

Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales)*

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The colonization, taxonomic succession and marginal growth and accretion rates of crustose corallines on artificial substrates in algal ridge and reef environments on St Croix, U.S. Virgin Islands were examined. Very thin *Leptoprolithon* and *Tenarea* species are the initial colonizers of glass and plastic plates placed in these environments. In strong light conditions, the colonizers are followed by *Neogoniolithon* and *Porolithon* species. In areas of high wave energy, where the activities of grazing organisms are greatly reduced, the climax species *Lithophyllum congestum* and *Porolithon pachydermum* are capable of building intertidal algal ridges.

The dominant coralline crusts showed marginal crustal extension rates of 0.9-2.3 mm/month and accretion rates of about 1-5.2 mm/year. Mean rates are about an order of magnitude greater than those previously measured in subarctic waters. The accretion rates are highly dependent upon the grazing activities of animals, especially parrot fish. Maximum rates in areas of minimum grazing are close to algal ridge accretion rates determined by C^{14} dating.

Introduction

Crustose coralline algae (Corallinaceae, Rhodophyta) are usually abundant in coral reef environments. In shallow, turbulent areas, they can be the dominant reef building organisms. In both the tropical Atlantic and Pacific oceans, crustose corallines build massive upper sublittoral and inter- to supra-tidal carbonate structures variously called algal rims, algal ridges, boilers, microatolls or cup reefs (see, e.g. Adey, 1975; Adey & Burke, 1975). Very few studies of algal colonization and succession on tropical shores or reefs have been undertaken (Doty, 1967; Littler & Doty, 1974). In their study of the importance of *Porolithon* on Pacific algal ridges, Littler and Doty examined the coverage of *Porolithon* and other algae on glass plates placed at various positions in a ridge system. However, the coralline species were not differentiated nor were growth rates or succession patterns determined. In this paper, we discuss the colonization and succession of corallines on artificial substrates in Caribbean coral reef and algal ridge environments on St Croix, U.S. Virgin Islands.

Studies of crustose coralline growth and accretion

rates are few (Adey, 1970; Adey & McKibbin, 1970), and virtually no *in situ* data are available for tropical waters. Goreau (1973) did obtain data on calcium accretion rates in several crustose corallines, but these are not easily converted to spatial units. We present several types of data relating to the growth, coverage and accretion rates of corallines in reef-ridge environments and discuss the effects of animal grazing on both the rates and the patterns of succession. From core-drilling and C^{14} dating, Adey (1975) interpreted the Holocene development of reefs and ridges on eastern St Croix. These actual reef accretion rates are compared with rates obtained on our artificial substrates.

The taxonomy employed in this paper is basically that of Adey & Macintyre (1973), with some generic and specific additions according to Adey (1975). *Paragoniolithon* and *Leptoprolithon* are newly described in the latter paper. The *Paragoniolithon* species are similar to *Neogoniolithon*, but the heterocysts are grouped (though not in pustulous fields as in *Porolithon*), the hypothallia are coaxial and the plants have a leafy habit. The *Leptoprolithon* species are very thin plants with a single-layered hypothallium and a perithallium that consists of a single layer or is absent. Some are strongly imbricate. Heterocyst fields are quite similar to those in *Porolithon* and the genera are apparently related. Of the species used here, *Neogoniolithon megacarpum*,

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Neogoniolithon imbricatum, *Neogoniolithon west-indianum*, *Paragoniolithon typica* and *Leptoporeolithon fragilis* are newly described by Adey (1975). *Neogoniolithon megacarpum* is a relatively smooth, flowing, well-developed crust usually yellow to light brown in colour and with highly-raised conceptacles often over 1 mm in outside basal diameter. Its heterocysts are large and conspicuous. *Neogoniolithon imbricatum*, with smaller heterocysts, is similar but with a redder colour, conceptacles 500–1000 μm in outside diameter and frequently irregularly imbricate by overgrowing. *Neogoniolithon west-indianum* is characterized by an irregular weakly-developed crust, and abundant, narrow (< 1–2 mm), irregular and generally short branches. It lacks the arcuate, peeling epithallium of the many species synonymized under *Neogoniolithon strictum*. *Paragoniolithon solubile* (Foslie et Howe) Adey is a leafy, bluish crust, speckled with white heterocyst fields and usually with scattered, raised, large conceptacles of about 1 mm in outside basal diameter. It is especially abundant on *Acropora cervicornis* thickets at 5–20 m depth. *Leptoporeolithon fragilis* is a thin crust, marginally consisting only of hypothallium and

epithallium, but quickly developing slightly-raised, discrete heterocyst fields and several perithallial cell layers. Usually the plant is an opaque pink-yellow colour similar to *Porolithon pachydermum*.

Non-coraline red crusts refer to Peyssonneliaceae (Squamariaceae) and related genera which are poorly known in the Caribbean (see Denizot, 1968).

Methods

During late 1972 and early 1973, numerous glass and polyvinyl chloride (PVC) plates were placed along transects in reef and ridge environments near the West Indies Laboratory in St Croix (Fig. 1). Several materials were tried as a substrate. Glass had too smooth a surface and the growing corallines tended to chip off when grazed. The unglazed backs of ceramic bathroom tiles worked well but were difficult to attach in rough areas. PVC that was roughened with sandpaper proved to be satisfactory and was easy to cut, drill and wire in place. Most of this study is based on the PVC plates.

Dead *Acropora palmata* is often the immediate

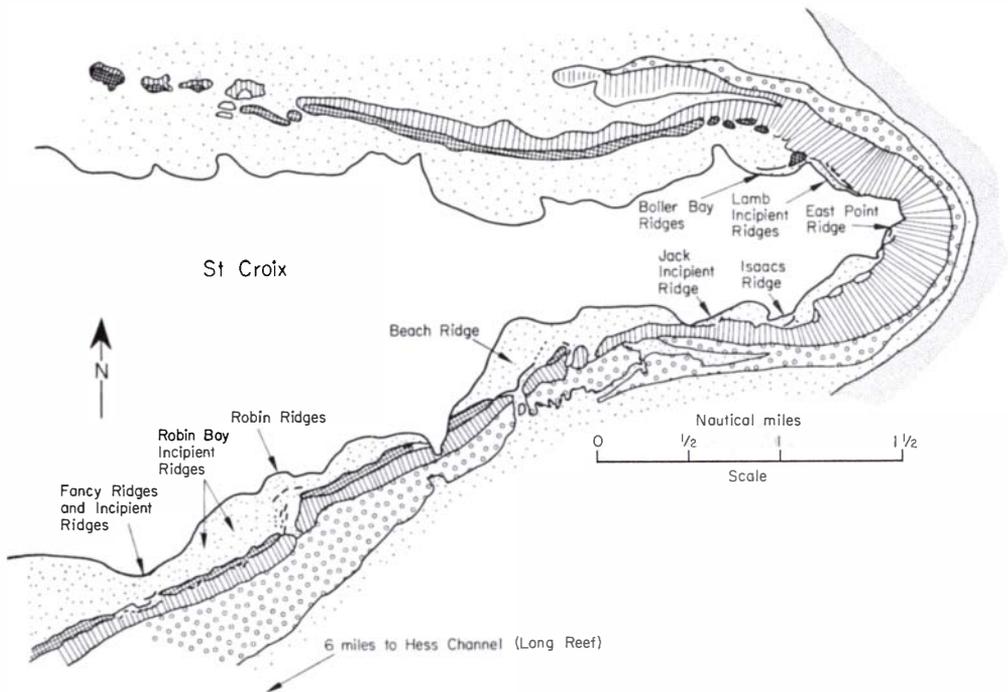


FIG. 1. The eastern end of St Croix with *Acropora palmata* reefs, reef flats, deeper fore-reef *Montastrea* and *Diploria* zones, shelf *Meandrina* hard ground, and algal ridges, sandy bottom, 4–5 m depth behind reef, 14–22 m seaward of reef (see Adey, 1974 for details).

substrate for the formation of extensive coralline pavements and probably most algal ridges on St Croix (Adey, 1975). Simulated arms of dead *A. palmata* were created by splitting in half PVC pipes of 10–12 cm diameter and 40–70 cm long and wiring these to standing arms of *A. palmata*. Our primary succession data are based on PVC pipes placed on *A. palmata* stands at depths of 0.5–1.5 m in the vicinity of the presently degenerating algal ridge in Boiler Bay on the northeast corner of St Croix. Six to twelve centimetre long sections of these PVC pipes were then removed at intervals and dried. The surface areas of all encrusting elements, remaining vacant areas and any newly dead coralline areas were then measured with clear plastic grids. We refer to these pipes as 'PVC palmata'.

Also, on the Boiler Bay algal ridges, as well as several of the south shore ridges (Fig. 1), transect series of PVC segments of 10–12 cm diameter pipe, about 100 cm², were nailed to the coralline surface. These were left in place for about a year. On the Isaac algal ridge, a series of PVC pipes 3 cm in diameter were hammered vertically into the ridge along a transect from the ridge crest to the coralline fore-ridge pavement at 1.15 m depth. These were left in place for 6.5 months. All surface coverage was measured with clear plastic grids, while rates (i.e. change in thickness) were measured directly from the PVC plates using calipers.

Marginal growth rates were obtained both by measuring the area increase of plants on the PVC pipes and also by direct measurement of plants on dead coral substrate. In the latter case, dead fragments of *Acropora palmata* and *Porites porites*, which abound on the shallow (1–1.5 m) reef flats of the northern Cruzan bank-barrier reef, were used. These were brought to the lab in buckets for short periods of time. Their surfaces were diagrammed and the distances of individual plant margins from natural or artificial reference points were measured. The coral fragments were then returned to their natural position in the reef for periods of up to several months. Fleishy and filamentous algae were present, though not abundant on the PVC palmata. Also, some of the ridge plates had considerable numbers of attached non-calcified benthic algae at the time of collection. However, these were taken into consideration only where the holdfasts were strongly enough attached or embedded in the coralline so as not to be removed with a light brushing. A small percentage (5–10%) of what we have tabulated as 'dead' surface consists of densely-spaced red algal basal filaments

and runners often packed with small carbonate fragments.

Results

The settling and succession of crustose corallines on a well-lighted, upward facing (45,000–90,000 lx) and weakly-grazed PVC palmata (surface per cent coverage of each species as a function of time for 259 days), is shown in Fig. 2. Figure 3 shows the succession pattern for a longer period (372 days), with some parrot fish grazing having occurred at about 200–260 days. On this PVC palmata some grazing apparently also occurred at about 100 days and, although 10–15% of dead coralline was present by collection at 155 days, distinct graze marks were not present.

Leptoporeolithon spp. followed shortly by *Leptoporeolithon fragilis* and a myrionematacean brown crust are the early colonizers at 20–60 days. These are then followed by *Tenarea prototypum* which tends to reach its peak of abundance at about 100 days. The three coralline primary colonizers are thin crusts of only a few cell layers, and they develop conceptacles on crusts of less than 1 cm in diameter. The *Neogoniolithon* spp. sometimes appear as scattered small plants in this early stage, but they do not become major elements, in terms of surface area occupied, until after about 100 days. In the absence of extensive grazing, the *Neogoniolithon* species, especially *Neogoniolithon megacarpum*, dominate after 100–200 days.

Typically, the initially bare or vacant surface of the PVC is covered by algal crusts by about 100 days. However, sometimes small areas of vacancy persist for considerable periods, even in the absence of obvious grazing (Fig. 3). This may result from low level grazing by small limpets on the *Leptoporeolithon* sp. The short, en echelon patterns of limpet grazing are common on thicker coralline surfaces. Apparently this usually does no permanent harm to the thicker crusts, and after only a small amount of new coralline growth, the patterns are no longer apparent. The 'dead' surface that often covers 10–50% of the PVC after 60–100 days is thicker coralline crust that has been killed, mostly by more intense grazing. However, the reason for some of this dead surface is not always apparent, and perhaps other elements such as fungal parasites are operating. *Diadema* grazing of corallines can be intense and is probably responsible for the degeneration of the shoreward ridge line at

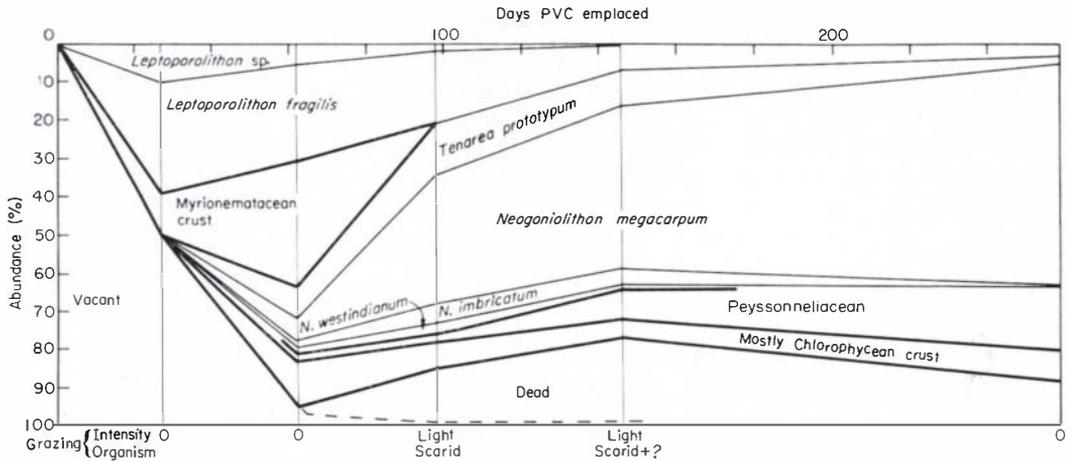


FIG. 2

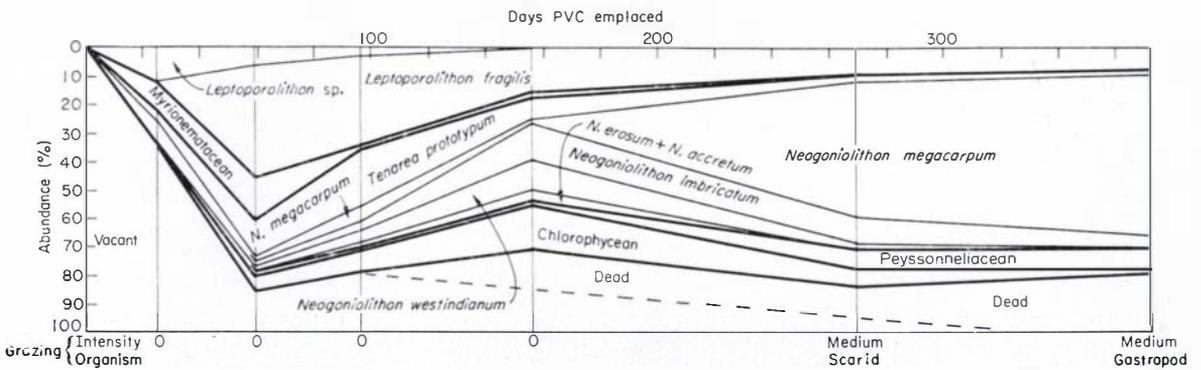


FIG. 3

Figs 2-10. Colonization and succession of encrusting organisms on PVC palmata settling arms. The vertical lines are times of collection and area measurement. The vertical axis represents total area on a PVC section with each segment being the percentage area occupied by each species or group as marked.

Figs 2 and 3. Upper or well-lighted sides of two PVC palmatas with little grazing apparent.

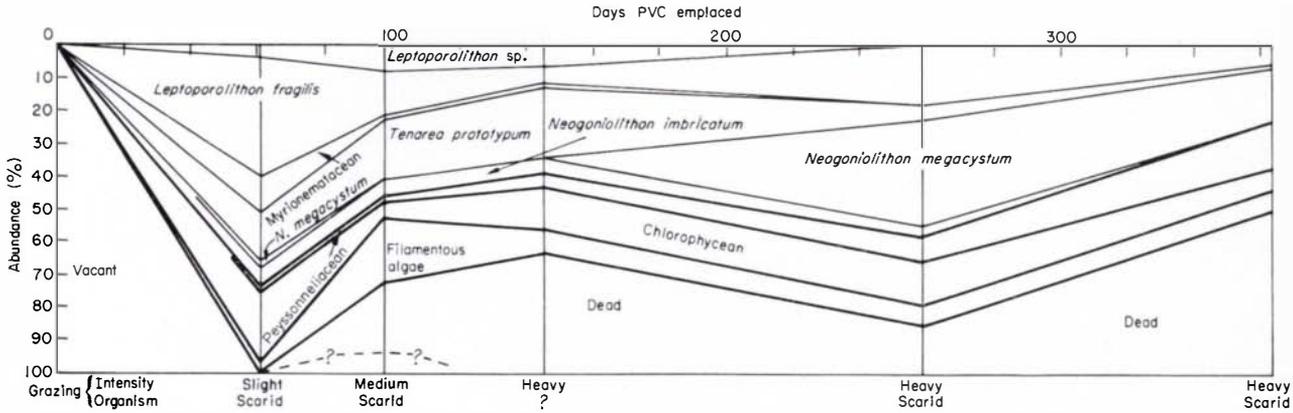


FIG. 4

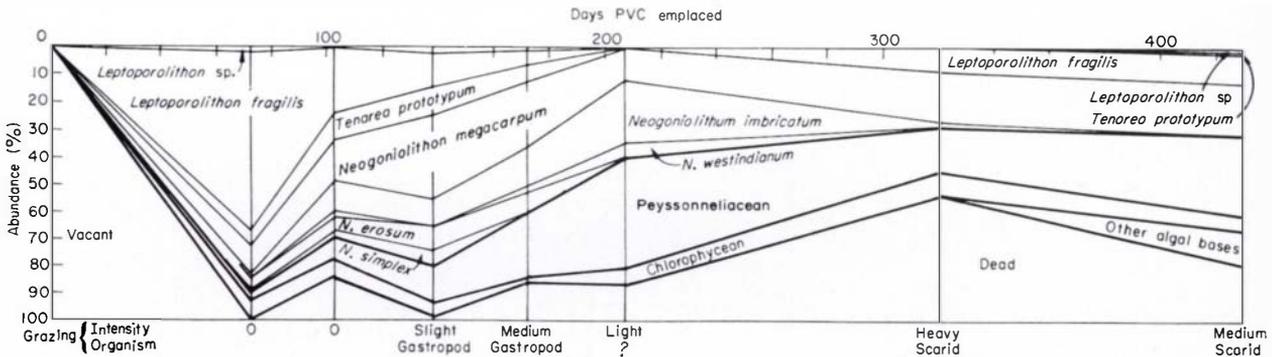


FIG. 5

FIGS 4 and 5. PVC palmata with intensive grazing on well-established crusts. The dashed lines with ? indicate the approximate amounts of vacant surface and crusts grazed to bare PVC.

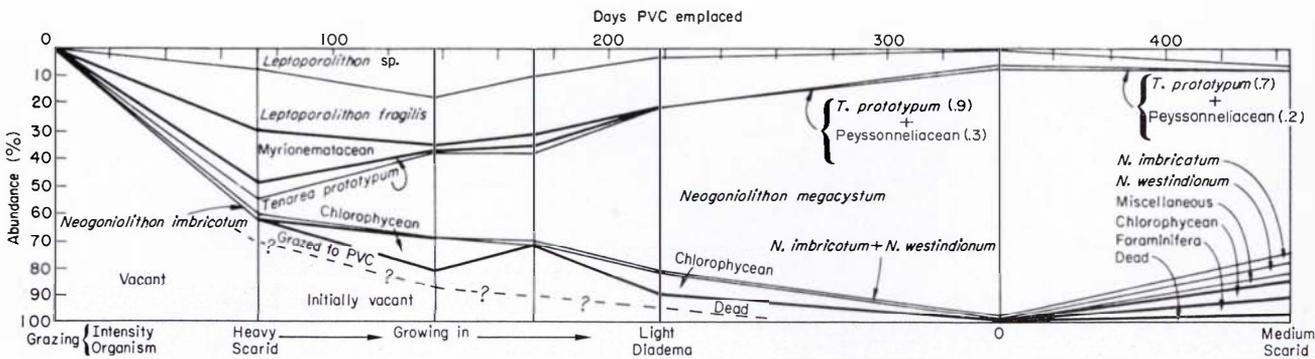


FIG. 6. PVC palmata with early grazing delaying succession but nearly complete coverage developing by 340 days.

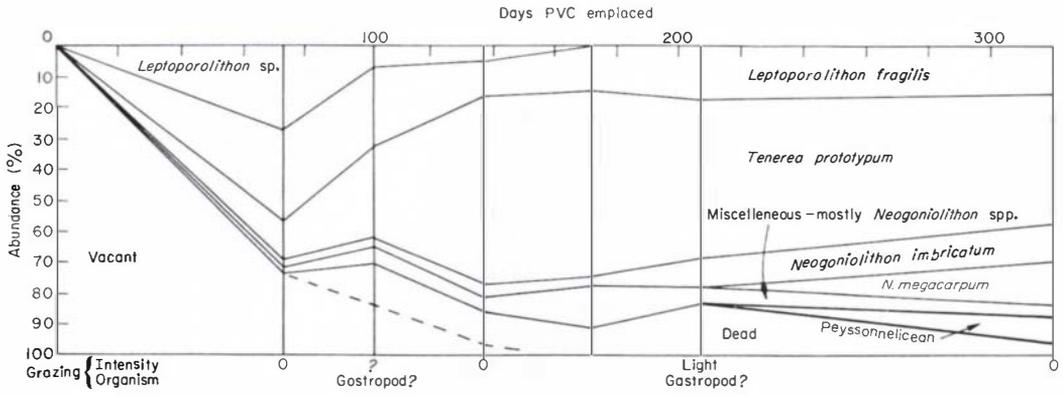


FIG. 7

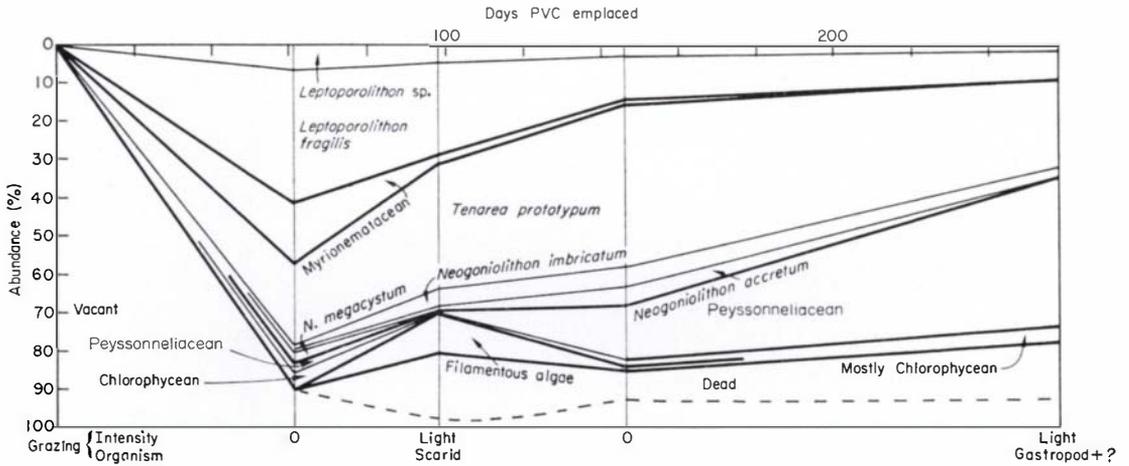


FIG. 8

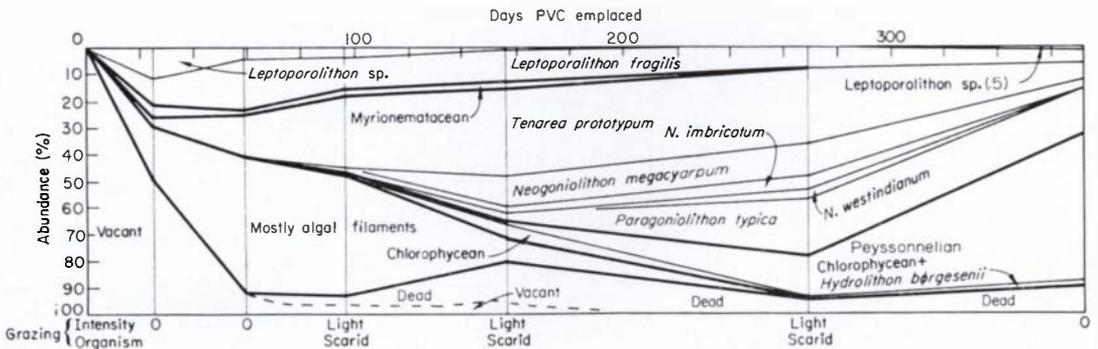


FIG. 9

Figs. 7-9. Under or shaded sides of PVC palmas showing little or no grazing.

Robin Ridge (see Fig. 1, Adey, 1975). However, *Diadema* is not common around the Boiler Bay ridges nor on the higher south shore algal ridges, probably because of the high turbulence levels. Only two of our plates showed even limited *Diadema* grazing (Figs 6 and 10).

Limpets (Acmaeidae and Fissurellidae) are abundant, perhaps averaging one per plate. The home territory of the limpets is marked by a vacant or dead coralline spot the size of the limpet on the plate. However, the resulting low-level grazing on the surrounding surface, while frequently apparent as a dense, arcuate, en echelon, series of scrapings, seldom appears to be deep enough to kill the corallines. Parrot fish grazing is common in these environments, except on or near the shallow, turbulent ridge crests, and parrot fish grazing on the PVC is often intense. Although it seldom covers a whole plate, the scrape marks can sometimes extend through several mm of crustose coralline and into the underlying PVC. Our PVC palmatas in Boiler Bay showed an apparent parrot fish visit rate (where extensive damage to the coralline surface occurred) of about 1.25 times per year. Occurring after 60–100 days of plate emplacement, intensive grazing tends to keep a part of the plate surface continually in the colonial stages. In this case, the *Leptoporolithon* species, accompanied by a relatively large amount of dead surface often with creeping algal filaments, remains present (Figs 4 and 5). On the other hand, the myrionematacean crusts seem to suffer particularly from grazing and are seldom re-established in any quantity after grazing. Noncoralline red crusts are not obviously grazed, even though many are weakly or not calcified. This implies a chemical or other built-in protection from grazing which may favour these softer crusts over corallines in areas of heavy grazing. When occurring within the first 100 days and not later, parrot fish grazing only serves to delay succession and coralline coverage of the plate (Fig. 6).

The undersides of the PVC palmatas have relatively low light intensities (1800–3000 lx). Both the *Leptoporolithon* spp. and *Leptoporolithon fragilis* colonization stages are present, as in higher light intensities. However, the myrionematacean crusts are less important, while *Tenarea prototypum*, which tends to be the third or fourth element of the well-lighted succession (Figs 2–6), dominates to apparent maturity in the shade (Figs 7, 8 and 10). Noncoralline red crusts and *Paragoniolithon typica*, both of which tend to be more important in the shade or in deeper water on natural substrates, are also

important elements, whereas *Neogoniolithon* spp. occur as only a few small plants usually at the plate edges where they would receive the highest intensities.

The undersides of the PVC palmata are only occasionally grazed (Fig. 10). This also appears to be a general characteristic of the well-lighted, internal spaces of dead, open *Acropora palmata* pavements in relatively quiet areas. Considerable coralline build-up (5–15 cm accretion) often occurs on the undersides of dead *Acropora palmata* in open pavements, whereas little or no accumulation is present on the uppersides even though 50–90% of the surface is encrusted with crustose coralline. Apparently parrot fish avoid grazing inside the *A. palmata* pavements, perhaps because of possible predation or the physical difficulty of working on an undersurface in a confined space. In turbulent areas, such as in shallow areas around the exposed algal ridges on the southeast side of St Croix, coralline accretion on the upper sides of dead *Acropora palmata* stands is at least as massive as beneath, often ranging to 10–20 cm thick. Presumably this results from the lowered grazing efficiency of parrot fish under turbulent conditions. In a little deeper water (1.5 m) in this same area, Steneck and Adey (in ms) found a coralline removal rate (due to grazing) of nearly 3 cm/year.

After 5–9 months on the upper sides of PVC palmata, the abundant *Neogoniolithon* plants that settled during the first few months of plate develop-

TABLE 1. Number, size and growth rates of *Neogoniolithon* plants on PVC palmata, and *Clathromorphum circumscriptum* on Gulf of Maine glass plates (Adey, unpublished data). (Most of the PVC plants measured are *N. megacarpum*. However, a few *N. imbricatum* and *Paragoniolithon typica* plants are included.) (a) Boiler Bay, St Croix—PVC; (b) Gulf of Maine—glass

(a)					
PVC no.	Plants (no.)	Total plate area (cm ²)	Area occupied (cm ²)	Days (no.)	Area/plant (cm ²)
1–3	25	99.5	55.7	138	2.2
2–3	21	59.7	21.5	259	1.0
3–4	20	78.7	23.6	156	1.2
4–4	29	62.9	37.7	218	1.3
8–4	28	85.8	41.2	147	1.5
Mean	24.6	77.3	35.9	184	1.5
Mean growth rate (marginal extension)				1.1 mm/month	
(b)					
Two plates	139	77.3	11.6	365	0.08
Mean growth rate (marginal extension)				0.13 mm/month	

TABLE 2. Marginal growth rates of shallow water coralline crusts on St Croix, April–September 1972. Note branch elongation rates for *Neogoniolithon westindianum* are also included along with marginal rates for several arctic boreal species. The latter rates were taken from the data of Adey (1970) using 0–12°C range for subarctic plants and 5–15°C for boreal species. The single maximum values given are large individual plants that could be surely identified to species

Substrate and location	Depth	Genus, species	Plants (no.)	Marginal extension (mm/month)		
				Max.	Mean	Min.
<i>Acropora palmata</i> back-reef area, northern barrier reef	30–120 cm	<i>Neogoniolithon</i> spp. and <i>Porolithon</i> spp. (all plants)				
		<i>A. palmata</i> topside	18	4.0	1.4	0.2
		<i>A. palmata</i> bottom	13	1.4	0.9	0.4
		<i>Neogoniolithon megacarpum</i>	1	4.0	—	—
		<i>Porolithon pachydermum</i>	1	2.2	—	—
Terrigenous pebbles, lagoon shore, northeast reef	30–100 cm	<i>Neogoniolithon westindianum</i> branch elongation	14 5	7.9 1.8	1.9 1.0	0.3 0.1
		<i>Hydrolithon borgesense</i>	46	4.4	1.0	0.1
<i>Porites porites</i> cryptic, around dead bases in dense patches	1–2 m	<i>Paragoniolithon</i> spp. <i>Hydrolithon</i> spp. <i>Neogoniolithon</i> spp.	16	8.7	2.3	0.2
		<i>Paragoniolithon solubile</i>	1	8.7	—	—
Glass plate pavement in algal ridge area of Boiler Bay	1–2 m	<i>Neogoniolithon megacarpum</i>	25	3.7	2.3	—
		<i>Neogoniolithon imbricatum</i>	25	2.7	2.1	—
Arctic-boreal shallow water corallines	Tanks	<i>Phymatolithon polymorphum</i> (boreale)		0.4	0.3	0.15
		<i>Lithothamnium glaciale</i> (subarctic)		0.4	0.2	0.06
		<i>Clathromorphum circumscriptum</i> (subarctic)		0.3	0.2	0.06
		<i>Lithophyllum orbiculatum</i> (boreale)		0.1	0.2	0.1

ment were beginning to fuse with one another, but the individual plants were still distinct. Using the number of *Neogoniolithon* plants present and the area occupied by them, a mean marginal extension rate of 1.1 mm/month was calculated (Table 1). Since not all of these plants settled immediately when the substrates were placed, 1.1 mm/month is a minimum rate. A rate of 1.3–1.5 mm/month is perhaps closer to the actual marginal extension rate. Table 1 also shows a similar calculation for *Clathromorphum circumscriptum* from two large plates at 1–2 m depth from coralline bottoms in the Gulf of Maine (Adey, unpublished data). The equivalent marginal extension rate is 0.13 mm/month. Also, theoretical calculations from laboratory experiments with northern species (Table 2, after Adey, 1970) give monthly values (based on a mean yearly rate) of 0.1–0.3 mm/month. Thus, a dominant shallow, subarctic species has a growth rate that is an order of magnitude lower than Caribbean plants occupying a similar habitat.

In Table 2, calculations of marginal growth rates based on measurements of coralline plants on coral

or rock substrate in several shallow-water environments on St Croix are shown. Mean rates are near to those found on the PVC palmata (from 0.9 to 2.3 mm/month). The smallest values were obtained from *Neogoniolithon* and *Porolithon* plants on the undersides of the arms of *Acropora palmata*.

Accretion rate or increase in thickness of coralline crusts is of special interest in terms of the build-up of carbonate structures. Adey (1970) showed mean yearly rates of 330 $\mu\text{m}/\text{year}$ for shallow water (< 6 m depth) *Clathromorphum compactum* in the Gulf of Maine. Although it is difficult to measure accretion rates on the PVC palmatas, since growth occurs on both sides, we have estimated an average of 0.8 mm/year on each side. Allowing for an initial settlement period of about 3 months, the mature rate is about 1 mm/year, including grazing, or nearly three times the rate for *Clathromorphum compactum*. Although the shaded side of the PVC palmata showed about the same total thickness as the topside, the dominant *Tenarea prototypum* and non-coralline red species have a leafy, imbricating or overgrowing habit which develops considerable underlying spaces. Since, as

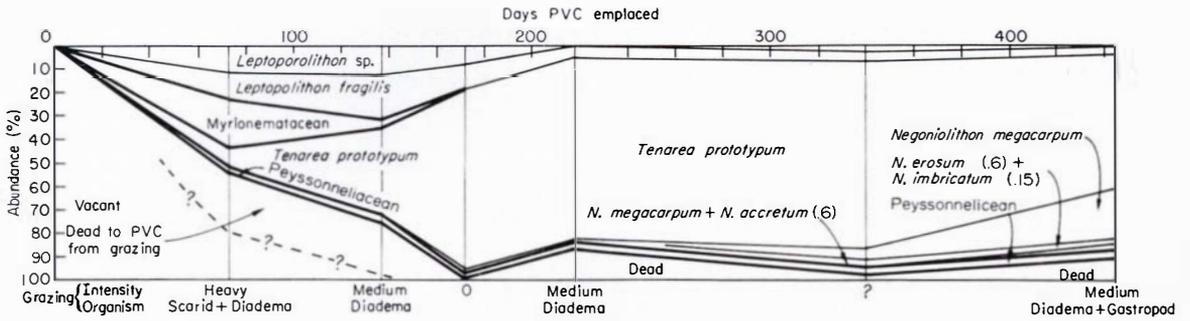


FIG. 10. Under or shade side of PVC palmata with both parrot fish (scarid) and *Diadema* grazing.

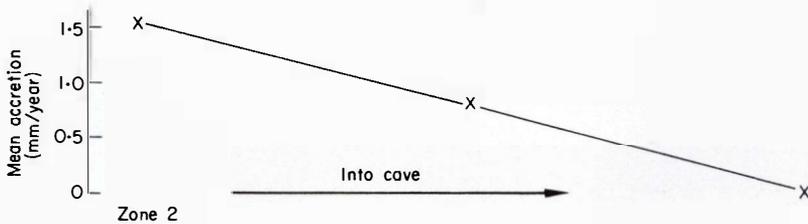
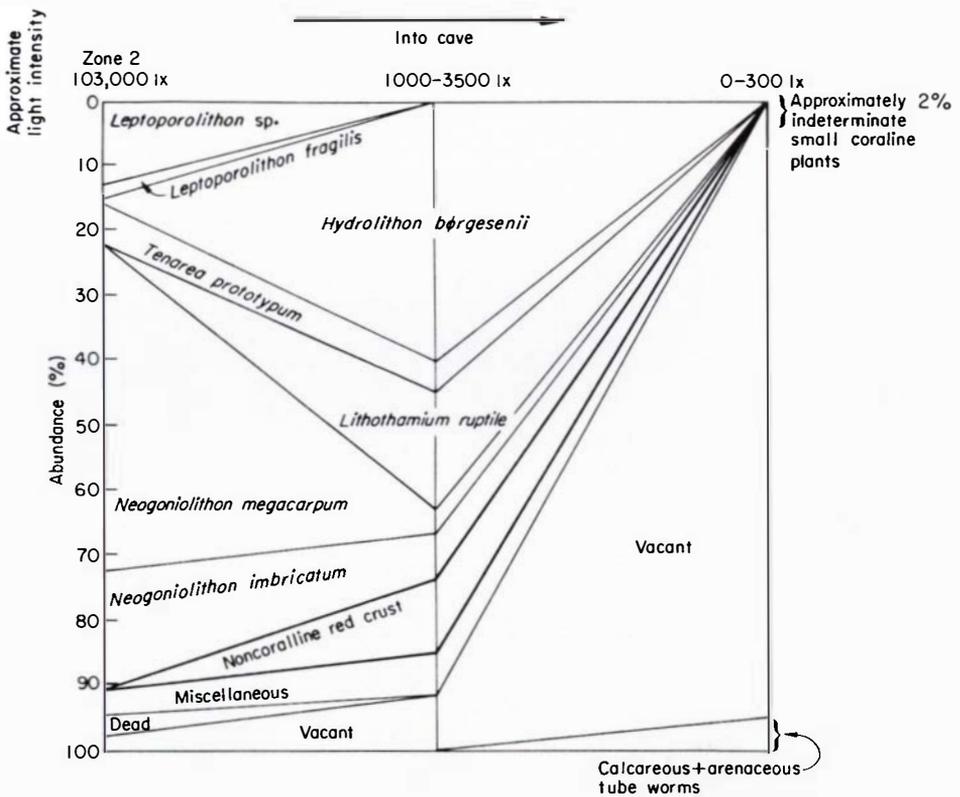


FIG. 11. Glass plates from cave-transect, outside to inside, in Shark Reef, Boiler Bay, 11-12 months after emplacement. No grazing is apparent in these plates. However, they were not monitored on a monthly basis.

discussed above, the undersides have also been subject to less grazing pressure, the production of carbonate on the lower sides must be considerably below that of the upper sides.

The algal ridges on St Croix have many caves, largely resulting from the lateral (and outward) growth of cup-reef lips at sea level and the subsequent merging of these (Adey, 1975). A series of three plates were placed from just outside a large cave in Shark Reef, Boiler Bay (at -10 cm) to well within the cave itself at about -30 cm (Fig. 11). After 1 year, the outside plate showed a coralline coverage and species composition that was similar

to that on the PVC palmata. *Neogoniolithon imbricatum* is considerably more important here than on the PVC palmata, and this is also characteristic of the difference between the crests of the Boiler Bay algal ridges and the *A. palmata* pavements. However, the accretion, measured by calipers, of about 1.5 mm/year (allowing 3 months settlement time) is nearly twice that of the PVC palmata. The cave entrance in this case is immediately behind the ridge crest at a depth of about -15 cm, zone 2 of the algal ridge (Adey, 1975), and even in Boiler Bay this area is subject to considerable turbulence. No grazing is apparent on this plate, and the increased accretion

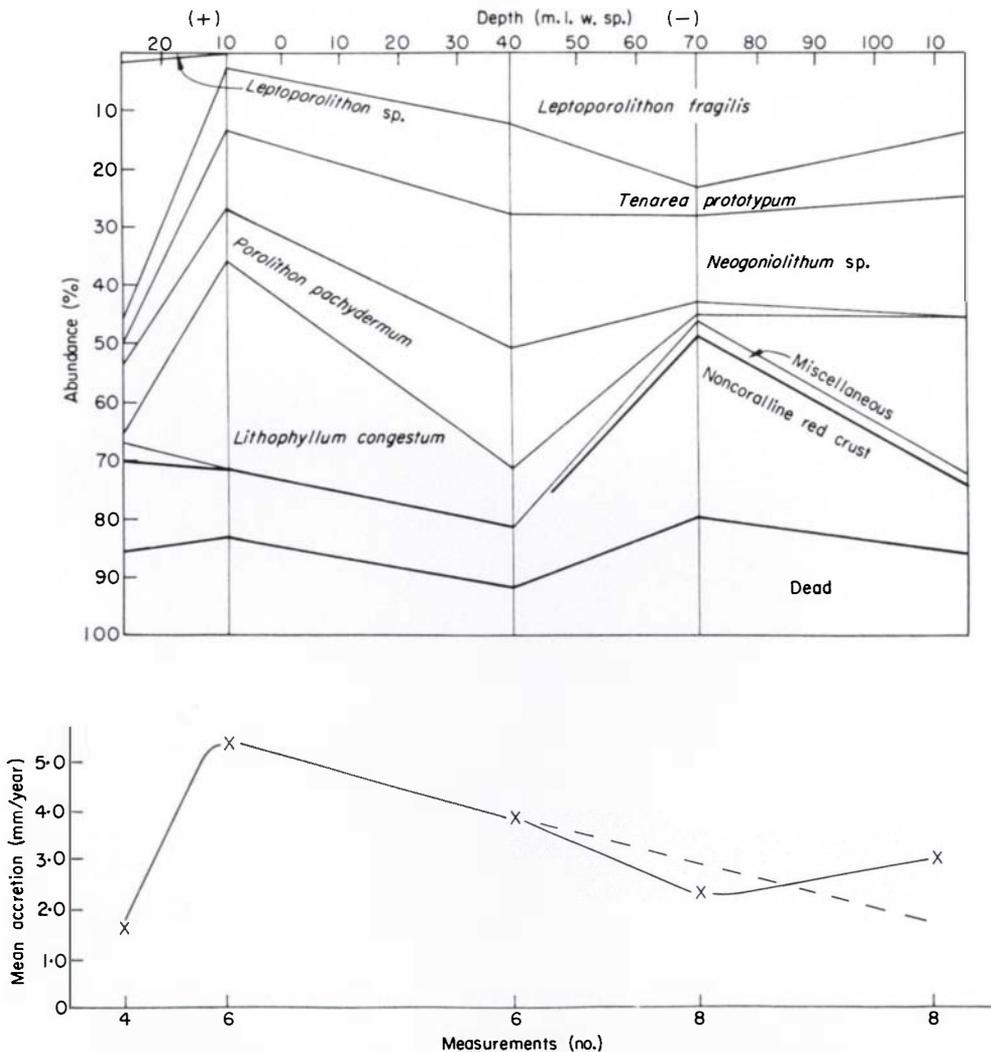


FIG. 12. PVC plate transect across Fancy algal ridge, +27 cm to -115 cm, showing encrusting populations at 6 months after emplacement.

over the PVC palmata at 1–2 m depth in relatively quiet water is likely in part due to lack of intense grazing and perhaps partly due to a slightly shallower placement.

Just inside the cave entrance, the light intensity drops markedly and the coralline populations change considerably. *Lithothamnium ruptile* (Foslie) Foslie is characteristic of cryptic situations in all of the algal ridges on St Croix. *Hydrolithon borgesense* (Foslie) Foslie is not characteristic of shade situations on the major ridges themselves, but is abundant on rhodoliths and on the pavements in the turbid back ridge area of Boiler Bay not far from the cave. The mean accretion rate on this plate is about 0.8 mm/year, which is only about half that on the outside of the cave even though evidence of grazing is also lacking. Just inside the cave, at daytime light intensities of 0–300 lx, after 1 year only a few small undeterminable plants of crustose coralline were present, and the accretion rate was near zero. The main occupiers of this plate are calcareous worms. Even these only occupy about 5% of the surface.

Figure 12 shows species composition and accretion on a series of 26 mm diameter PVC pipes placed from the crest at +27 cm to a depth of 115 cm on the east-facing front face of Isaac algal ridge, St Croix (see Steneck & Adey, in ms). The branching

Lithophyllum congestum dominates at and just above mean low water, a characteristic of all wave-exposed and active ridges on St Croix (Steneck & Adey, in ms). Although *L. congestum* sometimes occurs in abundance down to several meters depth, it usually lacks significant branches below about 50 cm. At higher levels (25–50 cm), on Isaac algal ridge, *Porolithon pachydermum* dominates. Apparently, this coverage requires a longer period than 6 months to reach climax, and the colonizer *Leptoporolithon fragilis* is still dominant on the pipes. The maximum mean accretion rate found was 5.2 mm/year at 10 cm above mean low water.

The algal-ridge pair off Fancy Mountain on the southeastern shore of St Croix is presently degenerating, the required wave action being blocked by a developing *Acropora palmata* reef just offshore. A series of PVC plates across these two ridges showed the accretion rates given in Fig. 13. Two of the plates in deeper water in front of and behind the outer ridge showed the effects of recent grazing. Number 4 showed massive parrot fish grazing and number 2 considerable limpet grazing. Both had accretion rates well below the plates with no apparent grazing. *Lithophyllum congestum* abundances are relatively low on outer Fancy Ridge (a maximum of 20% surface coverage per 0.25 m²) and nearly zero on inner Fancy Ridge (Steneck & Adey, in ms).

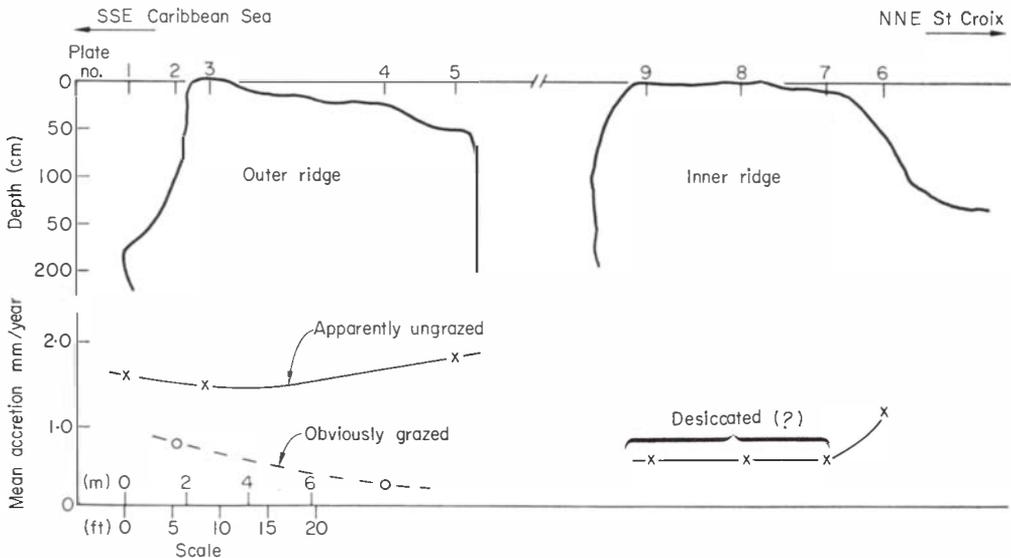


FIG. 13. PVC plate transect across Fancy algal ridges showing apparently ungrazed and grazed accretion rates 12 months after emplacement. Plates 7–9 show a large percentage of vacant and dead surface although grazing is not apparent. This is now a protected and very quiet ridge and the plates were probably subject to periodic kill-off by desiccation at periods of mid-day low tides.

Discussion

We have not tried to assess experimentally the differences between newly dead *Acropora palmata* arms and our PVC palmatas. Dead *A. palmata* usually has a rough surface that is a suitable substrate for many organisms. Sanded PVC, on the other hand, has a uniform surface that is apparently especially conducive to coralline settling, while not initially providing a good holding surface for crabs, worms, etc. It seems likely that a coralline surface is slower to develop on a dead *A. palmata* than a PVC plate or arm. However, once the surface is covered with a coralline crust, there should be little difference in accretion rates.

We have removed several specimens of shallow (1–2 m) *Acropora palmata* pavements just seaward of the algal ridges in Boiler Bay (Adey, 1975) and measured surface coverage of algal crusts. These surfaces can be assumed to be in the climax state and with 30–60% coverage of *Neogoniolithon megacarpum* they are similar to our PVC palmatas after 200 days or more in the ocean. *Leptoprolithon fragilis* is abundant on these surfaces, up to 20% total surface coverage, indicating the continued grazing pressure of parrot fish. However, *Porolithon pachydermum* was found up to 30% coverage, suggesting that this is a slow species to develop at this depth and that perhaps the plastic pipes are still subclimax even after 1 year in the water. Non-coralline red crusts are also not as abundant on these well lighted pavements as on our PVCs.

As suggested by the gradual reduction of *Tenarea prototypum* on the shaded sides of the older PVC palmatas (Fig. 10), a climax population is slower to develop at lower light intensities, even though considerable carbonate accumulates in the process. *Tenarea prototypum* is not a dominant on the shaded sides of dead *Acropora palmata* in Boiler Bay. As on two of our underside PVC palmatas, non-coralline red crusts dominate at surface coverages of up to 60% on the underside of standing dead *A. palmata*. In the pavements *Lithothamnium ruptile* and *Hydroolithon borgesensei* are minor elements which do not occur in our PVCs. More important, the encrusting forms, *Homotrema rubrum* and *Neogoniolithon accretum* are both major shade elements in the pavements, and we have not found them on the shaded sides of our PVCs. The cryptic pavement areas are more similar to the mid-cave plate in Shark Reef (Fig. 11), suggesting that the PVC palmata undersides receive higher light intensities than the

holes in the pavements. In any case, it would appear that several years are required to reach a climax state in shaded environments.

On two blocks removed from the Boiler Bay algal ridge crests, *Neogoniolithon accretum* followed by peyssonneliacean crusts dominated while *N. megacarpum* and *N. imbricatum* were only secondary elements. These low and degenerating ridge crests (0–17 cm above mean low water), and to a lesser extent the back ridge zones, have a dense fleshy algal cover reaching 3–4 kg/m² (wet) (see Connor & Adey, 1975). With this cover, the mature crusts are apparently shade adapted and, thus, dominated by *N. accretum* and non-coralline red crusts. The Shark Reef, zone 2, plate (Fig. 11) lacks the shade elements and is dominated by *N. megacarpum* and *N. imbricatum*, indicating that the climax state, dominated by a fleshy and leafy algal overstory with shade-adapted crust species, has not been reached.

The high (to 50 cm above mean low water) and actively growing algal ridges have a smaller standing crop of fleshy algae and an entirely different crust species composition. Two blocks from 20–30 cm (above mean low water) at Beach algal ridge and Lamb incipient ridge were dominated by the branching *Lithophyllum congestum* followed by the crustose *Porolithon pachydermum*. The *Neogoniolithon* and non-coralline red crust species are only secondary elements. This strong domination by *Lithophyllum congestum* from +20 to –20 cm has been documented for many active ridges by Steneck & Adey (in ms). At higher levels on these ridges (30–50 cm), *P. pachydermum* dominates strongly, with *L. congestum* occurring mostly in and around holes. *Lithophyllum congestum* and to a lesser extent *P. pachydermum* are the main builders of the algal ridges. This is even true of some of the degenerate types such as those in Boiler Bay and the Fancy algal ridge pair (Adey, 1975). Our PVC pipes at Isaac algal ridge show a species coverage which is similar to that found on the mature ridges. However, the relatively high percentages of *Tenarea prototypum* and *Leptoprolithon fragilis* suggest that at 6 months a climax state has not been reached. A 1 year incubation time would probably be more appropriate for reaching the climax state on these substrates.

At an average of 1–2.3 mm/month, marginal extension rates of shallow water tropical corallines are about an order of magnitude higher than boreal-subarctic crustose corallines. Maximum mean accretion rates measured at about 5 mm/year are fourteen times greater. However, due to con-

siderable grazing pressure, especially by parrot fish and limpets, accretion rates in most reef environments are normally considerably below the maximum and perhaps closer to 0.5–2 mm/year. Under the high energy conditions of the algal ridge environment, grazing is very limited (without monitoring plates on a weekly basis, it is difficult to be certain that grazing has not occurred at all) and rates of 3–5 mm/year are attained.

Large numbers of the boring echinoid *Echinometra* occur in the intertidal and uppermost sublittoral parts of algal ridges. They are especially abundant on the less turbulent back 'bowl' sections of the higher ridges and massively infest all intertidal sections of degenerating ridges. These animals enter small holes as juveniles and continue to enlarge the burrows as they grow and feed largely on floating algae (Abbott *et al.*, 1974). The efficacy of *Echinometra* burrowing is demonstrated by the subsurface sections of our verticle PVC pipes. Where these intersect an echinoid burrow below the ridge surface, they are virtually removed by scraping within 6 months. Our plates placed on ridge surfaces did not

show the degenerative effects of *Echinometra*. Whereas, our crest accretion rates for the Boiler Bay and Fancy algal ridges would seem to indicate continued growth at a low rate, both of these ridges are obviously degenerating and this is probably largely the result of *Echinometra* boring. We have examined some reef-blocked algal ridges in the eastern Caribbean that are honey-combed by such borings and probably have a large-scale porosity of well over 50%. It would appear that plate accretion rates of greater than 2–3 mm/year would be required for an actively growing ridge. Below that level, erosive effects dominate and a ridge degenerates.

Adey (1975) discussed the evolution of algal ridges and coral reefs on St Croix. These results are summarized in terms of yearly ridge or reef accretion rates in Fig. 14. In highly turbulent waters, the growth rates achieved in our plate studies would have been quite sufficient to allow algal ridges to follow sea level rise throughout the Holocene. Eastern Caribbean ridges apparently have typically formed on coral reefs developed on available hard shelves at –3 to –10 m as sea level rose 3000–5000

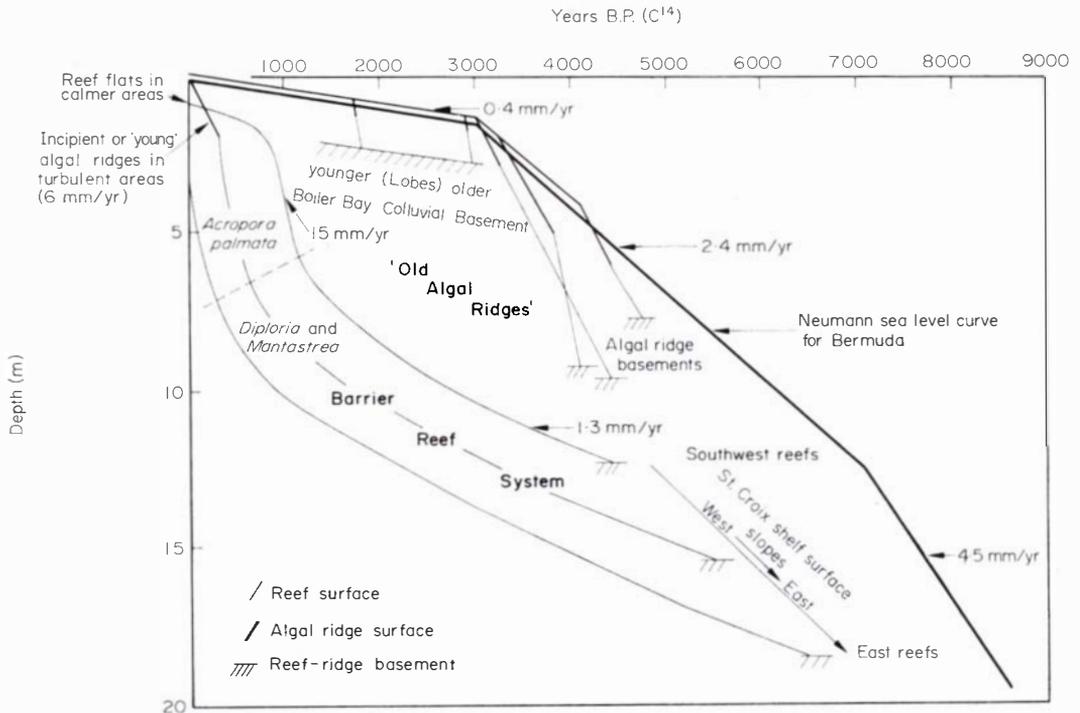


FIG. 14. Holocene development of coral reefs and algal ridges on St Croix showing rates of upward development. After Adey (1975).

years before present (BP). Open, wave-beaten conditions were required to prevent massive grazing and allow maximum accretion rates by corallines so as to offset considerable boring by burrowing filter feeders. Sediment 'packing' and resulting submarine cementation (Ginsburg & Schroeder, 1973), perhaps under the influence of extensive wave pounding, may also assist in strengthening a ridge once it is formed.

As coral reefs develop on deeper shelf levels in front of the algal ridges, eventually blocking the wave action, the ridges degenerate due to grazing and boring. A typical mature *Acropora palmata* reef has a low-sloping fore-reef profile which reduces the wave energy delivered to the reef crest. However, some recent or incipient ridges are developing on *Acropora palmata* reef crests in St Croix, and it remains to be seen whether or not this is a general pattern that will produce a new series of algal ridges. Accretional rates achieved in such incipient ridges, as measured by C^{14} dating, reach 6 mm/year (Adey, 1975).

Conclusions

We are only beginning to understand the ecological relationship of crustose coralline species to algal ridges and coral reefs. Although the picture is complex, we can make some generalizations that are especially applicable to a constant trade wind situation of medium levels of wave energy similar to that found on eastern St Croix.

At an early stage in ridge development, with a dominantly *Acropora palmata* and *Millepora* pavement formed in water of less than 1–2 m depth under considerable wave action, *Neogoniolithon megarcarpum* and *Porolithon pachydermum* will dominate as long as at least occasional calm water allows considerable grazing of fleshy algae. Partially shaded holes in the pavement are filled by *Neogoniolithon accretum*, *Homotrema rubrum* and non coralline red crusts, while a scattering of the corals *Diploria* spp., *Porites astreoides* and *Millepora* are also generally present. This combination builds towards sea level at the rate of about 5–6 mm/year, the resulting accumulation depending upon the rate and extent of sea level rise. On reaching sea level, *Lithophyllum congestum* replaces the crusts and rapidly builds to +20 to +30 cm. With a slowly rising or stable sea level, *Porolithon pachydermum* will be an increasingly important element building at higher levels of > +30 cm. Rapidly rising sea level may, however,

favour continued domination by *Lithophyllum congestum*. The extent of sea level rise and its rate will then determine the mass of ridge laid down by this combination.

The blocking of mechanical wave energy by a younger ridge or reef to windward at this stage will allow a new (degenerative) coralline sequence to develop. Perhaps, however, such a degenerative sequence would be preserved in the ridge carbonate structure only under optimum conditions of slow sea level rise. A reduction of wave action on a mature ridge allows a massive development of fleshy algae, a reduction of *L. congestum* and a domination of crusts adapted to lower light levels, especially *N. accretum* and non-coralline red crusts. With continued wave blocking, ridge height will be reduced by boring and eventually by grazing. Without a continued fairly rapid sea level rise, the degenerative shade sequence will be likely lost to the geological record and removal of ridge carbonate by burrowers will extend into the *L. congestum* and *P. pachydermum* structure as in the Boiler Bay algal ridge.

Erroneous statements concerning the relationship of carbonate deposition by corallines in cold as compared to tropical waters are common in the literature (see the discussion by Adey & Macintyre, 1973). The same late Holocene interval of sea level rise is available for carbonate build-up in boreal-subarctic waters as in the tropics, although glacial rebound may limit this in some northern areas. An order of magnitude difference in accretion rates, the lower subarctic-boreal rates probably basically being due to generally lower incoming light energy levels, is of course important. However, corallines would appear to generally cover more of the shallow, sublittoral, hard bottom in the subarctic than in the tropics, and even at +0.3–0.5 mm/year, 1–2 m of Holocene carbonate buildup would have been possible. That this may occasionally happen is shown by coralline buildups of nearly this magnitude in places in the Aleutians (Lebednik, personal communication). The lack of grazing fish and the heavy fleshy algal cover often present in shallow northern waters is probably important in limiting coralline accretion rates. Indeed, the areas where coralline buildup is greatest are areas with abundant urchins. However, in the North Atlantic, even where factors are apparently favourable, only 10–15 cm of total accretion is now present. (Several meters of maerl or rhodolith accumulations are known and are probably common, but a considerable admixture of terrigenous silt and sand or mollusc shells is also present in

these places.) In areas having 10–15 cm of accretion, blocks of coralline are frequently found broken out of the quite porous crust, baring the basement rock beneath, and it is usually not difficult to pry a large segment of the carbonate free. It is the boring filter and detritus feeders, largely worms and pelecypods, and not original porosity that is largely responsible for this lack of strength. Perhaps a general lack of submarine cementation also contributes to the usual failure of a substantial crust to develop.

In summary, parrot fish and *Diadema* grazing can greatly limit coralline accretion in tropical waters. High wave energy situations where these organisms cannot function are comparable to those of northern waters. Basic accretion ratios under favourable conditions, tropics/subarctic-boreal are about 4/0.3 (mm/year) and known total actual coralline accretion ratios (in the Atlantic) are about 5/0.2 (m). These ratios are at least similar, suggesting that the major difference involved is indeed only a physiological limiting of the amount of energy applied to building carbonate, possibly alternately to store food for the winter low solar energy periods. Also suggested here is that without intense parrot fish grazing in waters of medium turbulence, crustose coralline reefs or ridges would perhaps not be largely restricted to high energy situations and could perhaps greatly overshadow coral reefs in tropical waters. This could have considerable significance in understanding the importance of algal reefs in the early Cenozoic as related to the co-evolution of the Scaridae and scleractinian frameworks. The relationship of acanthurid grazing to fleshy algal cover is probably also important in determining coralline accretion rates. Detailed studies of the relationships of acanthurid to scarid to urchin grazings as a function of turbulence are critical to our further understanding of reef-ridge development.

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