *P. gardineri*) lies within the range reported for other reef primary producers with the exception of the contrastingly low rates calculated by Goreau (1963) and Marsh (1970) for unidentified crustose corallines. There may be various reasons for these low rates. Goreau and Marsh probably worked with different species from different habitats and used different techniques, so that dissimilar rates would be expected.

Just shoreward of the algal ridge, the abundance of *Sporolithon erythraeum* led Littler (1973a) to measure its productivity. The results showed that *Sporolithon*, and probably *Hydrolithon reinboldii* which occurs with it, are adapted to lower light intensities, although when compared with the *Porolithon* species they yielded similar productivity values. Thus on the algal ridge in the subclimax community, other corallines are suppressed and *Porolithon* dominates where the light is brightest; in shade deep within the algal ridge or inshore of it, *Hydrolithon* and *Sporolithon* dominate.

The reduction of wave force inland from the crest of the ridge, although still violent, seems to result in the slope downward to the general reef-flat level. Such causal events as reduction of wave force permitting growth of frondose algae and their reducing, in turn, *Porolithon* dominance through shading appear to be critical. Under such circumstances, removal of material, e.g. material eroded or weakened by boring organisms, exceeds coralline production until the general reef-flat level is reached.

ACKNOWLEDGMENTS

SUMMARY

Studies on Indo-Pacific algal ridges indicate the importance of the role played by *Porolithon*. *P. gardineri* (6% cover) and *Lithophyllum kotschyanum* (7% cover) are the major species on the crest portion of Hawaiian algal ridges; *Porolithon onkodes* (41% cover) is dominant on the heavily-grazed seaward slope of the algal ridge. *P. onkodes*, because of its role in maintaining and providing the surf-resistant reef edge, is one of the most important reef-building organisms.

The evidence shows that *P. onkodes* is physiologically adapted to withstand intense illumination and physically adapted to withstand intense surf and grazing. It requires continuous disturbance which prevents its competitive exclusion by frondose algae.

The estimates of the mean net contributions to the total reef productivity were about 0.5 g C/m^2 of fringing reef per day for *P. onkodes* and 0.2 g C/m^2 per day for *P. gardineri*. The net productivities of the two crustose corallines (2.2 g C/m^2 of thallus per day for *P. onkodes* and 2.4 for *P. gardineri*) lie within the range reported for other reef primary producers.

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