THE BENTHIC ALGAL COMPOSITION, STANDING CROP, AND PRODUCTIVITY OF A CARIBBEAN ALGAL RIDGE[1]

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ABSTRACT

The distribution and standing crop of benthic algal species on a Caribbean algal ridge (St. Croix) and its associated carbonate pavements is discussed and contrasted with that of other eastern Caribbean algal ridges and a Pacific algal ridge. Mean standing crops of 3 kg/m^2 (wet weight) and a species richness of about 40 species (for ten 0.25 m^2 samples) were encountered on St. Croix. Non-calcified or fleshy algae are greatly reduced in standing crop with depth away from the high wave energy ridge crests and species richness increases. This is correlated with the greater grazing abilities of fish and invertebrates under less turbulent conditions.

On reefs of typical lower eastern Caribbean islands, only where the force of water movement across intertidal algal ridges prevents intense grazing by fish and echinoids are general high levels of algal standing crop and productivity developed. However, in the more eutrophic waters of higher islands and where wave action is greater, dense standing crops of larger fleshy algae can also extend sublittorally to depths of at least 10 meters. We suggest that the extensive filling of grazing niches in tropical reefs and a general retreat of plant tissues to protective carbonate structures has caused a reduction of primary productivity in typical reef environments.

INTRODUCTION

The windward reef margins of large numbers of Pacific atolls and some high islands are rimmed by an algal ridge, a partly intertidal and supratidal calcareous reef framework built primarily by crustose coralline red algae. Less well known are the scattered but locally abundant occurrences of algal ridges in the Caribbean and tropical Atlantic. Adey and Burke (1976) describe the distribution of algal ridges in the eastern Caribbean, and Adey (1975) treats in detail the morphology, structure and geological history of the well-developed set of algal ridges on St. Croix. The latter author also summarizes the more important literature on algal ridges. In this paper, we describe the fleshy algal flora of the St. Croix algal ridges and its richness and ecology in terms of standing crop.

Few studies have been done on the standing crops of benthic marine algae on algal ridges or coralline-rich reef areas (coralline pavements). Taylor (1950) describes the difficulty of collecting on the Bikini ridge (Marshall Is.). He gives an account of removing algae from a particularly thick zone (a few millimeters to a centimeter in thickness) on the ridge. Dahl (1971) describes an algal turf association on the fringing reef flat of American Samoa. His algal associations of low standing crop and high diversity decrease in coverage across the reef flat to the seaward side where first crustose algae and then, further seaward, living corals predominate. Quantitative biomass measurements were not given by Dahl. Another Pacific account, Soegiarto's work on Kaneohe Bay, Hawaii (in Smith et al., 1973) indicates that standing crop and algal diversity are greatest in the reef flat surf zone, where water movement is greatest (250 g/m^2 dry weight) and decrease in all directions from there.

Doty's (1969, 1971) studies on the standing crop on an algal ridge and associated coralline pavements off Waikiki Beach, Hawaii are among the few detailed quantitative studies treating the attached flora of a coralline reef. Using Doty's data for November, 1967 as being about average for the entire period covered, the mean standing crop reaches a maximum of about 3400 g/m^2 wet weight on the algal ridge and a minimum of about 1300 g/m^2 in the deeper zone immediately behind the ridge (approximately 1 meter deep).

The upstream-downstream method of determining the organic productivity of an ecosystem has become a standard method of marine biology. Johannes et al. (1972), Gordon and Kelly (1962) and Odum (1956) discuss the method and cite its use on several reef structures in the Pacific. We have applied upstream-downstream analysis of dissolved oxygen to determine the gross and net organic productivity of a single lobe of an algal ridge on St. Croix.

SITE DESCRIPTION AND METHODS

Our study of fleshy benthic algae distribution was conducted on several of the algal ridges along the eastern shore of St. Croix. The collections were especially concentrated on the Boiler Bay algal ridge in the northeast (Fig. 1).

The south shore algal ridges are more or less directly exposed to a prevailing ESE trade wind of 10-20 knots and to seas with wave heights of 1-2 m.

The maximum elevations of these mostly actively growing ridges is about 20-50 cm above mean low water spring tide levels (m.l.w.sp.). Benthic algae were removed from quadrats located on Robin, Beach and Isaacs Ridges (Fig. 1).

The Boiler Bay algal ridge, in an intermediate stage of development, consists of a series of 30-35, more or less horseshoe-shaped coralline frameworks ranging in diameter from about 50 m to as little as 2-3 m. For convenience of reference, the larger of these "boilers", "microatolls" or algal ridge "lobes" are named as reefs in figure 2. The Boiler Bay algal ridge, essentially in its present plan, was actively growing from about 2000 to 500 years before present. However, wave action became blocked by growth of a coral reef at the mouth of the bay, and as surface degradation by borers exceeds carbonate accretion by corallines, the ridge is slowly being eroded. The trade wind swell is refracted about 90° over the coral reef and into Boiler Bay, and at the present time wave heights seldom exceed 30 cm. Maximum elevations of the Boiler Bay ridge now range from 5-10 cm above m.l.w.sp. on West End Reef to 17 cm above m.l.w.sp. on Shark Reef, though they were probably somewhat higher in the past.

Distinctive zones of crustose coralline algae, coral and coralline-coral pavement are visible on and around the ridges and were delineated by color patterns on aerial photographs. Color patterns on the ridges and the surrounding pavements are often due to the fleshy algae populations peculiar to each zone, which in turn are largely dependent on depth, wave action and the grazing of animals. Eight distinct algal zones were determined and are described below.

Zones 1 to 4 lie on the coralline-constructed algal ridge; the remaining zones lie on the associated carbonate pavements or other rock as described. The zone locations in Boiler Bay are indicated in figures 3 and 4. Detailed maps of the area, along with the methods used in mapping, are given in Adey (1975).

Zone 1 is the horizontal strip of algal ridge which lies above mean low water spring tide levels. Between wave crests, it is potentially exposed to desiccation and intense sunlight, though the wave wash is rather constant and severe drying did not occur during our two year stay in St. Croix. Zone 1 is characterized by a turf of Rhodophyta species up to 10 cm thick dominated by *Hypnea* spp., *Laurencia* spp., *Jania* spp., *Amphiroa* spp. and *Gracilaria mammillaris*. Smaller amounts of other reds, as well as scattered clumps of *Sargassum* spp., *Colpominia sinuosa* and other Phaeophyta with occasional small Chlorophyta species are also present.

Zone 2 lies at 0 to about 30 cm below m.l.w.sp. and slopes gently shoreward, averaging about 15 cm in depth. The substrate in this zone is also dominantly coralline algae, though an occasional *Porites astreoides* is also present. Zone 2 is chiefly populated by *Halimeda opuntia*, *Laurencia papillosa* and *Gelidiella acerosa*, though *Pterocladia americana* and *Jania* spp. are also important.

Below zone 2, the algal ridge continues to slope shoreward, tending to form open-backed basins behind each boiler or lobe with depths of about 30 to 60 cm. These basins are designated as zone 3. Here, *Porites astreoides* occupies about 15% of the surface area, and there are also scattered sand pockets in the coralline substrate. The flora here is similar to the second zone, but *Laurencia papillosa* and *Halimeda opuntia* are reduced and the total biomass of fleshy algae is one third less than in the second zone.

The vertical seaward faces of the algal ridge at about 1 to 1.5 m depth were designated zone 4. This is a relatively smooth coralline surface with a light cover of fleshy algae of many small species, the most obvious being *Dictyopteris delicatula*. All quadrats from zone 4 were taken centered at about 0.5 below m.l.w.sp.

Zone 5 occurs on the nearly flat and irregular seaward margin of the fore-ridge carbonate pavement at depths of 3.5 to 4.5 m. The substrate in this zone is a largely cor-algal pavement of dead corals cemented together by crustose corallines, foraminifera and probably submarine cementation of sediment. A few live corals, *Porites astreoides*, *Porites porites*, and *Siderastrea* spp., are also present. The dominant algae are *Halimeda opuntia*, *Dictyota divaricata*, *Amphiroa tribulus* and *Halimeda tuna*.

Zone 6 is also predominantly a cor-algal pavement, but about 11% of the surface is covered by the same living corals that characterize zone 5, *Porites astreoides* being especially important. This zone occurs around the sides and shoreward margins of the ridge lobes at depths of 0.5 to 1.5 m. The most abundant algae here are *Halimeda opuntia*, *Dictyopteris delicatula*, *Dictyota divaricata*, *Dictyota dentata*, *Sargassum vulgare* and *Jania* spp., but numerous other species also occur in small amounts.

Zone 7 lies in the shallow water (0.5-1.0 m) near shore landward of the algal ridge, where a band of carbonate and terrigenous cobbles and pebbles occurs along much of the shore of Boiler Bay. Some corallines and corals also occur here, but in rather small amounts. In this band, the dominant algal species are *Jania adherens*, *Padina sanctae-crucis*, *Sargassum vulgare*, *Halimeda opuntia* and *Cladophoropsis membranacea*.

Zone 8 occurs on the beachrock which runs parallel to the shore in the western and eastern sections of Boiler Bay. This zone is frequently well above mean low water, and since it is partly protected from wave action by the algal ridge, it is somewhat more subject to desiccation and temperature and salinity extremes. However, our quadrats were taken below mean low water springs at depths of about 0 to 0.5 m. Much of zone 8 is characterized by a turf of *Hypnea musciformis*, *Laurencia papillosa* and other Rhodophyta. However, at the east end of Boiler Bay, the Chlorophyta dominate this zone, particularly *Halimeda incrassata*, *Halimeda opuntia* and *Dictyosphaeria cavernosa*. At the west end of the bay, the beachrock is covered predominantly with *Sargassum vulgare* with considerable amounts of *Sargassum platycarpum*, *Dictyota dentata* and *Chaetomorpha linum*. Because of this difference in the two areas of beachrock and our inadequate sampling for the zone, we do not feel that we have properly characterized the algal populations of zone 8.

In each of the above zones, quadrats were subjectively chosen from several algal ridge lobes and their associated pavements as being typical in algal cover for that particular zone. Macroscopic benthic algae were removed as well as chunks of substrate from within a 0.25 m^2 area. The substrate was carefully examined for the smaller species and all algae collected was sorted, identified and weighed for wet biomass. Taylor (1960) was used extensively for identifications. Skeletal carbonate for *Jania*, *Amphiroa*, *Halimeda* and *Pencillus* was calculated using the data of Vinogradov (1953). The standing crops of crustose coralline, algal symbionts and boring algae are not included in this data.

Upstream-downstream dissolved oxygen analysis was applied to Reference Reef, one lobe of the Boiler Bay algal ridge (Figs. 2, 5 & 11). Sampling was accomplished at low water during spring tides when quiet weather permitted a gentle flow of seawater over the ridge with each wave crest. At that time, zone 1 is exposed except during a wave crest and zone 2 is exposed with each wave trough. The water flows southwestward over Reference Reef into the back-ridge lagoon. The boundary of the flow across the ridge (see figure 5), and the flow rates, were measured with standard float bottles. Flow volumes were calculated through section B-B' of the effluent channel. Because of the restricted area involved, the conjunction of spring tides, small waves and light ENE winds was required to provide a measurable channelization of effluent and a well defined area of measurement, as well as to reduce the possibility of significant atmospheric oxygen input from breaking waves. There was therefore often a considerable waiting period between water sample collections. Dissolved oxygen measurements were accomplished using standard Winkler techniques (Strickland and Parsons, 1968).

Oxygen exchange was also studied on 100 cm^2 segments of coralline and corals with their attached algal cover, which had been removed from Boiler Bay just prior to testing. Polarographic electrodes were used with a precision blood oxygen instrument (Radiometer model no. PHM-27) and a salt water chamber maintained at ± 0.1°C (see Adey, 1973). Full sunlight (early April) was employed, and following testing with an entire sample, the fleshy algae were removed and the coral or coralline substrate was tested again.

RESULTS

A list of the algal species commonly encountered in each quadrat and their standing crops is given in tables 1 and 2. The standing crops of all algae for the Boiler Bay algal ridge are shown in figure 6 according to zone. The total number of species encountered and the number of quadrats are also indicated. Fleshy algae are treated separately from those with carbonate skeletons. Summary graphs of the mean standing crops, relative to zone, exclusive of rare or infrequent species, are given in figures 7 through 9. Those quadrats taken from Robin, Beach and Isaacs Ridges on the south shore are summarized in figures 10A and 10B.

Winkler oxygen values obtained for the Reference Reef sampling stations shown in figure 5 are given in figure 11. On each sampling occasion, daytime oxygen levels increased as water flowed over the ridge and nighttime levels decreased. The oxygen thus produced or consumed by the ridge organisms and net and gross productivity in g carbon/m^2/day (translated by g O_2/m^2 x 0.3, Ryther; 1956) are calculated in table 3. Day and nighttime upstream samples were not taken at the same point, and the possible effect of this is discussed below.

Another estimate of the productivity of Reference Reef was determined from the laboratory polarographic electrode study of small samples. The rate of productivity for each zone of Reference Reef was calculated as the product of the total surface area of that zone times the photosynthetic and respiratory rate derived in the laboratory from the 100 cm^2 segment from the same zone. These calculations are shown in table 4.

Our range of gross productivity for Reference Reef is compared with other studies in table 5.

DISCUSSION

The Waikiki Beach study (Doty, 1968) of algal standing crops included algal ridge crest and back ridge or reef flat areas. For comparison, we have plotted the Waikiki data for November 1967 in figure 12. This month shows about an average level of standing crop for the 17 month period (see Doty, 1971).

In terms of total algal standing crop (not including crustose coralline, borers or symbionts), from the algal ridge crest back into the lagoon, Waikiki and Boiler Bay are quite similar. The peak of standing crop occurs on the ridge crest in both cases and this is markedly reduced on the back ridge pavements. The shallower Waikiki back ridge pavement has a higher standing crop than that of Boiler Bay. However, the most striking difference is an apparent lack of a beach rock and its accompanying secondary peak of standing crop at Waikiki. Even in the total number of macroscopic species present, these two areas are remarkably similar, Boiler Bay averaging about 33 species/zone (see figure 6) and Waikiki about 37 species/zone, the difference being easily attributable to collecting pressure (see figure 14).

In detail, however, the two areas are remarkably dissimilar. On the Boiler Bay algal ridge, the red algae dominate strongly, forming 48-62% of the standing crop. (If the crustose corallines were to be included, the dominance would be considerably greater.) This high level of red algal standing crop is not concentrated in a few species, but in over eight species of *Laurencia*, *Hypnea*, *Gracilaria*, *Gelidiella*, *Pterocladia*, *Jania* and *Amphiroa*. On the pavements surrounding the ridge (zone 6) and on the fore-beach cobbles (zone 7) this dominance is reduced, but still the red algae make up 20-40% of the standing crop. It is only in some areas of the beach rock (zone 8) that the red algae are largely replaced by the green algae *Halimeda* or the brown algae *Sargassum*.

In contrast, a number of species of *Laurencia*, *Hypnea* and *Gracilaria* are present on the Waikiki reef, but none of these exceed a mean of 80 g/m^2 in any one zone. Although *Spyridia filamentosa* reaches mean values of nearly 200 g/m^2, only *Acanthophora spicifera* reaches dominant levels. However, virtually all of the red algal standing crop that is present occurs on the back ridge flat, especially near shore. The 23 species of red algae in the quadrats on the Waikiki algal ridge proper formed only .04% of the standing crop in November, 1967, while in Boiler Bay's equivalent zones, 31 species (in quadrats) formed 41% of the standing crop.

Green algae are not important on the algal ridge crests in either Boiler Bay or Waikiki Beach. However, on the back and fore-ridge pavements and near shore in both areas, the greens become conspicuous. The 30-40% of green standing crop in back ridge and beach rock at Boiler Bay were mostly *Halimeda* spp. However, *Caulerpa*, *Cladophoropsis*, *Valonia* and *Dictyosphaeria* occur at mean levels of 20-160 g/m^2. The 20% of the standing crop in back ridge and shore Waikiki contains considerable *Halimeda*, but nearly equal amounts of *Dictyosphaeria cavernosa*. *Ulva reticulata*, near shore, is also important, perhaps due to higher pollution levels.

In contrast to the situation in Boiler Bay, the Waikiki ridge standing crop is almost entirely composed of brown algae: three species of *Sargassum*. These three species occur in varying amounts across the reef flat to the shore, and it is only in the zone 30 meters from shore, where *Sargassum polyphyllum* and *Acanthophora spicifera* share most of the biomass, that the brown algal dominance of the standing crop is challenged. At least three species of *Sargassum* occur on the Boiler Bay ridge, but only in a single quadrat did they occur at levels of more than a few grams. *Sargassum* is generally more important on the beach rock and *Padina sanctae-crucis* on the cobble zone near shore. Otherwise, *Dilophus*, *Dictyopteris* and *Dictyota* are all important minor elements on the pavements around the Boiler Bay ridges and may occasionally form blooms. In Hawaii, *Dilophus* does not occur, and at Waikiki relatively few *Dictyota* and *Dictyopteris* occur as compared to other Hawaiian areas (I. A. Abbott, personal communication).

In the context of these striking differences, it is interesting to examine the standing crop of the exposed algal ridges on the south shore of St. Croix. Green algae are virtually absent from the highest of these ridges as they are at Waikiki. Also, the brown algal standing crop, largely in the form of *Sargassum vulgare*, exceeds that of the red algae which consists mostly of three species of *Laurencia*. In the back ridge zones 2 and 3, the *Sargassum* drops rapidly in abundance. Even though it tends to be replaced by *Dictyopteris*, red algae (still mostly *Laurencia* spp.) begin to dominate again. This suggests that on algal ridges subject to very high wave energies, reds may be replaced by *Sargassum*. The considerably higher and more exposed algal ridges on the southeast shore of Martinique (studies in progress) show a similar relationship. There, the highest ridge tops, at > 1 m m.l.w.sp., are nearly bare, while the low crests and surrounding highly turbulent pavements have high standing crops of *Sargassum*. While Waikiki is not directly exposed to the trade wind, as are the southeastern St. Croix ridges, it does often receive a very large South Pacific swell. Boiler Bay, on the other hand is largely blocked by the northern Virgin Islands and rarely receives the equivalent large swells from occasional northerly winds developed from passage of continental fronts ("northers").

Adey (1974) discusses the relationship between exposure, wave action and algal ridge heights. The highest parts of the more exposed St. Croix ridges reach 40-50 cm above mean low water springs, with a mean spring tide range of about 30 cm. During some summer neap tide cycles, the ridge zone 1 can be 20-30 cm above sea level for four to six hours mid-day. Desiccation and heating are likely to be critical on occasional quiet days and, along with mechanical stress during more turbulent weather, probably accounts for the obvious bareness of the higher part of the ridges. These factors probably also account for the difference in standing crop decreasing from 3200 g/m^2 at Boiler Bay ridge crests with an average height of +14 cm to 2680 g/m^2 on the south shore ridges averaging +30 cm high. It seems likely that *Sargassum* species are better able to withstand both the turbulent water conditions and perhaps occasional periods of limited desiccation and heating.

In recent years, it has generally been considered that benthic algal standing crops are considerably lower in tropical than in temperate to boreal areas (see e.g., Taylor, 1960). This has been variously attributed to low ambient water nutrients, high insolation levels, lack of beds of brown algae or a shift of standing crop to crustose corallines, which are not usually included in standing crop analysis (Bakus, 1969). (Note that Adey and Macintyre (1973) point out that crustose corallines are probably as important in terms of bottom coverage in subarctic-boreal waters as they are in the tropics.) In our studies of the Boiler Bay algal ridge and that of Doty at Waikiki, average wet standing crops up to 3-3.5 kg/m^2 were found, with individual quadrats ranging up to 5 kg/m^2. On several considerably larger algal ridges and pavements that we are now studying in Martinique, algal standing crops are nearly twice as high. Typical lower intertidal *Ascophyllum*, *Fucus* and *Laminaria* stands in Norway have a standing crop of about 3.5 kg/m^2 (Baardseth, 1970). Upper sublittoral *Laminaria hyperborea* stands in the British Isles average 5.0-6.5 kg/m^2 (Kain, 1971). An especially rich *Gigartina stellata* stand in the lowest intertidal and infralittoral in Maine achieved nearly 10 kg/m^2 in the peak summer season (Burns and Mathieson, 1972). Thus, while perhaps temperate-boreal standing crops of larger algae tend to be higher than those in the tropics, algal ridge and beachrock standing crops (those in turbulent zones) can be similar, and, generally, in the seas around the older parts of the higher, volcanic eastern Caribbean islands (Adey and Burke, 1976) algal standing crops of reef structures are quite equivalent to or perhaps larger than the average for northern shores. While brown algae are less important than reds in the flora of the Boiler Bay ridge, *Sargassum*, *Dictyota* and *Dictyopteris* are major components. Similarly *Sargassum* actually exceeds the red algae in biomass on the south shore St. Croix ridges while at Waikiki and Martinique, it is highly dominant. Perhaps the main question to which our attention should be directed is not why tropical standing crops of larger benthic algae are so low, but why they only achieve high levels in special situations.

The importance of grazing in the shallow tropical marine environment has attracted considerable interest in recent years. Randall (1961) contrasted the luxuriant intertidal algal crop in Hawaii with the low stubble of the upper sublittoral and attributed it to fish grazing (Acanthuridae, Scaridae and Pomacentridae).

The conspicuous vegetation-free halo surrounding tropical reef areas has also been shown to result from either fish (Earle, 1972; Randall, 1965) or echinoid (Ogden, et al., 1973) grazing, and removal of urchins from reef areas can result in massive increases in algal standing crops (Sammarco, et al., 1974). Grazing by urchins in northern waters can also be extremely important in limiting standing crop (Jones and Kain, 1967; Paine and Vadas, 1969). In the northern North Atlantic, Adey is familiar with extended areas, virtually bare of fleshy algae dominated by echinoids and coralline algae, and Lebednik (personal communication) has seen similar areas in the Aleutian Islands. Mead (1970) has suggested that the main group of fish grazers, the percoid fishes, which are tropical and Cenozoic in evolution are largely responsible for the present reduction of the sublittoral algal "forests" in the tropics. It is difficult to escape the logic of this conclusion - an algal ridge or shallow pavement is a special, turbulent water environment which is usually inaccessible to grazing fish and *Diadema*. A few invertebrates (mostly crabs, snails, limpets and chitons) do graze in this zone, although their effectiveness is apparently limited. *Echinometra* is often abundant on algal ridges and beachrock, however, the wave energy is apparently generally sufficient to largely confine the echinoids to their holes and to feeding on drift (Ogden, Abbott and Abbott, 1974).

Below the shallow highly turbulent levels of the ridges and pavements, the grazing marks of parrot fish, urchins and gastropods are often strikingly apparent on the typically bare coralline or rubble surfaces. In Caribbean waters, grazing, especially by parrot fish, is critically important in the colonization and carbonate buildup of the crustose corallines themselves (Adey and Vassar, 1975; Steneck and Adey, 1976) and probably is an important factor restricting algal ridges to the most exposed windward shores.

Our research group has spent a considerable amount of time in daytime snorkeling around the algal ridges in Boiler Bay. Our collective casual observations on the intensity of fish grazing are as follows: zones 1 and 2 on the ridge, zone 8 on the beachrock and perhaps to a lesser extent, zone 7 near shore are rarely grazed by larger fish. These zones are either exposed in wave troughs or continuously washed by waves. Zone 3, the algal ridge bowl is periodically grazed, sometimes heavily depending on sea conditions. Zones 4 and 6, on the other hand, are heavily and consistently grazed. Not only are these zones easily reached by grazing fish, but cover for the fish is abundant in the form of holes in the pavements and coral structures, especially *Acropora palmata*. Zone 5, the deep pavement, is the zone over which we have greatest disagreement concerning fish grazing pressure. Generally, we do agree that it is less than the pavement zone 6 because of lack of cover for the fish. Periodically, however, it is probably massively grazed, especially by schools of tangs and parrot fish. Figure 13 shows this subjective index of grazing potential plotted against standing crop. Generally there is indicated a strong inverse relationship between the ability of fish to graze effectively and the standing crop of fleshy and filamentous algae.

The upright calcareous algae, on the other hand, show no apparent relationship between grazing pressure and standing crop. Zone 1, no fish grazing, and zone 4, intense grazing, have about the same level of calcareous standing crop. The only striking feature of the plot is the very high standing crop of calcareous algae on the deep fore-ridge pavement, zone 5, as compared to the other zones. This largely results from the abundance of only two species, *Halimeda opuntia* and to a lesser extent *Amphiroa tribulus*. *Halimeda opuntia* has secondary peaks in zones 2 and 6 and the reason for this distribution pattern is obscure.

In figure 14, the total number of non-calcified algal species for each zone are plotted as a function of the number of quadrats taken (i.e., total area collected for collecting pressure). The Waikiki data of Doty are also included and are converted to 0.25 m^2 quadrats on the basis of total area per zone (see Fig. 12). The relationship indicated further suggests that the larger number of species taken at Waikiki was a result of greater collecting pressure. In figure 15, the Boiler Bay data are plotted, species number/zone as a function of quadrat number/zone. Since species number is a function of collecting pressure, a correction factor is thus derived as shown to correct all zones to 10 quadrats. (Note that a plot of number of species occurring at mean levels of > 1 g/.25 m^2 is not or only slightly quadrat dependent in the range that we worked.) Thus, in figure 16, the total number of non-calcified algal species, corrected to 10 quadrats, as well as the number with a standing crop > 1 g/.25 m^2, is plotted as a function of zone. Both measures show a consistent drop in number shoreward.

Proceeding shoreward, daytime temperatures and suspended sediment generally increase markedly in Boiler Bay, a feature very obvious to the swimmer. Equivalent night temperature drops are to be expected, especially in the winter. These physical characteristics are likely responsible for the shoreward drop in species number.

Figure 17 indicates the variations in number of species from the mean total species curve (Fig. 16) for Boiler Bay. Zones 3, 4 and 6 have four to six species above mean levels. These are zones of heavy to intermediate grazing pressure, suggesting that due to a reduction in space competition, grazing has increased richness. On the other hand, the poorly grazed zones, especially 1 and 2, which have a high standing crop are poor in the rarer species. Zone 8 is the chief anomaly in the pattern. If lack of fish grazing is the controlling factor, and this is indicated by a relatively high biomass, one would expect total species number to be low. Ogden, Abbott, and Abbott (1974) found 20% fewer species on the west beachrock in Boiler Bay as compared to the offlying ridge crests. Their extensive search for species should represent a large number of quadrats. We suggest that our species number for zone 8 is too high, probably as a result of insufficient sampling.

In table 5, our range of gross productivity values for Reference Reef are compared with other areas. As is perhaps to be expected, our values for a dominantly algal area are somewhat higher than those previously given for coral reef communities. Also as can be seen in table 4, algal ridge zones 1 and 2 are responsible for 55% of the area productivity, and in terms of those zones alone, the productivity is about 30 g C/m^2/day. The contribution of crustose coralline algae is indicated as 12.1 g C/m^2/day. This is probably higher than normal, since on the Boiler Bay ridge, the coralline surface is usually shaded by the fleshy algal cover. In any case, it is considerably higher than the previous figure of 1.5 g C/m^2/day given by Marsh (1970).

Because of the critical importance of tide level to our process of taking data on the ridge, it was not possible to take successive oxygen readings at different light levels during a single day. This could however be done on different days as the time of low water springs changes. Presumably our daytime values being taken near noon are maximum levels. On the other hand, Marsh (1970) indicated that in ridge corallines, photosynthesis levels are constant for 10 hours of the day. If this is true for other ridge algae, then our upper value of gross productivity (Table 5) is high by about 15%. The productivity of these ridges and especially the higher ridges of the eastern islands (Adey and Burke, 1976) should be examined in further detail.

CONCLUSIONS

The intertidal wave-washed crustose coralline algal ridges of St. Croix, Virgin Islands develop a dense standing crop of fleshy algae and have a gross productivity which is high for the tropical reef environment. In caged areas and areas with considerably greater wave action, especially in the presumably more eutrophic waters around the higher volcanic islands such as Martinique, the standing crop is often denser and also extends to greater depths. In St. Croix, where wave energy is moderate, the heavy coverage of fleshy algae is greatly reduced with depth away from the ridge crests. Thus, lack of intense grazing pressure under turbulent water situations is probably responsible for the rich algal area on the ridges. In a relatively low-turbulence coral dominated reef environment, the maturity of the tropical ecosystem with extensive filling of grazing niches, especially by fish and echinoderms, results in a generally reduced primary productivity. Cenozoic tropical reefs are characterized by coralline algae and hermatypic schleractinian corals. The domination of this combination perhaps resulted from the evolution of grazing bony fish and some echinoid species. Algal ridges, and in some cases exposed beachrock, are specialized turbulent water situations in a carbonate environment where grazing niches cannot be filled either by fish or by the key grazer *Diadema antillarum*.

Given favorable conditions of marine salinity and low levels of marine erosion and suspended sediment, the frequency and extent of fleshy algal-dominated reef environments, as well as the nature of the flora developed, is thus largely dependent upon the strength and constancy of the accompanying trade wind and sea. Since well-developed sublittoral algal pavements are especially prominent around the older parts of the higher eastern Caribbean islands, it is suggested that more eutrophic conditions, with greater algal growth rates, are also critical.

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