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OF EASTERN MARTINIQUE, FRENCH WEST INDIES**

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## THE HOLOCENE REEF SYSTEMS OF EASTERN MARTINIQUE, FRENCH WEST INDIES

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and Leslie Kaufman<sup>3</sup>

### ABSTRACT

The windward east coast of Martinique ranges from high, eroding Pleistocene volcanic cliffs in the north, to relatively low, early Tertiary, embayed shores partly capped by Pleistocene limestones, in the southeast. An extensive shallow carbonate shelf is developed off the central part of this coast. The types of Holocene reefs found on Martinique correspond to the pattern that is characteristic for Lesser Antillean islands: the volcanic northern coast is barren; massive algal ridges have developed on benches cut in the limestones and other early Tertiary rocks of the southeast coast; on the central east coast, where the shelf is well developed, an extensive and double bank barrier system has formed. Parts of the bank barrier reef system are reaching the mature stage typical of high energy coasts and have algal ridge caps built primarily by crustose corallines.

The bank barrier reefs of Martinique are unusual in that the corals have been replaced on the crests by a carbonate pavement covered with dense, diverse stands of fleshy algae, Sargassum spp. being especially common. The term "fleshy algal pavement" has been applied to this type of reef. Based on upstream-downstream measurements of dissolved oxygen, a winter productivity level of 33 gO<sub>2</sub>/m<sup>2</sup>/day indicates that these extensive reefs with their dense plant cover may be the most productive in the eastern Caribbean.

Though transitional and less extensive, reefs with fleshy algal pavements also occur on Grenada, St. Lucia, southeastern Basse Terre, and Nevis. All of these island shores are locally characterized by high sea water turbidities, presumably resulting from run-off, indicative of eutrophic conditions. However, where algal pavements are well developed,

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the reef surface also generally lacks extensive large scale porosity and large populations of Diadema antillarum. Large parrot fish of the genus Scarus are also very poorly represented, although this may result from a general lack of filamentous algal turfs normally characterizing their diet.

Based on  $C^{14}$  dating of cores, we have concluded that about 600 years B.P., the Martinique inner bank barriers shifted from Acropora palmata to fleshy algal domination. We postulate that the surfaces of these reefs developed into pavements by the filling of the interstitial reef spaces by either gradual or catastrophic means. This eliminated the large scale porosity required by algal grazers such as Diadema (and perhaps some parrot fish) in this high energy area.

In the reefs of the Grenadines where the surrounding waters are quite clear, similar carbonate pavements occur in the high energy areas, but lack a fleshy algal cover. We conclude that flat, featureless carbonate surfaces in areas of strong wave or current energy are conducive to the development of stands of fleshy algae. Especially where nutrient levels are high, massive stands of fleshy algae can become dominant on the reefs.

#### INTRODUCTION

Recent studies of Caribbean coral reefs, especially those of Adey and Burke, 1976, Macintyre and Glynn, 1974, and Adey, 1975, have demonstrated the existence of extensive reef structures with considerable accumulations of Holocene carbonate. In addition, massive algal ridges have been found in numerous localities throughout the Lesser Antilles (see Adey and Burke, l.c.). While there are undoubtedly fewer species of reef organisms in the West Indies than in the Indo-Pacific, this is probably largely due to the great difference in geographical area and to the relative isolation of the Caribbean during the Neogene. There is no field evidence for climatic inhibition of the rate of Holocene or earlier carbonate reef build-up in the Caribbean, a conclusion that correlates with new evidence for long term stability of Caribbean sea temperatures (Climap, 1976).

Research on living Lesser Antillean reefs has not been extensive. Prior to the recent work out of West Indies Laboratory, St. Croix (see W.I.L. Special Publications, beginning 1972), and the reconnaissance study of Lewis (1975) in the Grenadines, most studies had been done in areas of very limited Holocene reef development. Areas such as the east coast of Martinique had been considered devoid of reefs, in part due to the fact that the structures found in the area did not correspond to the popular conception of what a reef should be. The waters around Martinique tend to be turbid, with visibilities ranging from three to twelve meters, depending upon wave activity. Coral growth on the reefs is restricted, and has commonly been replaced on the crest by carbonate pavement covered with a heavy, diverse growth of fleshy algae, which we refer to as "fleshy algal pavement". Fish biomass is reduced as compared

to that found on the rich Caribbean Acropora palmata reefs. In spite of their unusual morphology, it would appear that Martinique's Holocene carbonate reef systems are among the most massive and extensive in the eastern Caribbean and biologically they may be among the most productive in the West Indies.

In the island arc extending from the Virgin Islands to Grenada, approximately eight hundred kilometers of windward coast is available for potential reef development (not including Barbados). As part of the present study, a reconnaissance survey of this coast has been made by boat and plane (Adey and Burke, 1976). As a result of these observations, the windward island shores of the Lesser Antillean island arc are found to fall into four categories: (1) barren, terrigenous (volcanic) sediments, 30% of total shoreline; (2) barren, non-volcanic, 14%; (3) bank barrier reefs on carbonate shelves at depths of 12-25 m, 38%; (4) reefs on shallow (<10 m) pre-Holocene benches, 18%. Approximately 52% of the bank barrier reef shores are dominated by fleshy algal pavement reefs such as found on Martinique, 36% by Acropora palmata reefs, and 12% by an A. palmata-algal ridge transition type characterized by crustose corallines and Millepora. Algal ridges in all stages of development occur in some areas as scattered caps on the bank barriers. Shallow benches, which occur primarily on the shores of limestone islands, are dominated by high algal ridges in exposed areas, and in more protected areas by A. palmata and coralline-Millepora reefs. In category (2) listed above are found some limestone island shores which are steeply cliffed, unbenched and without shallow reefs (5% of total), as well as some shores where the carbonate shelves are deep (>30 m) and also lack well developed reefs (9% of total).

Adey and Burke (1976) discuss the distribution of these reef types throughout the Lesser Antilles. These same authors (in ms.) present a model for control of Holocene reef development by the height of pre-Holocene shelves or benches, wave energy and water turbidity. The young northeastern coast of Martinique is characterized by steep cliffs cut in volcanic sediments, a narrow steeply sloping shelf and very minimal reef development. The older eastern and southeastern coasts, on the other hand, have a well developed shelf and are rich in Holocene reefs. Martinique is located in a peak of trade wind energy and constancy in the eastern Caribbean, and an index of wind strength and constancy shows a reduction to the north as well as the south (Adey and Burke, in ms.). East to southeastern Martinique is characterized primarily by bank barrier reefs with well developed fleshy algal stands on their crests. The southernmost part of the coast is dominated by a bench algal ridge system. These areas and their reef biotas are described below.

All of the authors listed took part in both the field work and the preparation of this paper. However the various sections were largely the responsibility of the following individuals: geological structure and history - Adey and Burke; corals - Burke; algae and productivity - Adey and Adey; fish - Kaufman.

## DESCRIPTION OF THE REEFS

The following description includes the reefs from Presqu'ile de la Caravelle to Baie des Anglais (Fig. 1). It is based on three aerial reconnaissance flights, extensive examination, including coring and diving, at four sites (Vauclin Point reef, Cayes de Pinsonelle algal ridge, Islet de Ramville reef and Islet Lezard algal ridge) and numerous short visits to other points.

The reef between Passe du Vauclin and Cap Ferré has not been explored by diving. Aerial reconnaissance indicates that it is dominated by a fleshy algal pavement and with coralline-Millepora mounds on the crest in the north and a high algal ridge in the south, northeast of Point Macré. Thus, it is intermediate in character between the inner and outer systems that will be described below. Aerial reconnaissance also indicates that fleshy algal dominated reefs, with scattered coralline-Millepora mounds, exist near shore to the north of Caravelle, as far as Pte. Lahoussaye. This is apparently equivalent to the inner system to the south. Further to seaward, extending northwestward of Caravelle, a deeper ridge-like structure also occurs. This could be either a developing Holocene bank structure or a Pleistocene equivalent of the shelf edge features. We have not examined either of these areas in the water.

The major Holocene reefs of Martinique lie on the east coast between Presqu'ile de la Caravelle and the southeastern corner of the island. North of Passe du Vauclin they are arranged in a double (inner and outer) bank-barrier system. South of Cap Ferré, a single bench algal ridge system is predominant.

The double reef system, from Passe du Vauclin to Presqu'ile de la Caravelle, morphologically appears to be a set of bank-barriers developed during the middle Holocene atop the carbonate island shelf (Fig. 2). Bank barriers, which are common on many eastern Caribbean carbonate shelves, where depths are 15-25 m, typically consist of a coral or coralline framework cap (5-10 m thick) overlying a sand, rubble and head coral base. Adey and Burke (1976) suggest that these formed as "bars", largely during mid-Holocene, by coral head trapping of carbonate sand and rubble. Although the inner reef group in Martinique, which extends irregularly from Pte. du Vauclin to Baie du Galion, is rather atypical in form, paralleling the shore in a manner that is more characteristic of "bench" reefs, a series of holes bored in the Vauclin Point reef consistently penetrated the lower limit of the Acropora palmata facies at depths between 4-5 meters (Fig. 3), below which carbonate sand with occasional coral rubble is the major component. In the deepest hole in Vauclin Point reef drilling character abruptly became very hard at 14 m. We were unable to obtain core at this point, but this suggests a basement contact. It may be that the particular orientation and embayed nature of the shoreline has allowed the formation of a bank, based upon a bench. Such circumstances would require the bench to be relatively deep, at least 14 meters. Profiles across the Martinique shelf suggest that it shoals landward to such a degree that, if such a bench is present, it does not rise far above the shelf proper. These inner reefs may be bank barriers formed against an abrupt change of slope at the contact of the carbonate shelf and the volcanic rocks forming the shore.

The outer system is also unusual for the Lesser Antilles in that the apparent basement is relatively deep (25-33 m). This may result from unusually massive sand and rubble buildup on an embayed and north-south oriented coastline. Another possibility is the presence of a Pleistocene reef structure lying under the outer system. Our deepest core at Pinsonelle (Fig. 5) extended to only 13 m, however repeated drillings through the bank barrier in St. Croix (Adey and Burke, in prep.) as well as the minimum bank thickness at Vauclin reef (Fig. 3) and the shelf profile (Fig. 2), suggest that such an old reef core is not likely. Although other double bank-barrier systems are known in the Lesser Antilles (e.g., World's End and Horseshoe Reefs in the Grenadines), the Martinique system is the most extensive of these.

Profiles across several other points on the inner reefs (Figs. 5-7) are generally similar to that of Vauclin reef. Although it is not obvious on figure 1, it can be seen on the standard marine chart (HO 1009) that Sans Souci (inner), Pte. de la Prairie and especially Ramville Island reefs are more exposed than Vauclin Point reef. As a result, these reefs tend to be shallower near the crest, and both Ramville and Pte. de la Prairie have numerous low algal mounds and spurs (incipient algal ridges). These features are particularly apparent from the air, especially during low tides, but can be very difficult to see from a boat unless the sea is calm.

The inner reef system apparently developed extensive Acropora palmata caps over the bank-barrier foundation in the late Holocene. Large samples, extracted from the "clean" cores of several A. palmata arms, from the top and bottom of this facies in Vauclin reef gave  $C^{14}$  dates of 560 and 1670 years B.P. respectively. Most of the A. palmata excavated in a 3 m<sup>2</sup> hole dug to a depth of 2 m into the reef crest (Fig. 3) appeared to be in growth position. Today this coral only dominates a narrow and irregular band on the front faces of these reefs just below the zone of heavy algal growth.

Coring on the very high energy ramparts of Pinsonelle algal ridge (Fig. 4), indicates that crustose corallines have dominated the frameworks of the algal ridges on this system for at least two thousand years; a single  $C^{14}$  date from a narrow A. palmata band at a depth of 4-5 m was 2110 years B.P. Although we cored only in an emergent area on the outer system, the similarity in position and appearance of these structures would indicate that the results obtained at Pinsonelle are valid generally. It would be especially desirable to obtain a coring through to the Pleistocene shelf in an area where no algal structures have reached surface level, such as at Cayes de San Souci (see Fig. 8). However, there is little reason to believe that the basement in such cases is any shallower than at Pinsonelle. At Passe du Brigot an algal ridge is developed on both sides of the channel, and a section across the north ridge (Fig. 9) is very similar to that at Pinsonelle both with regard to depth profile and animal and plant populations (Fig. 10).

A single hole was drilled in the southern Martinique "bench-ridge system" at Lezard Is. (Fig. 11). At eight and one half meters below the surface of the ridge, drilling resistance increased markedly, suggesting

a transition from predominantly crustose coralline material to rock basement. However, a drill rod broke at this point, and we were unable to retrieve the bit and obtain core from the base of the hole. Our interpretation of these structures as "bench type" is based primarily on their location near shore, very shallow lagoons, and association with several predominantly limestone islands upon which wave cut terraces could have been formed at a period of lower sea level (see Adey and Burke, 1976). A similar drilling pattern was encountered in the bench algal ridge at Chateaux Point, Guadeloupe, where limestone basement was obtained with great difficulty from 7 m down.

The present eastern Martinique reef complex is characterized by an overwhelming dominance of large standing crops of fleshy benthic algae in crest and upper fore-reef areas, especially of the genera Sargassum and Gracilaria. This characteristic is also shared by some of the reefs of southeastern Basse Terre, St. Lucia, Grenada, and Nevis (see Adey and Burke, l.c.). Otherwise, such extensive fleshy algal reefs do not generally occur on Lesser Antillean islands except locally on sheltered and low "old" algal ridges (Connor and Adey, 1976). (Note the apparent fleshy algal covered pavement on high energy eastern Curacao (Van den Hoek et al., 1975.) The reasons for this somewhat unique algal dominance is surely due in part to the limitation of grazing by fish (Scariidae and Acanthuridae) and echinoids (Diadema antillarum) by the high wave energy. However, similarly shaped reefs with about equivalent wave action (see Adey and Burke, in ms.) in the Grenadines lack a fleshy algal cover. Through the Lesser Antilles, there appears to be a correlation of algal pavements with high turbidity; all of this is discussed below.

#### CORALS

P. J. Roos, in his 1971 study of the stony corals of the Netherland Antilles referred to a private collection of twelve species from Martinique made by P. W. Hummelinck. Eleven of these species were found during the course of the present study, Solenastrea bourni being the only exception, which was perhaps overlooked due to its similarity to the more abundant Montastrea annularis. Twenty-two additional species, including four major carbonate-producing Hydrozoans, have been identified and are listed in table 1. Their distribution along several inner and outer bank barrier transects is shown in figures 5-10.

Coral diversity on the lower fore-reef zones of the inner system is rather high, but total populations do appear to be generally low relative to comparable reef surfaces in St. Croix, Antigua or the Grenadines. The number of scleractinian species observed is about fifty percent of that reported from the intensive investigations in Jamaica (Goreau and Wells, 1967). However, as Roos (l.c.) noted "...there is considerable variation in important (diagnostic) characteristics...and great variation in growth form (of many of the corals and therefore) the great number of species of Agaricia in Goreau and Wells (1967) has to be interpreted with care." We conclude that this caution must be applied to some other genera as well. Thus, no attempt has been made to differentiate beyond the generic level for numerous morphologies of

Agaricia spp., Mycetophyllia spp., and what are apparently Colpophyllia spp. The list of coral species presented here (Table 1) could probably be increased by thirty to forty percent if taxonomic distinctions were clearer.

Inside the inner reef system water circulation and turbulence are restricted, creating conditions suitable for well developed lagoonal communities. Many of the inner bays have extensive mangrove populations, and coral production is low. However, in the lagoon area immediately behind the inner reefs, extensive beds of Thalassia testudinum and Syringodium filiforme as well as a complementary benthic algal population (see below) are found. The primary corals found here are Manicina areolata, and four species of the family Poritidae, Porites astreoides, Porites divaricata, Porites furcata, and Porites porites, the latter three species being most common. Also, associated with these are the two species of the family Siderastreidae (Siderastrea radians and Siderastrea siderea), which inhabit all other zones of the reef as well. Occasional scattered colonies of Diploria clivosa, Diploria strigosa and Oculina valenciennesi (near shore) are also common. An extremely delicate form of the Hydrozoan Millepora alcicornis is abundant in the shallow seagrass zone adjacent to the immediate back reef. Apparently this species prefers these shoal areas, which are characterized by a considerable current but low turbulence. This is also a common location for the formation of circumrotary corals (free nodules) by both Siderastrea species.

Except for the reef crest, which is locally dominated by the Hydrozoans M. complanata, and M. squarrosa, the back and upper fore reefs are characterized by large standing crops of fleshy algae and generally only a few scattered corals.

The area of coral dominance on the inner reef system is restricted to the fore reef and extends from just beneath the zone of heavy algal growth at a depth of 3-4 meters, to the sand at 10-15 meters. Because of the turbid water and the resultant reduction of light penetration, the corals within this zone represent a community usually found within a much wider depth range, and many colonies have assumed the plate-like form usually associated with deep water, although these are generally of less fragile construction.

Below the algal zone, the abundance of the various species of the order Faviidae increases with depth and then decreases again near the base of the deep fore reef. The members of the family Faviinae, including Favia fragum, D. clivosa, D. strigosa, Diploria labyrinthiformis and Colpophyllia natans, are common over the entire reef, although the latter two species are more common on the fore reef. The family Montastreinae (represented by Montastrea annularis and Montastrea cavernosa) is generally more common near the break in the fore reef slope and on the deep fore reef. Although there are some marked species preferences in the upper and lower portions of the fore reef slope (Acropora palmata above and D. labyrinthiformis and Colpophyllia spp. below), the most striking change in coral populations is in their morphologies.



The general trend of coral morphology, changing with increasing depth from crusts to heads to foliose, is similar for most major corals at all locations carefully examined on Martinique. The trend, however, is especially marked in Diploria spp., Montastrea annularis and Porites astreoides. Primarily encrusting forms of Diploria clivosa and Diploria strigosa and hummocky mounds of P. astreoides are found in the areas dominated by fleshy algae near the outer part of the algal pavement. Further seaward, they assume a hemispherical shape and are locally associated with patches of Acropora palmata. On the steeper fore reef, most corals gradually adopt the foliose morphology. Foliose Diploria spp., M. annularis, P. astreoides and Colpophyllia spp. shingle wide areas of the reef face and associated pillars, from the break in the fore reef slope to the base of the deep fore reef, over a depth range of up to ten meters.

Additional components occurring near the base of the deep fore reef community include Scolymia lacera, Meandrina meandrites, Mycetophyllia spp., and Siderastrea siderea.

On the outer reef system (Figs. 4, 8-10), the scleractinian corals are concentrated along the deep fore reef and also occur locally in back reef (reef flat) areas behind the algal ridges. The deeper fore reef community seems to be rather homogenous from our observations of three different localities, Pinsonelle, Cayes du Vauclin and Cayes de San Souci. Where the slope steepens markedly, there is a sharp decrease in fleshy algae and a corresponding increase in the frequency of corals. The Hydrozoan Millepora squarrosa, and three Diploria spp., especially D. labyrinthiformis, occasional A. palmata, along with the secondary corals (e.g., Favia spp., Siderastrea spp., P. astreoides) dominate the transition across the slope break. A gradual increase in M. annularis, Colpophyllia spp., Montastrea cavernosa, and large S. siderea then occurs down the reef face. These coral communities also occur on the sides of the deep sand channels and patches that are scattered over the fleshy algal pavements.

The back reef areas behind the algal ridges of the outer system are much more complex in that large patches of less energy tolerant species (A. palmata, P. porites) are locally very abundant. The back reef slope (sand cliff) is mostly occupied by seagrass communities, though well developed faviid reefs of M. annularis, Diploria spp. with abundant alcyonarians occur locally. Occasional A. palmata colonies also occur in this area.

There are a few major Caribbean coral species that are relatively rare in the Martinique reef system. Agaricia agaricites, which characteristically shingles vast areas on deep reefs in Jamaica and shallow areas in Belize, is rather uncommon here. Similarly, Acropora cervicornis, which is moderately common on fore reefs of the Grenadines, Guadeloupe, Antigua, and the Virgin Islands and is a mid-reef framework builder in the central and western Caribbean, was found living only at the base of a patch reef in Havre du Robert.

## BENTHIC ALGAE

As described above, on Martinique the crustose corallines are the main builders of the algal ridge caps on the outer reef system, the near-shore bench ridges in the south, and the incipient ridges forming on the crest and upper fore reef along the inner system. They also form a thin crust over much of the surface of the algal pavements of both the outer and inner reef systems. The taxonomy and ecology of crustose corallines in the Caribbean is presently under study (WHA), and, as many of the species are as yet undescribed, only a brief treatment of the dominant elements is given here.

In the deeper zones of the reefs throughout the Caribbean, the crustose corallines are poorly represented, although the genera Paragoniolithon (n. gen.), Neogoniolithon, Hydrolithon and Tenarea do occur. However, in the shallower zones that are dominated by Acropora palmata and Millepora complanata, the corallines typically encrust large portions of the usually abundant dead coral substrate. Porolithon pachydermum, Neogoniolithon megacarpum (n. sp.) and Lithophyllum congestum are dominant in well lighted areas, and Neogoniolithon accretum, Hydrolithon borgesensei and sometimes Lithothamnium ruptile and Paragoniolithon solubile are important in shaded situations (see Adey and Vassar, 1975; Van den Hoek et al., 1975). On rubble fragments scattered around the corals and patches, Hydrolithon borgesensei and sometimes Neogoniolithon mamillare are usually the dominant encrusters. The coralline populations on the inner reef system of Martinique is generally typical in the narrow A. palmata band and deeper fore-reef zones.

Although some Caribbean algal ridges are characterized by frameworks of the anastomosing branching type of L. congestum (Steneck and Adey, 1976), this has not been found to be the situation on Martinique and Guadeloupe, perhaps due to physical damage to this plant caused by higher energy levels. Although L. congestum occurs in this area, the ridges appear to be built largely by Porolithon pachydermum with a considerable admixture of Millepora.

On the fleshy algal pavements (which occupy the zones ordinarily dominated by A. palmata in other areas) the crustose coralline population is quite unusual beneath the heavy plant cover. Here Neogoniolithon n. sp., Mesophyllum n. sp., Lithophyllum n. sp. and Archeolithothamnium n. sp., all shade plants, are abundant. Most of the plants usually associated with A. palmata, with the addition of Archeolithothamnium dimotum, also occur on these pavements, but are much less abundant than those listed above. All of the species, except Archeolithothamnium n. sp., have been found in scattered localities elsewhere in the Caribbean, where they occur locally under fleshy algal patches. The Archeolithothamnium n. sp., a large, coarsely branched plant, is presently known only from Martinique.

The fleshy algae dominating the crest of Martinique reefs are both diverse and abundant. The Vauclin Point pavement, with over 100 species of macro-algae and an average standing crop of about 4 kg/m<sup>2</sup> (wet), is richer than any previously described equivalent tropical area (see Connor and Adey, 1976). (Van den Hoek et al., 1975, reported 142 algal species

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from a transect across the shore in south west Curacao. However, the transect included both shore and deeper zones. The maximum number in that study for a community-zone was 55. An equivalent number for the back algal pavement in this study would be over 90.) A series of 0.25 m<sup>2</sup> areas were collected in transects across Vauclin Point reef and Pinsonelle algal ridge. Standing crop measurements of the dominant species found are shown in figures 12 and 13. Numbers of quadrats, species encountered, frequency and standing crop by species are given in table 2.

On the Vauclin Point pavement, the maximum standing crops of fleshy algae are found on the upper fore reef (seaward of the surf zone) and on the back reef areas. There is a marked decrease in the standing crop in the surf zone, mostly due to a reduction of Sargassum platycarpum. On the algal ridge at Pinsonelle, the reduction of standing crop in the very high energy zone (which is also largely intertidal) is much more marked. Here, except for a small amount of Sargassum vulgare, virtually all of the species occurring on the fore and back ridge pavements are absent, and several Laurencia species dominate.

The Sargassum species are the major elements on the Martiniquan reef and ridge crests, although several Gracilaria, Dictyopteris, Dictyota and Laurencia species also occur in abundance. Floating Sargassum is frequent on these shores during periods of rough seas, suggesting that it is torn off by wave action (the relationship between wave action and algal standing crops over several years was described by Doty (1971a) for a Hawaiian algal pavement). On the other hand, heavy wave activity seems often to be associated with the presence of dense algal growth, perhaps serving to inhibit the predation of Diadema antillarum and parrot and surgeonfishes (mainly Sparisoma rubripinne and Acanthurus bahianus). Thus, Sargassum appears to reach high densities within a relatively narrow range of wave energy. Large algal stands do occur intertidally (on algal ridges) in relatively quiet St. Croix, but in Martinique, they extend down to 3-4 m on the medium-high energy inner reefs, and reach 10-15 m on the very high energy outer system.

With adequate protection, D. antillarum can probably survive long periods of intense wave action without moving from shelter. Within the area of dense algal growth behind the crest at Vauclin Point reef are several bare depressions occupied by large groups of Diadema. These typically cover an area of about 3 x 5 meters and are approximately 50 cm deep, sharply delineated at the upper rim by the surrounding algal forest. Apparently the urchins are kept within these patches by the force of current and swell as well as the whipping action of the long Sargassum fronds. During periods of especially intense wave activity these patchy Diadema seem to be restricted even more narrowly and pioneer algal growth begins to encroach upon the bare carbonate areas. As conditions return to normal, however, this new growth quickly disappears. Areas adjacent to the barren Diadema depressions, when cleared of their heavy algal growth are usually kept clear by Diadema grazing when wave energy stays at moderate levels. However, under rough conditions these areas are slowly re-covered with fleshy algae. It would appear that if wave action were to diminish greatly for a considerable length of time, the Diadema already present on the reef could decimate the algal stand. Therefore consistency of wave

action would seem to be as critical as intensity. This might provide one explanation for the extent of the algal pavements that are present on Martinique, located as it is in the zone of maximum trade wind constancy.

Our studies have indicated that three factors are related to the presence of sublittoral fleshy algal pavements: strong wave energy, smooth carbonate pavement and turbid waters. In addition to the inhibition of grazing activities that has been discussed above, it is also likely that wave energy plays an important role in the formation of smooth carbonate pavements by reduction of the coral population through breakage and the filling of the reef matrix with transported sediment and debris. Once such a smooth pavement is formed, grazing is further reduced because holes and niches used for protection by reef organisms are drastically reduced in number. However the combination of high wave energy and smooth carbonate pavement is usually not enough in itself to stimulate the formation of heavy fleshy algal growth, as is evidenced in many reefs in the Grenadines where the water is quite clear. It would seem that turbid water, probably rich in nutrients, is also required for the general heavy growth of fleshy algae, as has been observed by Adey and Burke (1976).

As has been discussed above, the crests of Martinique reefs were not always covered by fleshy algal pavements, but were dominated in the past by Acropora palmata, although it is probable that the water turbidity and energy conditions were not significantly different during that period than they are today. It seems likely that the changeover occurred when the A. palmata reef grew to near sea level and gradually was transformed by wave energy into a carbonate pavement upon which fleshy algae could flourish in the turbid water.

#### PRODUCTIVITY

Coral reefs are biologically among the most productive systems known. Oxygen exchange rates (based on changes in oxygen concentrations in water flowing over reefs and transformed to organic carbon), have been used to obtain gross figures of about 5 to 25g C/m<sup>2</sup>/day. In a typical Caribbean A. palmata reef environment, living corals and coralline algae cover a relatively small proportion of the total reef surface. Usually, much of the total area at any one time consists of dead coral substrate with a short, dense turf of small filamentous algae, blue-greens often being abundant. An algal ridge or pavement with a large standing crop of fleshy algae might be expected to be more productive than a typical coral reef; Connor and Adey (1976) suggested this in the study of an algal ridge lobe on St. Croix, where values of 24 to 45 C/m<sup>2</sup>/day were obtained.

Preliminary oxygen exchange studies were undertaken on both Vauclin Point reef and Pinsonelle algal ridge, using the Winkler method for measuring dissolved oxygen. At Vauclin Point reef, the breaker zone begins approximately one third of the way back from the seaward margin of the algal pavement. For each of the 15 sets of oxygen data taken, five samples were collected: seaward of the reef; beginning of the algal zone;

beginning of the breaker zone; end of the breaker zone; at the landward limit of the pavement. By plotting these data as a function of position and measuring water flow (float bottles) over the reef, it was possible to determine gain or loss of oxygen in the breaker zone and the net exchange of oxygen between reef surface and the water in terms of  $\text{g}/\text{m}^2/\text{hr}$ . Dissolved oxygen values of 6 to 7.2  $\text{mg}/\text{l}$  were found across the Vauclin Point reef and mid-winter results for both clear and partly cloudy (overcast) days are shown in figure 14. From these data, a gross productivity for the clear day of approximately  $33\text{g O}_2/\text{m}^2/\text{day}$  or  $10\text{g C}/\text{m}^2/\text{day}$  was determined. This is well below that obtained by Connor and Adey (l.c.) for the St. Croix algal ridge in April. However, the marked difference between the cloudy and the bright days suggests that, even at this latitude, daily and seasonal differences may be considerable. Summer productivity probably is considerably higher.

Only a single series of oxygen samples were taken across the Pinsonelle algal ridge, on the second of January. The oxygen concentrations rose from 6.8 $\text{mg}/\text{l}$  in front, to nearly 8.1 $\text{mg}/\text{l}$  immediately behind the ridge pavement system. About two-thirds of this rise occurred on the rather short back ridge algal pavement, indicating that this very shallow area is considerably more productive than the deeper Vauclin Point pavements. This further suggests strong limitation of productivity with decreasing light in sublittoral reef systems. Adey et al. (studies in progress) found gross oxygen production in Rod Bay, St. Croix during November to be  $17\text{g O}_2/\text{m}^2/\text{day}$  for a 1 m deep mixed coral and algae back-reef and  $13\text{g O}_2/\text{m}^2/\text{day}$  on a typical Acropora palmata-algal turf fore-reef with an average depth of about 4 m. (Very similar levels of 17 and  $10\text{g O}_2/\text{m}^2/\text{day}$ , respectively, were also predicted using species productivity values of Doty (1971b) and the standing crops of algal turfs typical of the reef.) Thus, for approximately the same depth (1m), productivity on the Martinique algal pavement was twice that of the back reef on St. Croix. This agrees with the theoretical consideration that while filamentous algae generally show 10-20 times greater productivity per unit weight than the more massive algae (Doty, l.c.), the standing crops of massive fleshy algae on these algal pavements are 20-30 times greater than that of filamentous algal turfs in a "coral" reef.

These data suggest that with very extensive algal pavements at depths of 1-2 m, the reef systems of Martinique are probably the most productive in the eastern Caribbean.

#### FISHES

The fish assemblages of the algal-dominated Martinique inner reef system differ markedly from those of typical A. palmata and mixed A. palmata-coralline-Millepora reefs of the eastern Caribbean. The fishes associated with coral and bare carbonate areas are similar to those of the mixed reefs, although certain conspicuous species are rare or absent. The fleshy algal pavements are heavily populated with typical grass bed populations usually alien to the mixed and A. palmata reefs. This contrast in fish assemblages may be explained by the general

disruption of small scale habitats as the formerly Acropora palmata dominated reefs of Martinique acquired their fleshy algal pavement caps.

During February-April 1975, about one hundred hours between 0900 and 1900 were spent observing fishes at five general locations on Martiniquan reefs: Ramville Island, Sans-Souci channel and Pte. du Vauclin on the inner bank barrier system; at Lezard algal ridge on the southern bench system; and on the more protected parts of Loup Garou on the outer bank barrier system. Assemblages were described by snorkeling or SCUBA diving within a broadly defined habitat (e.g., fleshy algal pavement) and recording the relative abundances of the fishes seen. Data were recorded with time from the beginning of each observation period, allowing the construction of sampling effort (time)/species number curves. From these curves it was determined that even in the most heterogenous environments, where frequent crossing of broad habitat boundaries complicated data recording, fifty to sixty minutes was usually sufficient to record over ninety percent of the visible species. The required time was somewhat longer in regions of high wave energy and turbidity. The major patterns discussed here include only the most abundant species. These were often observed within the first thirty seconds, without significant change in relative abundance estimate over several hours of observation. The relative merits and drawbacks of visual population estimates of reef fishes have been discussed by Bardach (1959) and reviewed by McVey (1972) and Gunderman and Popper (1975).

Table 3 lists all species encountered during the Martinique study, grouped in order of greatest relative abundance. Table 4 compares the relative abundance of several characteristic fishes on fourteen eastern Caribbean reefs, including Martinique. The reefs have been categorized on the basis of dominant surface features; Union Island, Goyave and Nevis reefs include patches of two categories.

As seen from Table 4, compared to mixed A. palmata-coralline-Millepora reefs, "pure stands" of A. palmata had fewer parrotfishes and were missing many other species. Randall (1967) noticed smaller populations of fishes on "Luxuriant reefs of Acropora palmata..." and attributed this pattern to "...limited food for fishes which feed on attached marine life or organisms therein," in spite of the excellent shelter provided by the continuous coral cover. Our experience on Rod Bay Reef, St. Croix, where living A. palmata occupied less than 30% of the surface and algal turfs are responsible for 80% of the productivity, further suggests that grazing fish may be food limited on extensive "pure stands" of A. palmata.

The Martiniquan reefs differ even more dramatically from those with both patchy A. palmata and coralline-Millepora pavement. Many species are missing from Martinique and even Sparisoma viride and Scarus vetula have a very restricted distribution. However the reefs support a much greater proportion of grass bed fishes such as the bucktooth parrotfish, mutton hamlet, and blackear and dwarf wrasses (occurrence in grass beds cited from Randall, 1968; Bohlke and Chaplin, 1968). This peculiarity of the fish populations is almost certainly not biogeographical, since all of the absent species are found on reefs both to the north and south, and

no special biogeographical boundaries fall through this area. Furthermore, at the reef at Goyave, Gaudeloupe (which is apparently in the process of developing from a typical Acropora palmata reef into one with a fleshy algal cover) there are adjacent patches of fleshy algal pavement and A. palmata surrounded by coralline-Millepora pavement. The assemblage on the fleshy algal pavement is similar to that of Martinique, while the assemblage on portions dominated by A. palmata is typical of this type of reef.

From Table 4 it can be seen that the Martiniquan fish assemblages resemble those of other reefs with extensive fleshy algal pavements much more than those with extensive A. palmata or mixed patches of A. palmata and coralline-Millepora pavement, even where they occur on the same island. This suggests that the fish assemblages on fleshy algal pavement reefs are due to either structural or food resource characteristics of these reefs which differ from those of A. palmata or mixed reefs.

The large Scarus spp. and Sparisoma viride are characteristically grazers and scrapers of carbonate surfaces rather than browsers on the larger fleshy algae. Their main food in a typical A. palmata reef is probably the abundant algal turfs growing on dead coral (Randall, 1967), often the most significant primary producers in this environment (Adey, studies in progress). It is possible that pavement reefs with dense fleshy algal stands do not have sufficient food resources of the proper type to maintain these big turf grazers.

Most parrot fishes form herds in open water, a behavior which is probably facilitated by bright color patterns (Hamilton, in press). When encountering the snorkeler (and presumably any other potential danger) large Scarus spp. and S. viride disappear beneath ledges or among interlocking arms of A. palmata. Since reefs dominated by fleshy algal pavements usually lack this shelter as well as grazeable algal turfs, these fishes would be forced to adopt rather different habits to survive there as adults. Apparently this has not occurred for any of the larger parrotfishes excepting the yellowtail, Sparisoma rubripinne. When encountered away from shelter, this species assumes a mottled, cryptic color pattern and nestles down against the algal cover. On the pavements at Martinique, Nevis and Guadeloupe it was usually observed browsing on fleshy algae rather than grazing on the small amount of turf-covered coralline pavement that was available. Ten S. rubripinne were shot for stomach analyses. Stomach contents were difficult to identify to species, however most were filled with fleshy fragments. Thus S. rubripinne seems much better suited to life on the fleshy algal pavements than S. viride or any of the large Scarus spp.

Sparisoma radians is also capable of cryptic coloration and behavior on fleshy algal pavement, as well as feeding on the algae growing there. Randall (1967) found it feeding primarily on Thalassia in grass beds. The mutton hamlet and dwarf and blackear wrasses are cryptic carnivores that are capable of matching any mottled green or brownish substrate. Since they are abundant both in grass beds and on fleshy algal pavement, they apparently do not prey exclusively on organisms peculiar to one or the other of these habitats.

Many fishes which can reach great abundance on all reef types are of extremely localized distribution on fleshy algal pavements. For example, it has been demonstrated that juvenile Eupomacentrus planifrons (threespot damselfish) inhabit live, branching coral ("bushes") which the fish kills as it matures (studies in progress - Kaufman). Adults prefer dead corals of similar morphology, on which they "farm" small fleshy algae by chasing herbivores from a territory. This study was performed at Jamaica and St. Croix, but similar patterns of micro-distribution for this and other species were observed throughout the eastern Caribbean and the Florida Keys. In Martinique, juvenile E. planifrons were fairly abundant on back-reef Porites porites shoals and fissured rocks, but nowhere else. Adults were restricted almost entirely to small patches of A. palmata on the fore-reef, where they defended territories on dead coral.

Observations on the local distributions of many other species tend to support the hypothesis that differences in fish assemblages between reefs dominated by fleshy algal pavements and those dominated by living A. palmata and/or algal turf-covered coralline-Millepora pavements are primarily due to differences in either or both habitat structure and food resource availability. The reefs of Martinique assumed their present character approximately 600 years B.P., before which the reefs were dominantly A. palmata. Presumably, the fish assemblage at that time was as different from that found today as are those of existing A. palmata reefs. In assessing the historical effects of fishing on local populations, one should note that major changes in the distribution and abundance of Caribbean reef fishes probably have occurred as the reefs themselves have matured. In many respects, these changes may be independent of man's activities, and are probably still in progress today.

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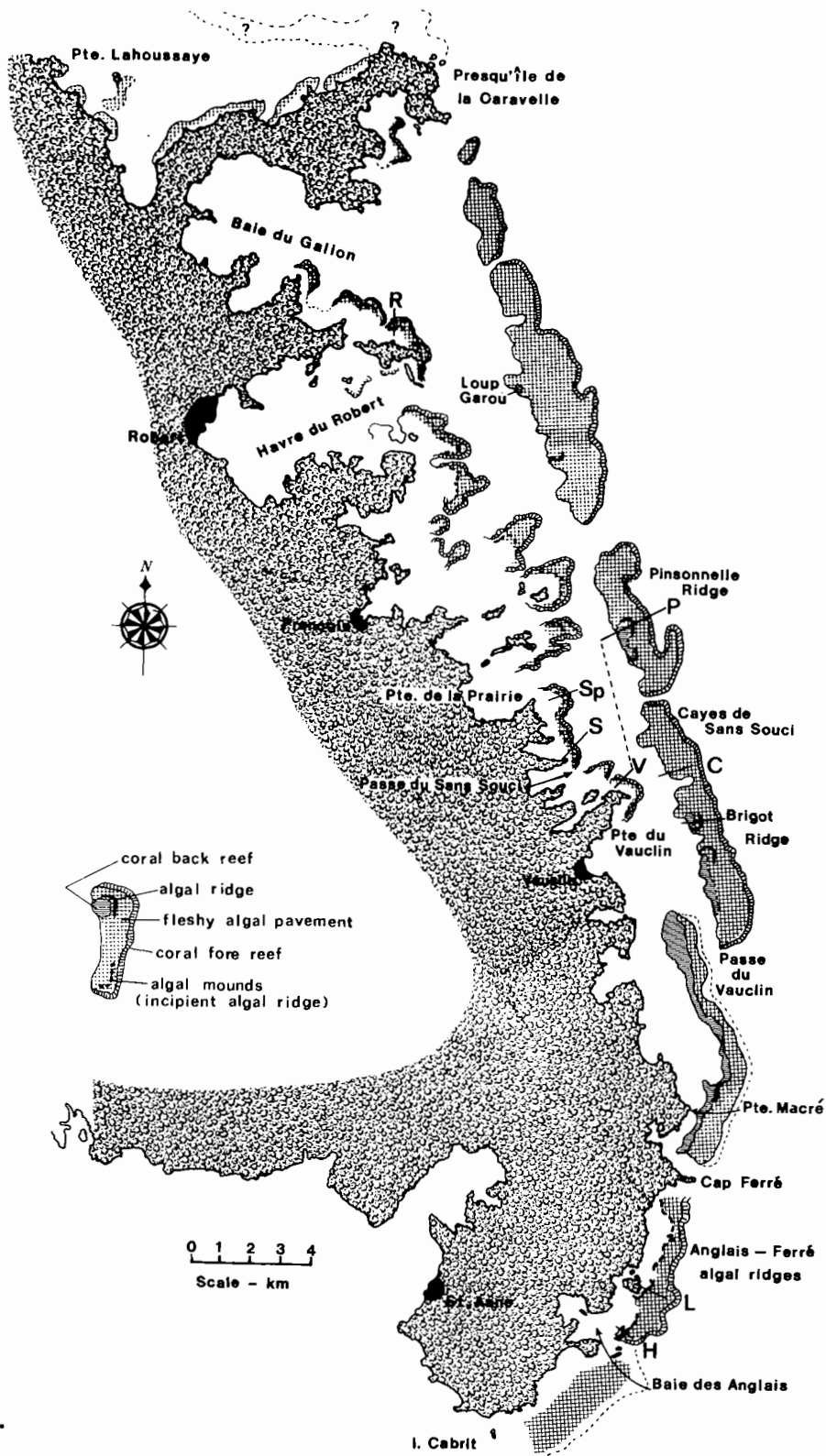


Fig. 1.

Holocene bioherms on eastern Martinique. Transects: H - Hardy Is., L - Lezard Is. (Fig. 11); Brigot Ridge - Cayes du Vauclin (Fig. 9); C - Cayes de San Souci (Fig. 8); P - Pinsonnelle algal ridge (Figs. 4, 10); V - Vauclin Point (Fig. 3); S - San Souci channel (Fig. 7); Sp - Pointe de la Prairie (Fig. 7); R - Ramville Is. reef (Fig. 5)

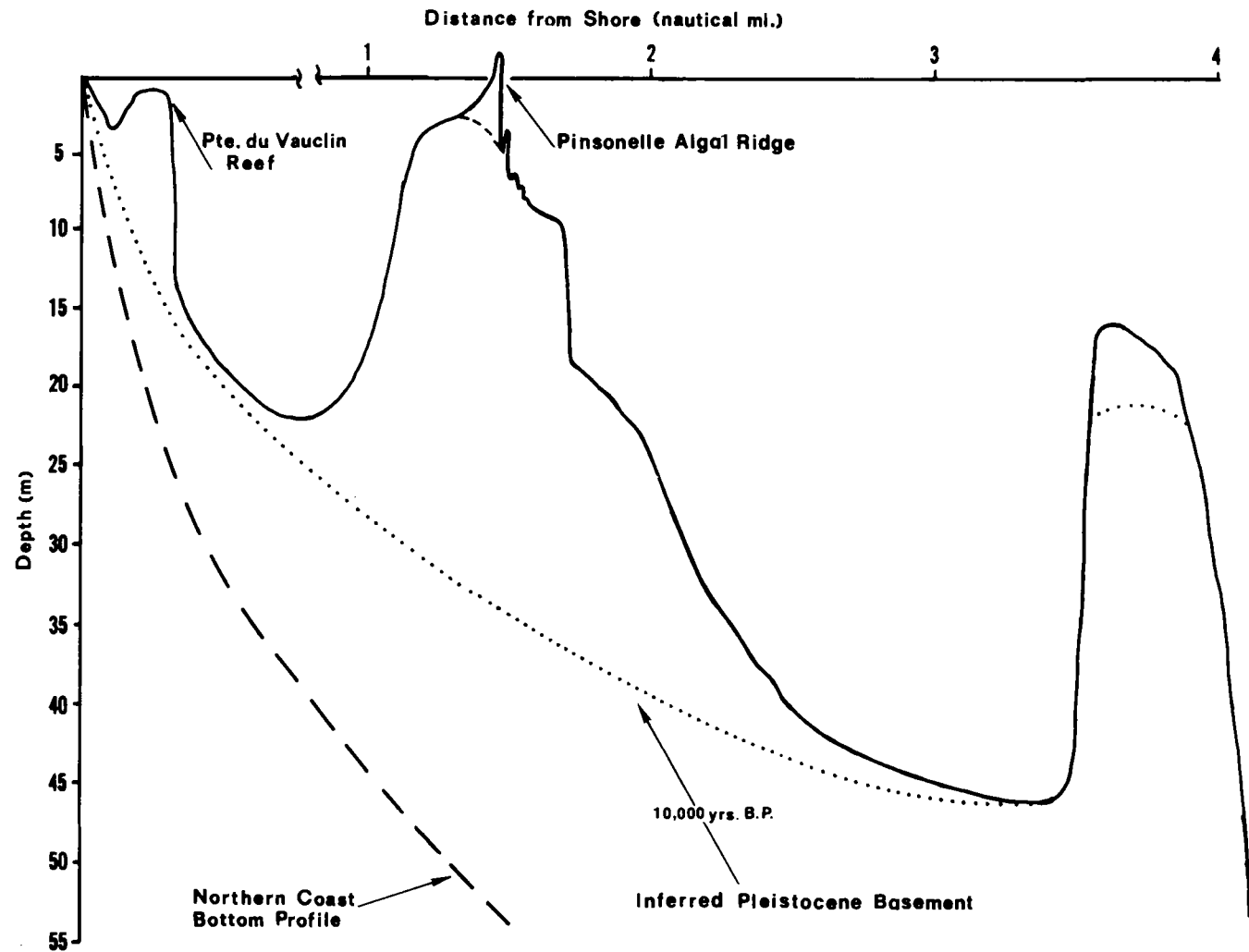


Fig. 2. Bottom profile (see V--P on Fig. 1 for location) across eastern shelf showing inner and outer reef systems and the shelf edge feature (Macintyre, 1972; Adey and Macintyre, in prep.). The sub bottom profile inferred is discussed in the text. The northern coast profile was taken off Point Chateauque.

Fig. 3. Section across Vauclin Point reef, V on figure 1.

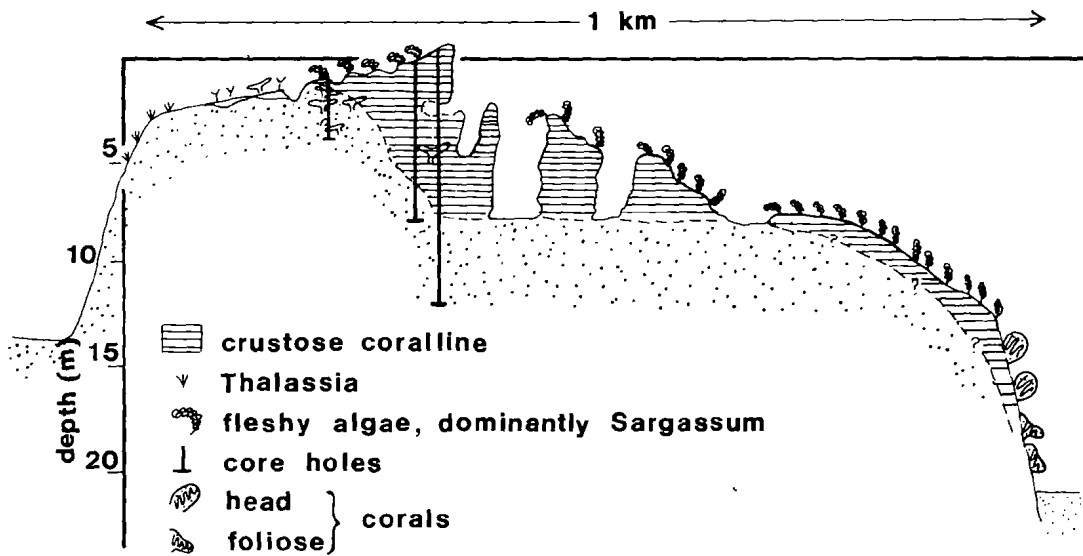
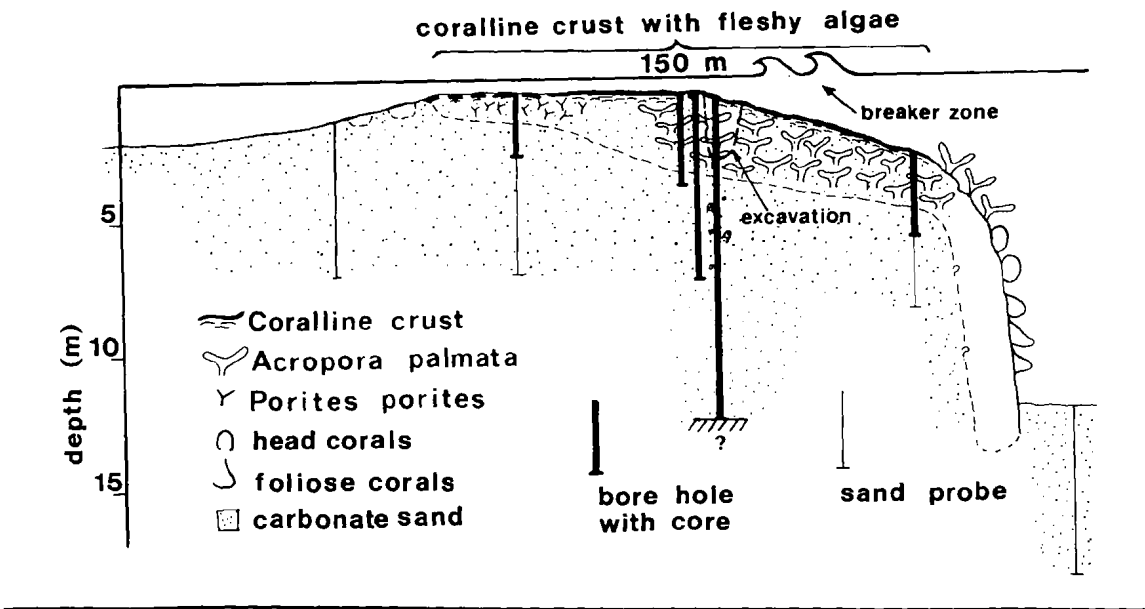


Fig. 4. Section across Pinsonelle algal ridge on the outer reef system, P on figure 1.

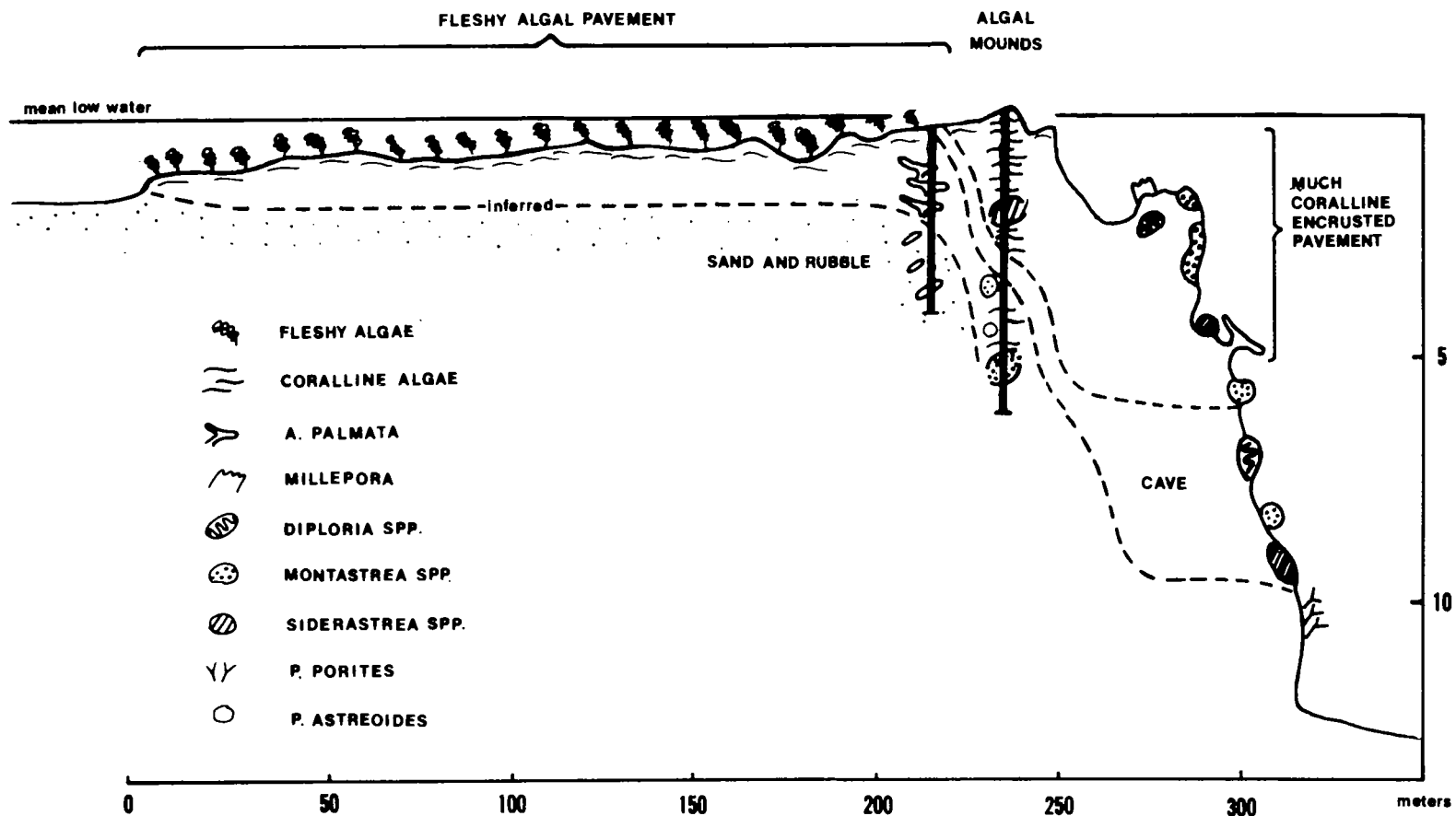


Fig. 5. Section across Ramville Island reef, R on figure 1.

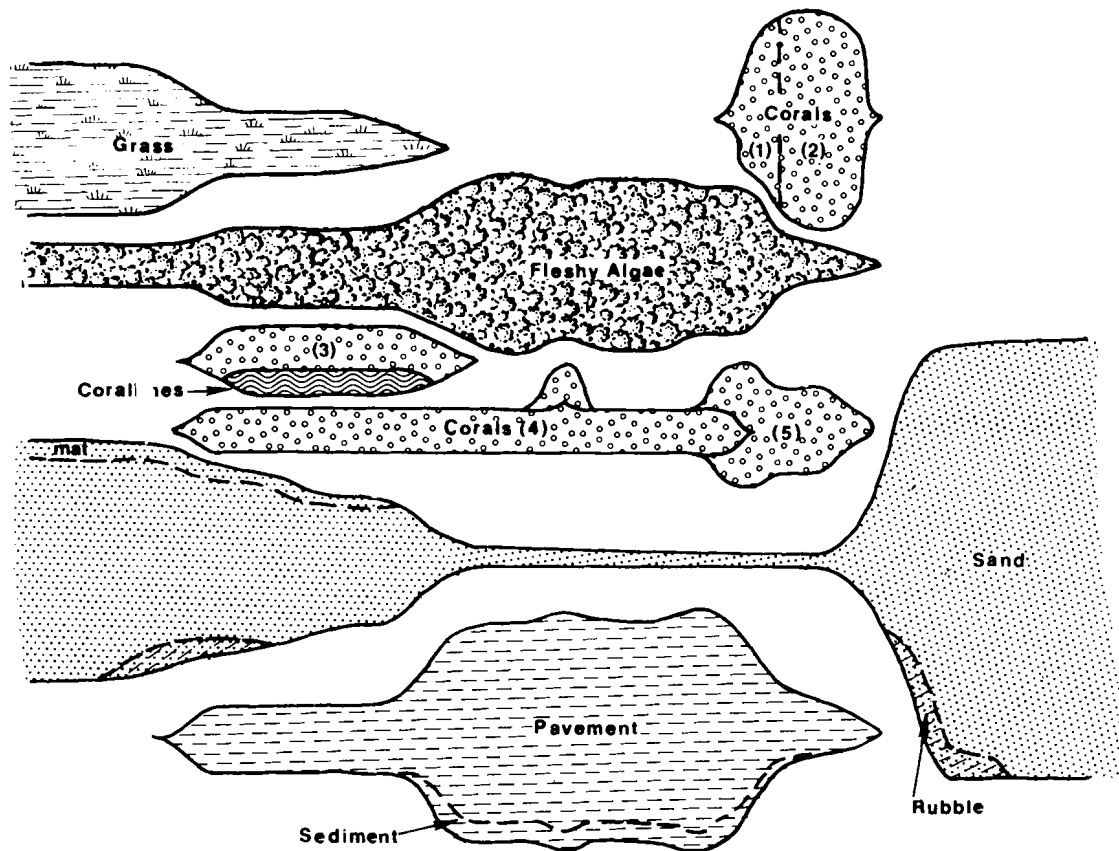
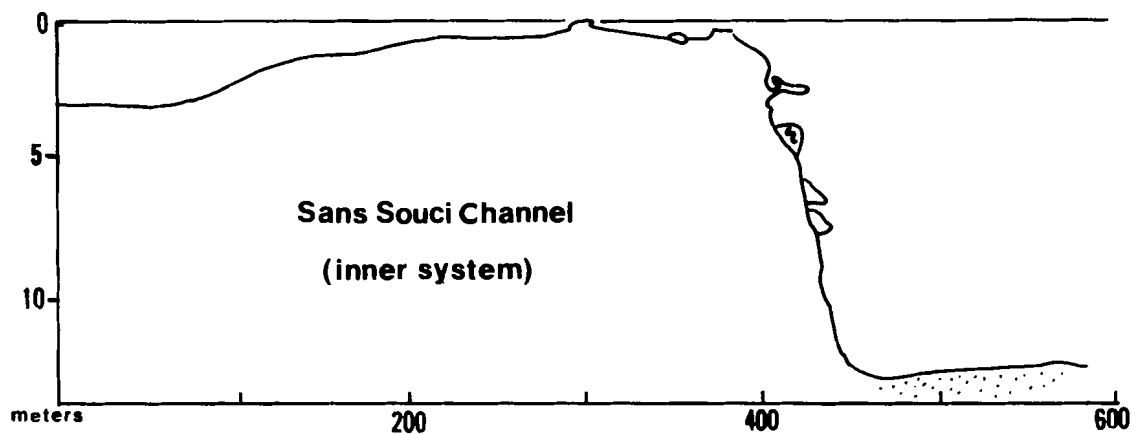


Fig. 6.



Profile and surface zonation across San Souci Channel reef. Section S on figure 1. Corals: (1) *Porites porites*. (2) *Montastrea annularis*, *Diploria clivosa*, *D. strigosa*. (3) *P. furcata*. (4) *P. astreoides*, *Dichocoenia stokesii*, *Manicina areolata*, *Favia fragum*, *M. annularis*. (5) *Millepora* spp., *Acropora palmata*. Corallines: *Neogoniolithon westindianum*. Pavement: grazed coralline encrusted. Mat: algal stabilized sediment.

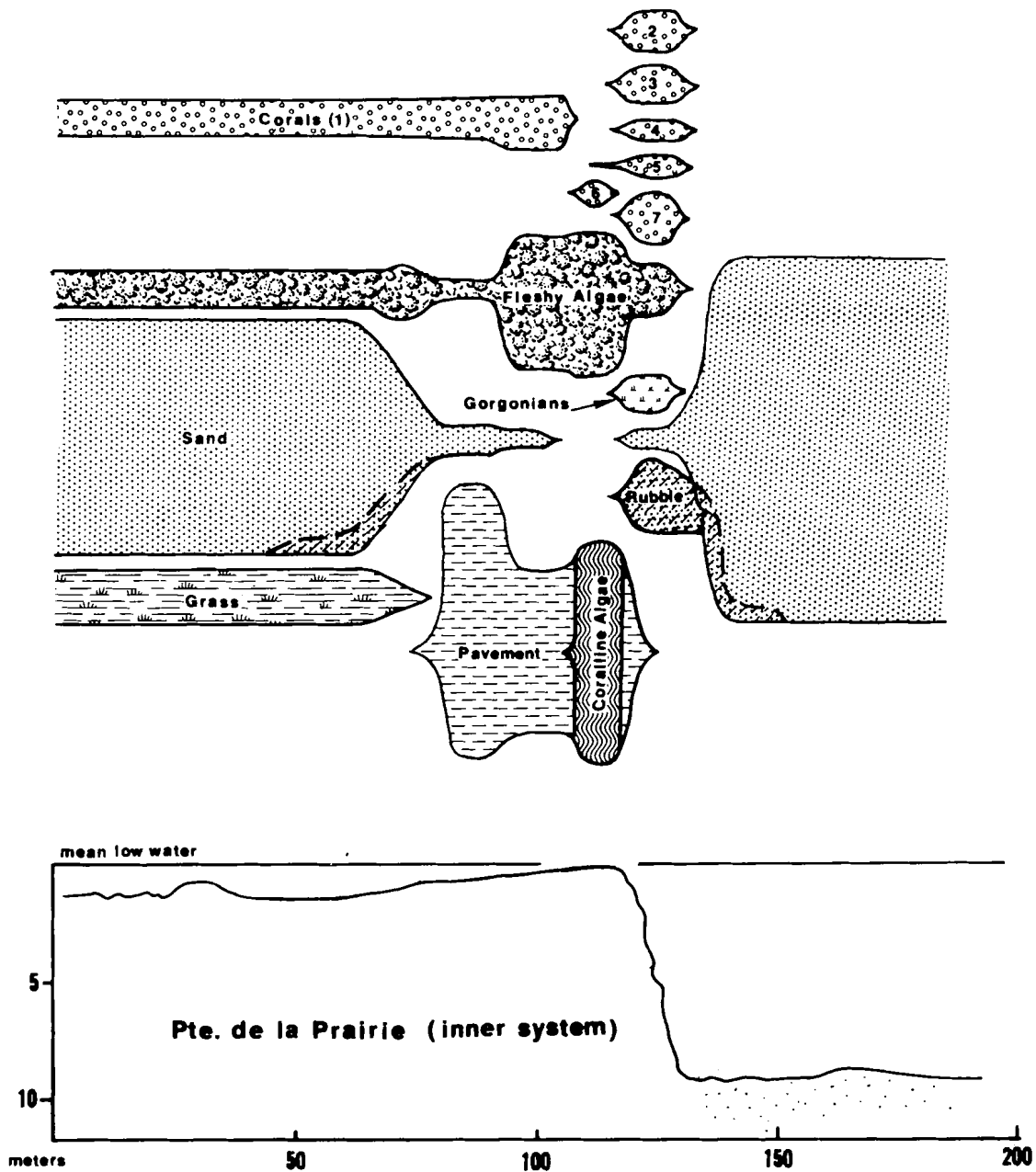


Fig. 7. Profile and zonation across Pte. de la Prairie reef. Section Sp on figure 1. Corals: (1) Porites porites, P. astreoides, Siderastrea siderea, S. radians, Manicina areolata, Favia fragum. (2) Diploria spp. (3) Montastrea annularis. (4) Acropora palmata. (5) P. astreoides. (6) Millepora squarosa. (7) P. porites, P. furcata, Mycetophyllia sp., Agaricia sp.



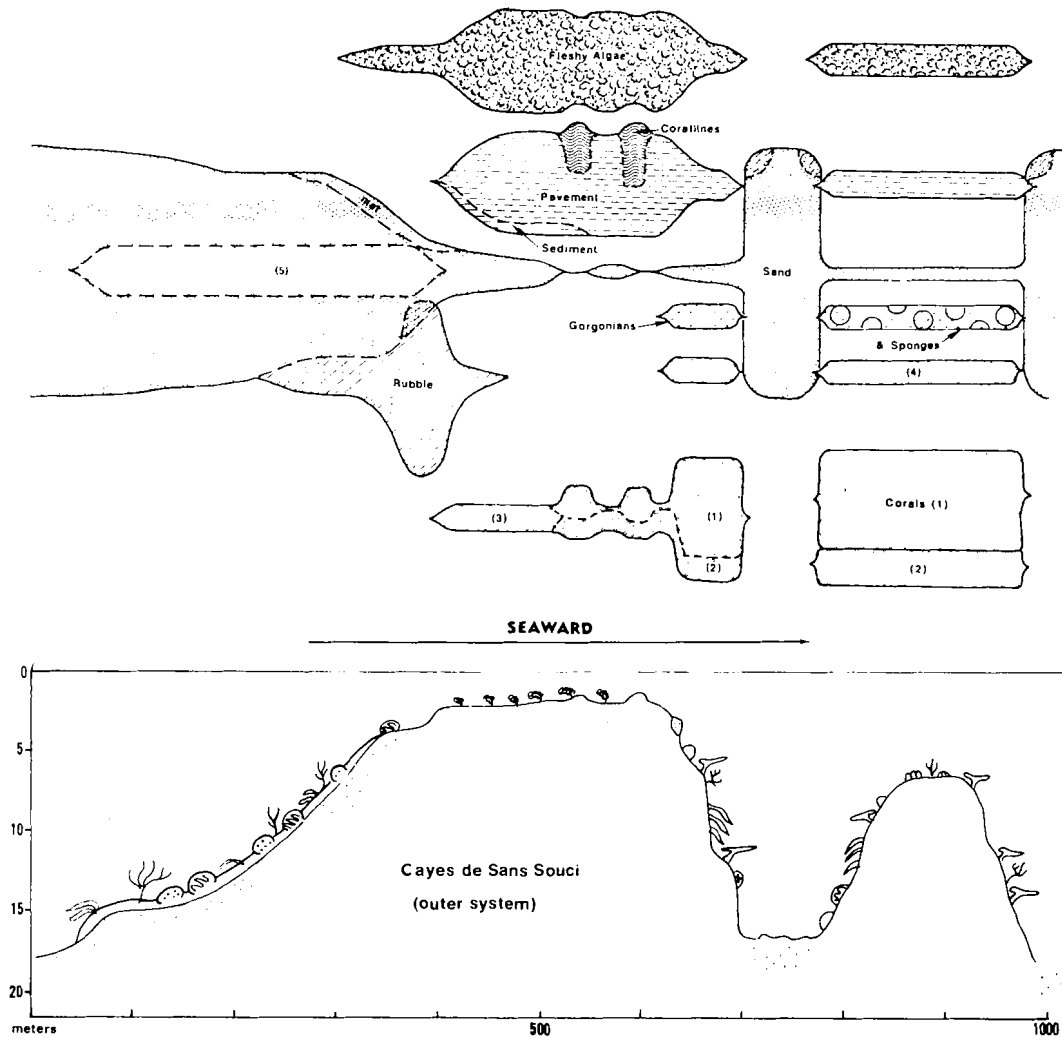


Fig. 3. Profile and zonation across Cayes de San Souci. Section C on figure 1. Corals: (1) Diploria labyrinthiformis, D. clivosa, Millepora spp., Montastrea annularis, Agaricia agaricites. (2) Isophyllia sp. Mycetophyllia sp., Porites astreoides. (3) Favia fragum, Diploria sp., Siderastrea siderea, P. astreoides. (4) Acropora palmata. (5) deep reef community growing on carbonate spurs. Corallines: Lithophyllum congestum, Neogoniolithon sp.

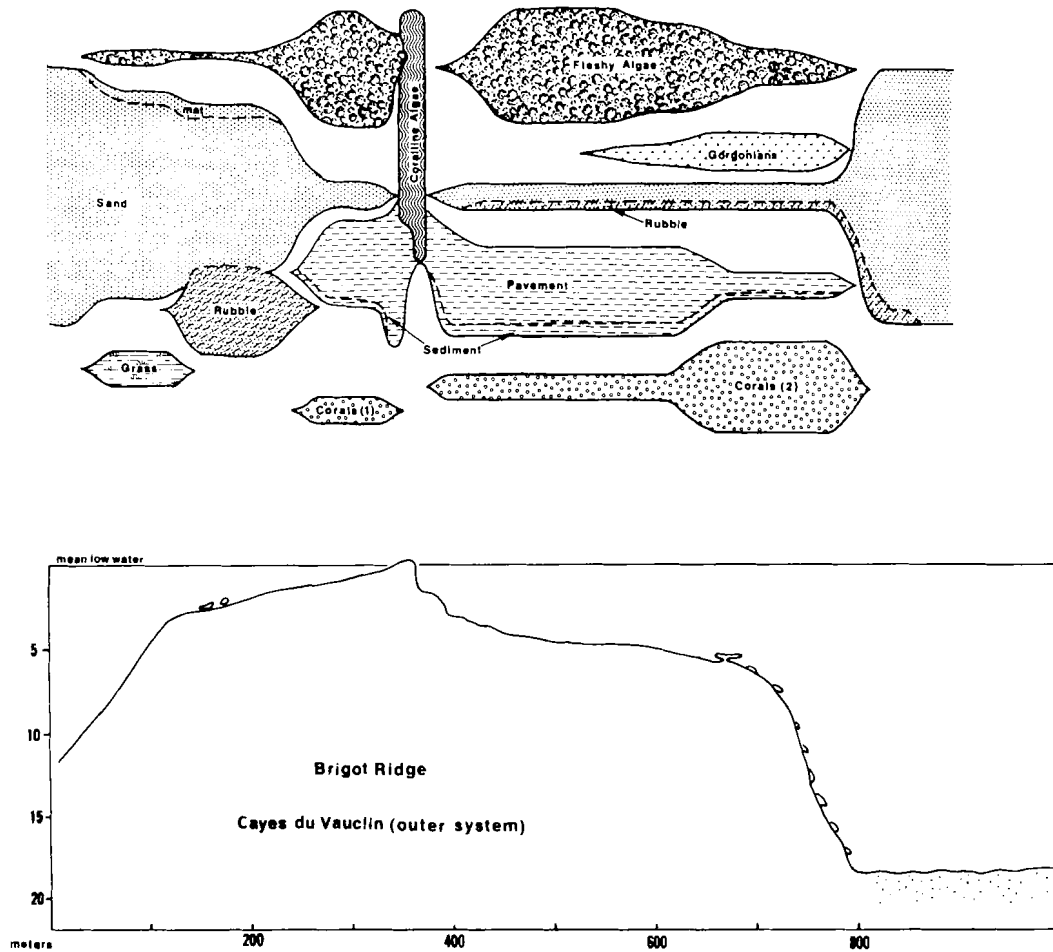


Fig. 9.

Profile and zonation, Cayes de Vauclin (Brigot). Marked Brigot Ridge on figure 1. Corals: (1) Millepora sp. and Porites astreoides. (2) Millepora sp., Diploria clivosa, upper section; Siderastrea siderea, Montastrea annularis, Isophyllia sp., lower section. Coralline algae, about 75% living - Lithophyllum congestum, Neogoniolithon megacarpum, Neogoniolithon spp., Porolithon pachydermum.

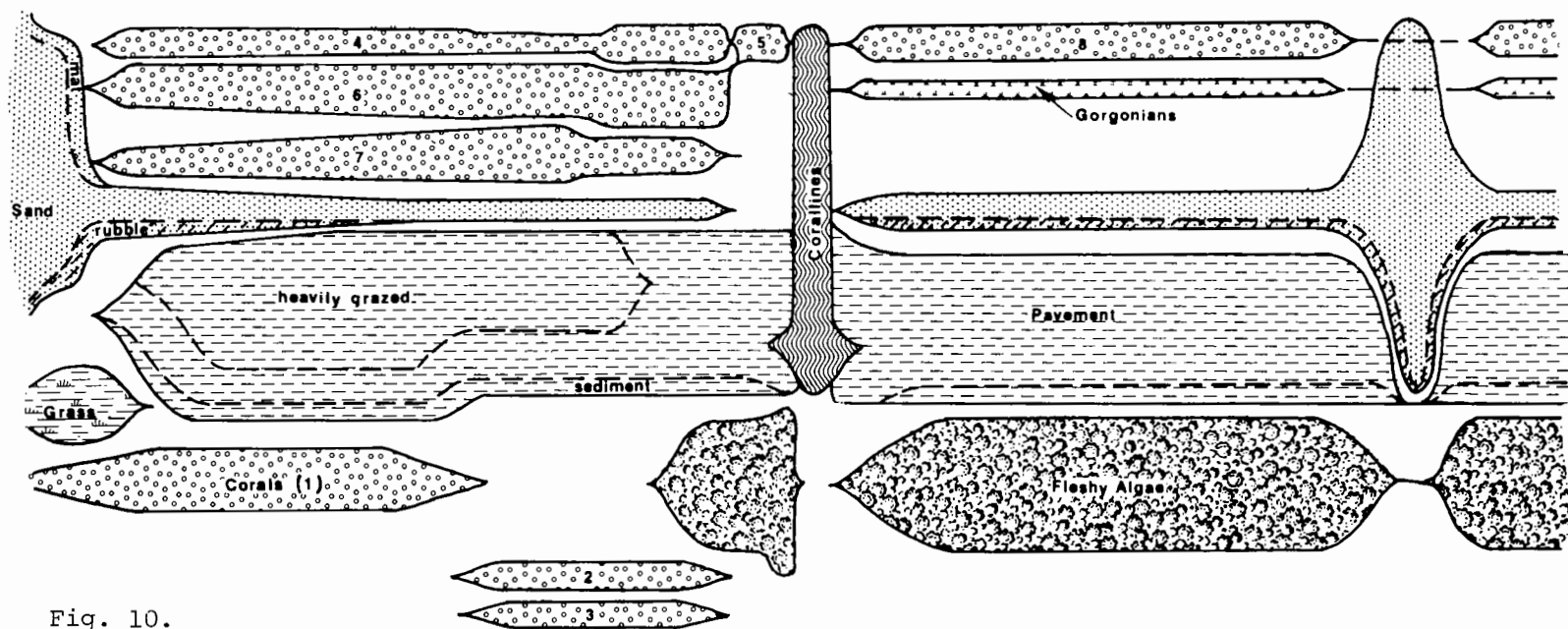
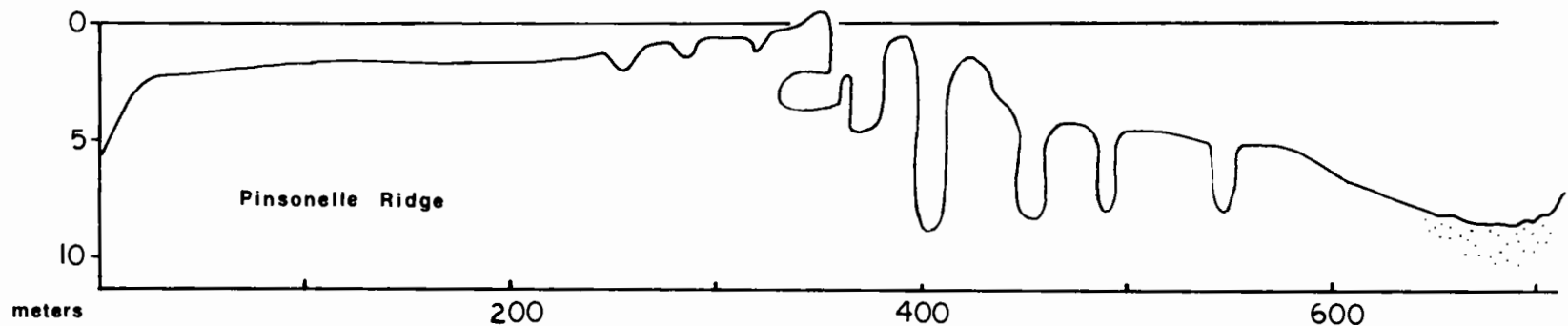


Fig. 10.



Profile and zonation, Pinsonelle algal ridge. (1) Acropora palmata. (2) Millepora spp. (3) Montastrea annularis. (4) Agaricia agaricites, Favia fragum, Diploria clivosa. (5) Siderastrea siderea, Diploria clivosa, Porites astreoides. (6) Porites astreoides. (7) P. porites. (8) Millepora alcicornis, F. fragum, D. clivosa. Corallines: Porolithon pachydermum, Lithophyllum congestum, Neogoniolithon megacarpum. Fleshy algae: dominantly Dictyopterus and Sargassum

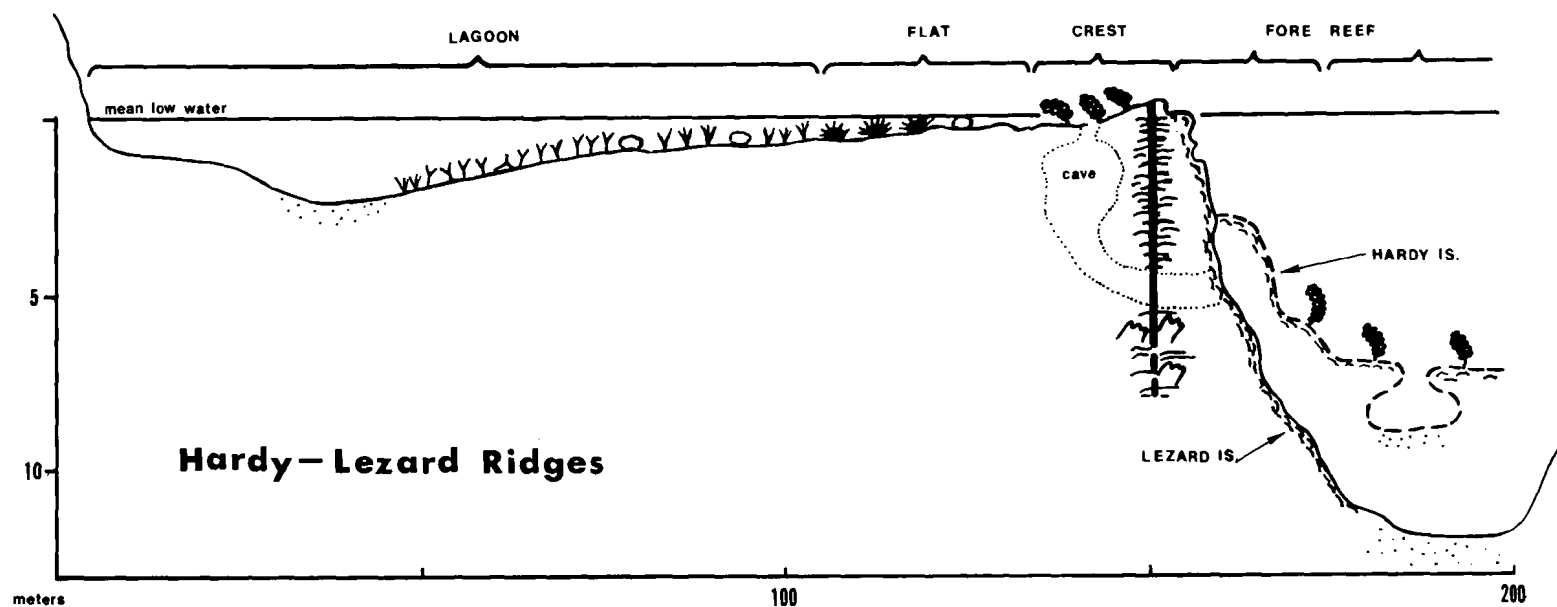


Fig. 11. Composite section across bench algal ridges at Hardy and Lezard Is., showing location and composition of core drilled at Lezard. H and L on figure 1. Lagoon - sand, *Porites* spp. and sea grasses. Flat - heavily grazed coralline encrusted pavement, abundant *Diadema* and *Porites astreoides*. Crest - abundant fleshy algae, especially *Hypnea* and *Laurencia*. Fore reef - upper section, coralline pavement, often heavily grazed, scattered corals; lower section, fleshy algal pavement with sand channels. Symbols as in Fig. 5.

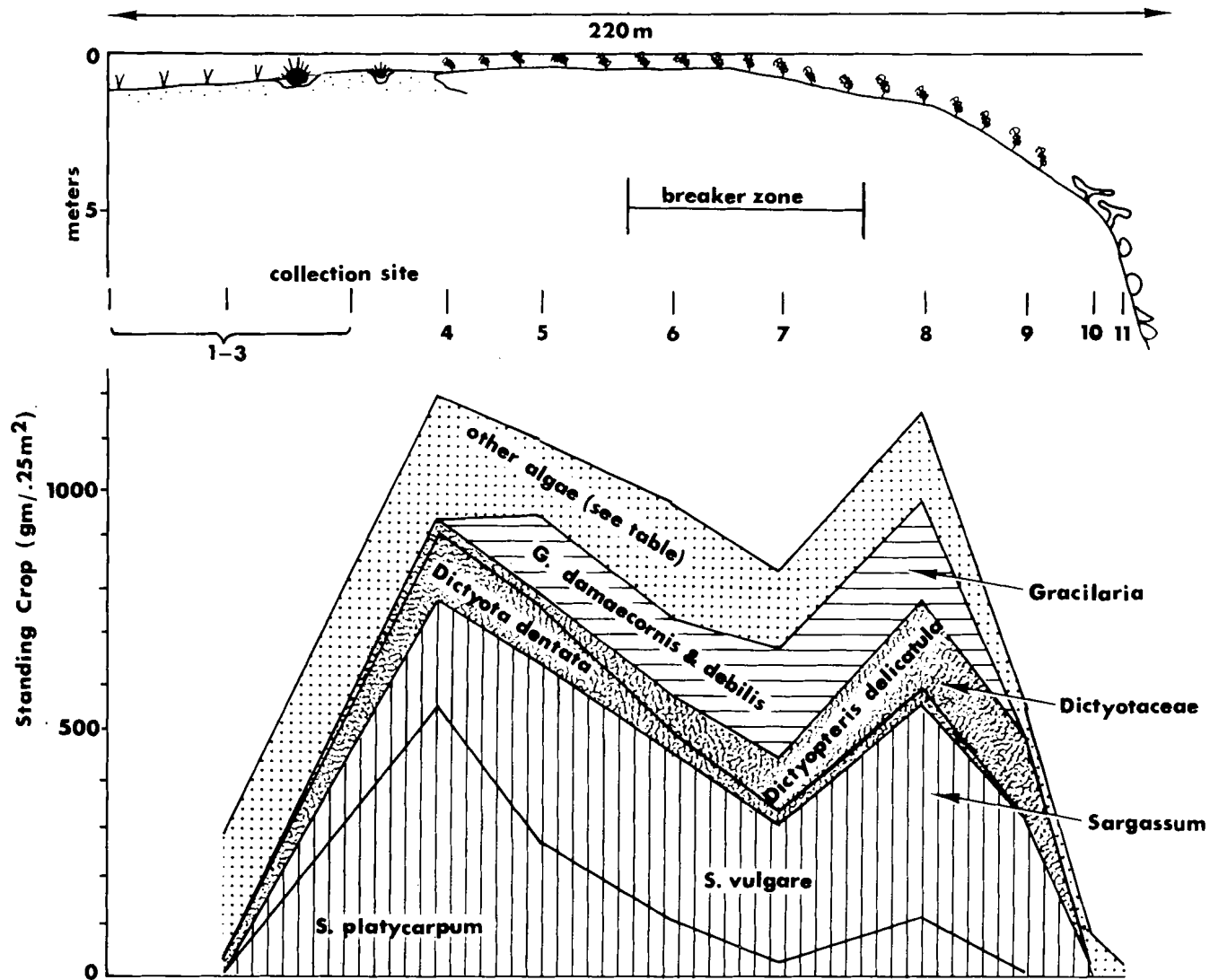


Fig. 12. Dominant species of benthic fleshy algae and standing crop on Vauclin Point algal pavement.

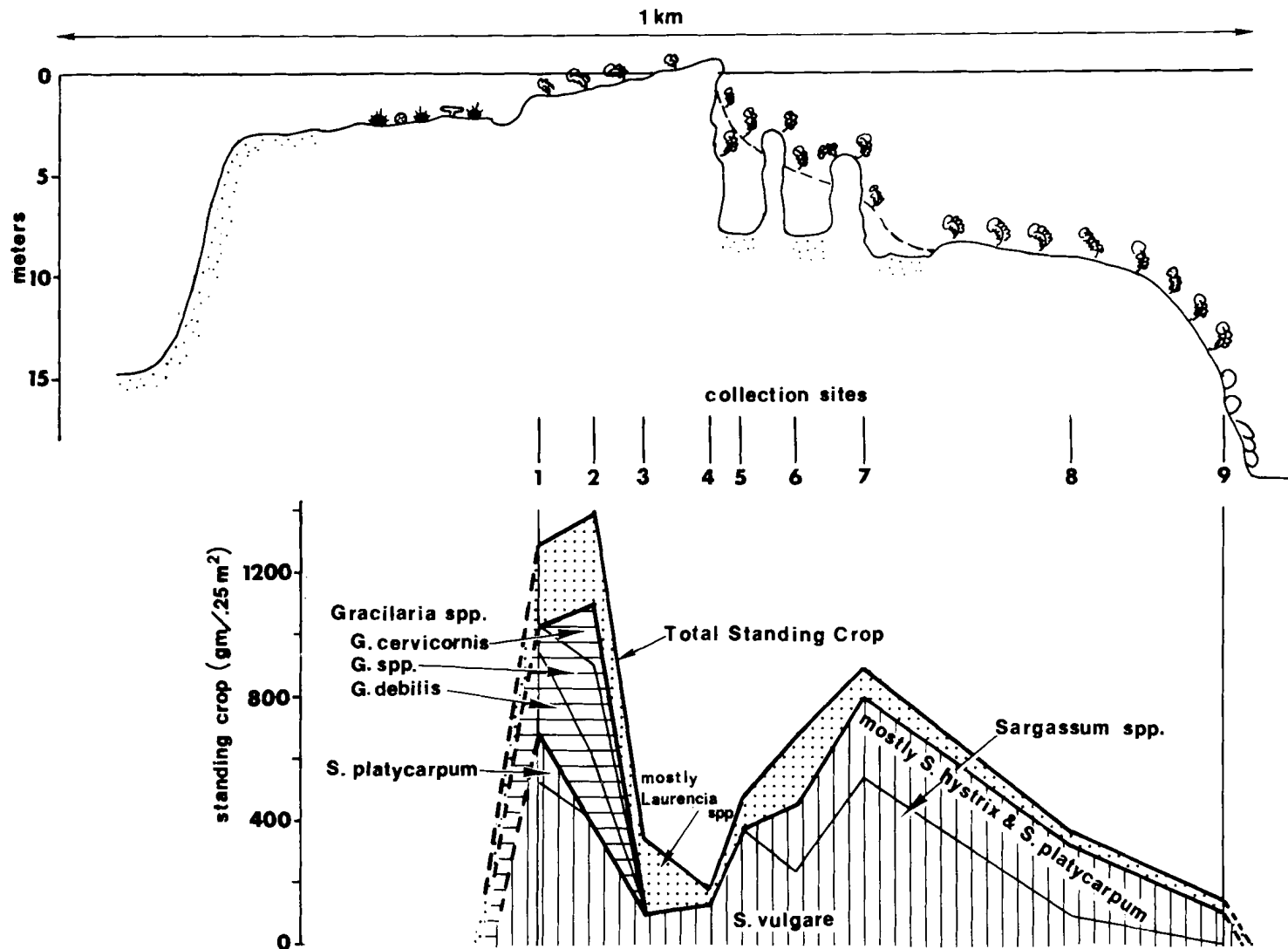


Fig. 13. Dominant species of benthic fleshy algae and standing crop on Pinsonelle algal ridge.

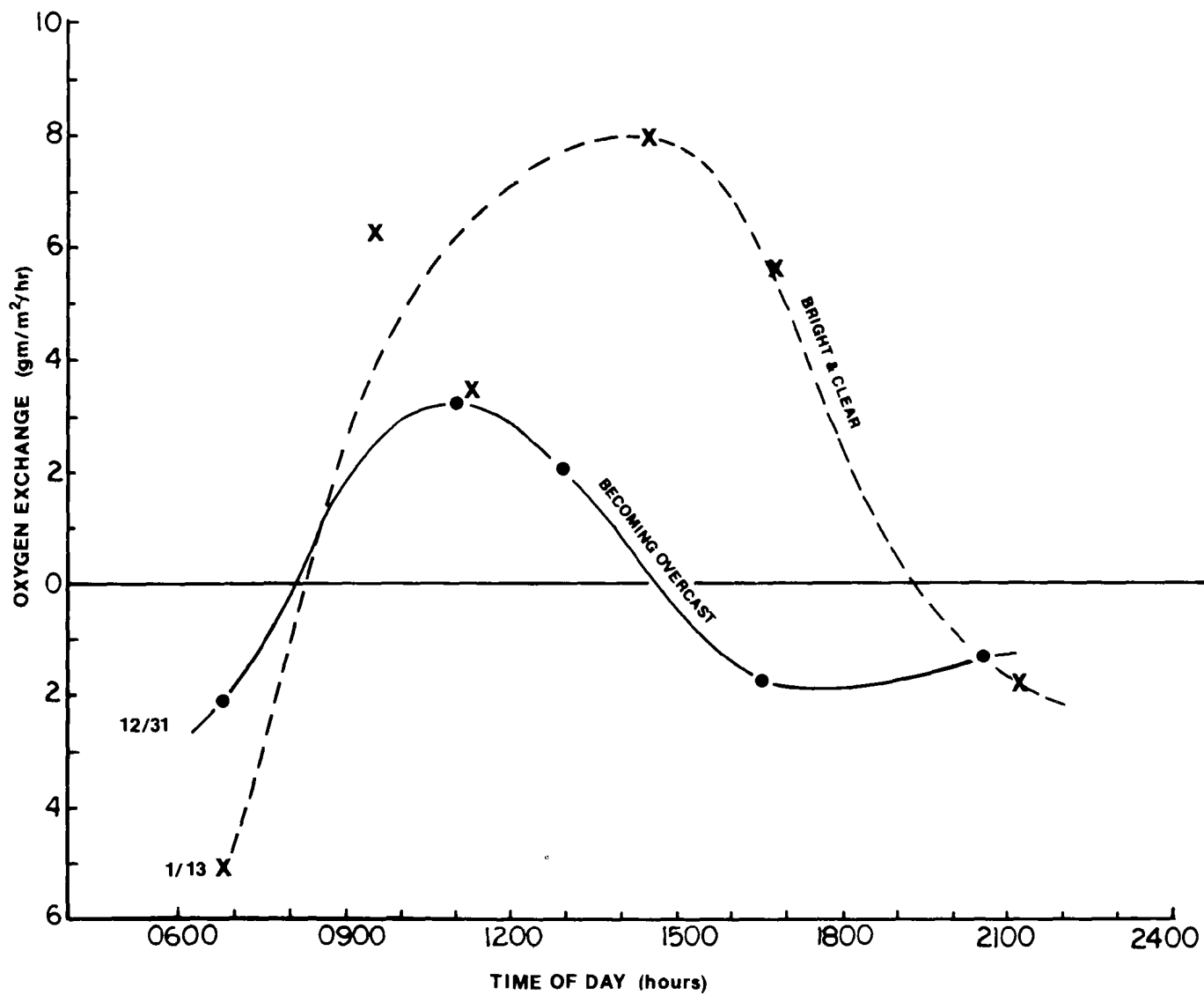


Fig. 14. Rate of oxygen exchange between reef surface and water for two different days on Vaucelin Point inner algal pavement.

Table 1. Corals Recorded from the Reefs of Martinique

## ANTHOZOA

## Scleractinia

## Acroporidae

Acropora cervicornisA. palmataAgariciidae<sup>1</sup>Agaricia agaricites

## Poritidae

Porites astreoidesP. poritesP. divaricataP. furcata

## Siderastreaeidae

Siderastrea radiansS. siderea

## Faviidae

Montastreinae<sup>2</sup>Montastrea annularisM. cavernosa

## Faviinae

Favia fraguumDiploria strigosaD. clivosaD. labyrinthiformisManicina areolataColpophyllia natans<sup>3</sup>

## Rhizangiidae

Astrangia solitariaPhyllangia americana

## Oculinidae

Oculina valenciennesi

## Trochosmilidae

Meandrina meandritesDendrogyra cylindrusDichocoenia stokesii

## Mussidae

Scolymia laceraMussa angulosaIsophyllastrea rigidaIsophyllia sinuosaMycetophyllia lamarckiana

## Cariophylliidae

Eusmilia fastigata

## HYDROZOA

## Milleporina

## Milleporidae

Millepora alcicornis<sup>4</sup>M. squarrosaM. complanata

## Stylasterina

## Stylasteridae

Stylaster roseus

1. Three additional morphologies were observed.
2. Solenastrea bournoni was observed by P. W. Hummelinck but we did not encounter it.
3. At least three different morphologies were observed.
4. Extremely variable morphologies were encountered including a long, thin, fingered variety and a wrinkled vase-forming variety, apparently ecovariants.



Table 2. Benthic macro algae, Pte. Vauclin algal pavement, 0.25m<sup>2</sup> quadrats; site locations shown in figure 12. Fractions to left in columns indicate number of quadrats in which species appeared/total quadrats collected; figure to right indicates mean net weight in grams (less than 0.1 gm not indicated).

SPECIES	SITE									
	1,2,3	4	5	6	7	8	9	10	11	
CHLOROPHYTA										
Cladophoraceae										
Chaetomorpha sp.	2/3 0.1	1/3	2/6		1/3					
Cladophora sp.		1/3	1/6				1/2			
Dasycladaceae										
Acetabularia spp.			1/6							
Neomeris annulata	1/3									
Valoniaceae										
Anadyomene stellata	1/3	3/3 0.1	3/6 0.3	2/3	1/3 2.2		1/2			
Struvea	1/3		1/6	1/3	1/3					
Cladophoropsis membranacea	1/3 7.1									
Ernodesmis spp.	2/3 0.8	1/3 0.3	4/6 0.5	1/3	1/3		1/2			
Valonia ventricosa	2/3 0.1		1/6 0.1							
Dictyosphaeria cavernosa	3/3 6.6	3/3 8.4	5/6 4.1	2/3 4.0	2/3 1.7	1/3 3.4	1/2 1.4			
Chamaedoris penicillium		3/3 4.4	6/6 3.9	2/3 1.3	2/3 4.3	2/3 3.3				
Caulerpaceae-Bryopsidaceae										
Bryopsis pennata			1/6	1/3						1/1
Caulerpa spp.			1/6 3.1			1/3 1.3				

<i>C. prolifera</i>	2/3 1.8		1/6 1.8						
<i>C. sertularioides</i>	2/3 0.2		3/6 1.0		1/3 6.0				
<i>C. floridana</i>		1/3 0.5							
<i>C. verticillata</i>						1/3			
<i>C. peltata</i>			1/6 0.5						
<i>C. vickersiae</i>		1/3	1/6	3/3	3/3				
<i>C. cupressoides</i>	1/3 0.1		1/6 0.5						
Codiaceae									
<i>Codium repens</i>	2/3 0.9				2/3 11.0				
<i>C. taylori</i>	1/3 5.0	1/3 27	2/6 1.4	2/3 11		1/3 2.7			
<i>C. intertextum</i>				1/3 1.7		1/3 0.7			
<i>Codium</i> spp.			1/6 6.6						
<i>Avrainvillea nigricians</i>	2/3 17.8								
<i>A. rawsoni</i>	2/3 9.3	1/3 10.0					1.1 84	1/1 20	
<i>Udotea flabellum</i>	1/3 0.5								
<i>Halimeda</i> spp.	1/3 9.8								
<i>H. discoidea</i>	2/3 2.1	2/3 7.2	4/6 7.7	2/3 10.		3/3 3.5			
<i>H. incrassata</i>	1/3 9.0								
<i>H. simulans</i>	1/3 0.5								
<i>Penicillus capitatus</i>	3/3 13.0	1/3 0.9							
<i>P. dumetosus</i>	1/3 1.0	2/3 2.1							
<i>Thalassia</i>	3/3 70	1/3 16							
<i>Syringodium</i>	2/3 18.5								
PHAEOPHYTA									
<i>Colpomenia sinuosa</i>	1/3 5.3	1/3 0.3		1/3 0.1	1/3				
Dictyotaceae									
<i>Dictyota</i> spp.		1/3 1.5	3/6 1.4			2/3 2.3	1/2 1.5		
<i>D. dentata</i>	2/3 0.5	3/3 133	6/6 117	3/3 41	3/3 24	3/3 31	2/2 11.0		

Table 2 (cont'd.)

<i>D. divaricata</i>	3/3 69	1/3 23	1/6 3.7	2/3 13.	2/3 11	1/3 1.2	2.2 1.2	
<i>Dilophus quiniensis</i>	1/3 12.8		1/6 0.8					
<i>Dictyopteris membranacea</i>	2/3 0.1	1/3 0.3	5/6 1.3		1/3 3.0	3/3 7.5	2/2 38	
<i>D. delicatula</i>	1/3	3/3 28	6/6 28	3/3 67	3/3 108	3/3 56	2/2 136	1/1
<i>D. justii</i>	1/3 0.5	2/3 22	3/6 8.2		1/3 11	2/3 11		
<i>Spatoglossum schroederi</i>	1/3	3/3 1.0	2/6 2.3	1/3 1.7		1/3 0.5	1/2 2.3	
<i>Lobophora variegata</i>		1/3 1.9	5/6 17	2/3 1.0	2/3 22	3/3 16	2/2 2.5	
Sargassaceae								
<i>Sargassum platycarpum</i>		3/3 565	5/6 292	2/3 109	2/3 23	2/3 122		
<i>S. vulgare</i>		3/3 224	6/6 368	3/3 348	3/3 294	3/3 448	2/2 330	
RHODOPHYTA								
Nemalionales								
<i>Asparagopsis hamifera</i>				3/3			1/2	
<i>Liagora</i> spp.	1/3	1/3	1/6	1/3 0.5				
<i>Galaxaura</i> spp.	2/3	1/3 1.7	3/6 1.4		1/3			
<i>G. oblongata</i>			1/6	2/3 1.5	1/3	1/3		
<i>G. marginata</i>		3/3 6.2	4/6 9.0	2/3 2.3	1/3			
<i>G. subverticillata</i>		1/3 3.5		1/3 1.2	1/3			
<i>G. squalida</i>		1/3	2/6 2.5					
Gelidiales								
<i>Wurdemanina miniata</i>	2/3		1/6 0.8		1/3	1/3	1/2	
<i>Gelidiella acerosa</i>	2/3 5.8	2/3 5.1	6/6 4.6	2/3 2.2	1/3 0.5			
<i>Pterocladia americana</i>	1/3					1/3	2/2	
<i>Gelidium pusillum</i>	1/3	1/3 0.3	4/6	3/3	2/3	2/3	2/2	
Rhodymeniales								
<i>Botryocladia pyriformis</i>		2/3	5/6 1.0	2/3 2.5	3/3 3.7	3/3 7.0	2/2 1.2	

<i>B. occidentale</i>					1/3 0.8				
<i>Champia parvula</i>		2/3			1/3 1.0	1/3			
<i>C. salicornoides</i>	1/3				1/3 0.8				
<i>Coelothrix irregularis</i>		1/3 5.0							
<i>Chrysymenia sp.</i>							1/2		
<b>Cryptonemiales</b>									
<i>Halymenia spp.</i>					2/3 0.5				
<i>Jania spp.</i>	1/3 1.4	1/3	3/6	1/3		1/3		1/1	1/1
<i>J. capillacea</i>				1/3		1/3			
<i>J. pumila</i>						1/3			
<i>Amphiroa spp.</i>			1/6 0.2		1/3	2/3 0.8			
<i>A. fragillissima</i>		1/3		1/3	1/3				
<i>A. tribulus</i>							2/3 1.4	1/2 3.5	
<i>A. rigida</i>							1/3		
<b>Gigartinales</b>									
<i>Gracilaria spp.</i>	1/3 0.5	3/3 8.9	4/6 5.0				1/3 1.1		
<i>G. ferox</i>	1/3	3/3 5.3	3/6 6.3	3/3 42	2/3 25	3/3 45	2/2 20		
<i>G. debilis</i>			6/6 154	2/3 157	3/3 97	3/3 212	1/2 1.4		
<i>G. damaecornis</i>		1/3 26	1/6 10	2/3 9.5	2/3 55	1/3 16			
<i>G. mammillaris</i>		1/3	2/6 1	1/3 1.4	2/3 15	3/3 18	1/2 1.5		
<i>G. cuneata</i>		1/3 4.1	2/6 1.9	1/3 6.8	2/3 4.5	2/3 14	2/2 11		
<i>Hypnea spinella</i>				2/3 0.1					
<i>H. musciformis</i>	1/3	1/3	1/6						
<i>Euclima spp.</i>		2/3 3.6	3/6 3.7	3/3 10	2/3 4.9				
<i>Meristotheca floridana</i>			1/6	1/3 1.4	1/3 0.2	1/3			
<b>Ceramiales - Ceramiaceae</b>									
<i>Callithamnion spp.</i>			1/6			1/3			
<i>Antithamnion spp.</i>				1/3					
<i>Wrangelia penicillata</i>			1/6	2/3 6.8	2/3				
<i>Ceramium nitens</i>			1/6 0.9						

Table 2 (cont'd.)

Centroceras clavulatum		3/3	3/6 0.2	2/3 1.3	1/3 6.3				
Spyridia aculeata				1/3 4.6					
Griffithsia globulifera	1/3	3/3	3/6	3/3	2/3 0.8	1/3			
Spermothamnion spp.	1/3	1/3	2/6	2/3	2/3 0.8				
Ceramiales - Dasyaceae									
Heterosiphonia									
Ceramiales - Delesseriaceas									
Nitophyllum spp.									
Ceramiales - Rhodomelaceae									
Polysiphonia spp.	1/3	1/3	1/6						
Bryothamnion triquetum	1/3 1.6	1/3 6.0							
Lophosiphonia spp.			1/6						
Acanthophora muscoides				1/3 3.5	1/3 2.3				
A. spicifera	1/3 0.4	1/3			1/3				
Digenia simplex	3/3 58.6	1/3	1/6						
Laurencia spp.						1/3 5.0	1/2 2.0		
L. intricata			2/6 0.1	1/3	1/3	2/3 0.6			
L. corallopsis		3/3 3.3	1/6 0.8	1/3 5.0		1/3 1.3			
L. poitei	1/3 1.0	1/3 13	4/6 7.8	1/3 10	1/3				
L. papillosa	3/3 3.9	3/3 5.2	4/6 11	2/3 11.9	1/3 7.6				
L. obtusa	1/3	1/3	1/6 1.0	2/3 14	2/3 13				
L. gemmifera	1/3 0.8	2/3 16.6	1/6 1.4	3/3 21	2/3 50				
Chondria spp.		1/3	1/6						
Enantiocladia duperreyi	2/3 4.6	1/3 18	5/6 8.9						
Vidalia obtusiloba	1/3 0.1		1/6 3.7						
Total mean wgt. gm/0.25m <sup>2</sup>	341	1209	1108	927	809	1033	565	84	20
Total number of species	55	58	68	53	51	41	25	3	3
Total sp. with wgt 1gm/0.25m <sup>2</sup>	23	32	36	34	25	24	16	1	1
Total sp. occurring	7	15	6	10	6	10	11		

Table 3.

## Martinique Fish, Grouped by Relative Abundance

Typical habitat: FR(fore reef), AP(algal pavement), BR(back reef).  
(T) indicates uncertainty in identification.

## Class I

		FR	AP	BR
1	<i>Jenkinsia lamprotaenia</i> (T)		x	x
2	<i>Holocentrus ascensionis</i>	x		x
3	<i>H. rufus</i>	x		x
4	<i>Atherinomorus stipes</i>		x	x
5	<i>Allanetta harringtonensis</i>			x
6	Planktivorous Carangid (T)	(on Pte. du Vauclin) x		
7	<i>Ocyurus chrysurus</i>	x		x
8	<i>Haemulon chrysargyreum</i>	x		x
9	<i>H. sciurus</i>	x		x
10	<i>Mulloidichthys martinicus</i>	x		x
11	<i>Pempheris schomburgki</i>	x		x
12	<i>Kyphosus sectatrix</i> (T)	x		
13	<i>Eupomacentrus fuscus</i>	x	x	x
14	<i>E. partitus</i>	x	x	x
15	<i>Microspathodon chrysurus</i>	x		x
16	<i>Abudefduf saxatilis</i>	x	x	x
17	<i>Chromis multilineatus</i>	x	x	x
18	<i>Halichoeres bivittatus</i>	x	x	x
19	<i>H. radians</i>	x	x	x
20	<i>H. maculipinna</i>		x	
21	<i>Thalassoma bifasciatum</i>	x	x	x
22	<i>H. poeyi</i>		x	
23	<i>Sparisoma rubripinne</i>		x	
24	<i>S. radians</i>		x	
25	<i>Scarus croicensis</i>	x		x
26	<i>Ophioblennius atlanticus</i>	x	x	x
27	<i>Labrisomus nuchipinnis</i> et al.		x	
28	<i>Malacoctenus aurolineatus</i>	x	x	x
29	<i>Malacoctenus macropus</i>	x	x	x
30	<i>Malacoctenus erdmanni</i>	x	x	x
31	other <i>Malacoctenus</i> spp.	x	x	x
32	<i>Acanthurus coeruleus</i>	x		x
33	<i>A. bahianus</i>	x	x	x
34	<i>A. chirurgus</i>	x	x	x
35	<i>Coryphopterus glaucofrenum</i>		x	
36	<i>C. hyalinus</i> et al. (T)	x		

Table 3 (con't.)

		Class II	FR	AP	BR
37	<i>Synodus intermedius</i>	Sand Diver	x		x
38	<i>Aulostomus maculatus</i>	Trumpetfish	x		x
39	<i>Adioryx coruscus</i>	Reef Squirrelfish			x
40	<i>Myripristes jacobus</i>	Blackbar Soldierfish			x
41	<i>Cephalopholis fulva</i>	Coney	x		x
42	<i>Alphestes afer</i>	Mutton Hamlet		x	
43	<i>Hypoplectrus puella</i>	Barred Hamlet	x		x
44	<i>Serranus tigrinis</i>	Harlequin Bass			
45	<i>Priacanthus cruentatus</i>	Glasseye Snapper	x		x
46	<i>Lutjanus griseus</i>	Grey Snapper	x		x
47	<i>L. apodus</i>	Schoolmaster	x		x
48	<i>Haemulon flavolineatum</i>	French Grunt	x		x
49	<i>H. plumieri</i>	White Grunt	x		x
50	<i>Eupomacentrus planifrons</i>	Yellow Damselfish, 3-spot	x		
51	<i>E. variabilis</i>	Cocoa Damselfish	x		
52	<i>E. leucostictus</i>	Beaugregory			x
53	<i>Doratonotus megalepis</i>	Dwarf Wrasse		x	
54	<i>Hemipteronotus splendens</i>	Green Razorfish		x	
55	<i>Sparisoma viride</i>	Stoplight Parrotfish	x		x
56	<i>S. chrysopterum</i>	Redtail Parrotfish	x	x	x
57	<i>Gnatholepis thompsoni</i>	Goldspot Goby	x	x	x
58	<i>Gobiosoma evelynae</i>	Sharknose Goby		x	
59	<i>Balistes vetula</i>	Queen Triggerfish	x		x
60	<i>Cantherhines pullus</i>	Tail-Light Filefish	x		x
61	<i>Canthigaster rostrata</i>	Sharpnose Puffer	x		x
62	<i>Diodon holocanthus</i>	Spiny Puffer		x	

## Class III

63	<i>Synodus synodus</i>	Rockspear			x
64	<i>Echidna catenata</i>	Chain moray		x	
65	<i>Strongylura</i> spp.	Needlefish		x	x
66	<i>Hemiramphus brasiliensis</i>	Ballyhoo			x
67	<i>Adioryx vexillarius</i>	Dusky Squirrelfish			x
68	<i>Sphyræna barracuda</i>	Great Barracuda	x		
69	<i>Epinephelus guttatus</i>	Red Hind	x	x	x
70	<i>E. adscensionis</i>	Rock Hind		x	
71	<i>Gramma loreto</i>	Royal Gramma	x		
72	<i>Rypticus sapnoaceus</i>	Soapfish	x		x
73	<i>Caranx ruber</i>	Barjack	x		x
74	<i>Trachinotus goodei</i>	Palometa	x		
75	<i>Scomberomorus regalis</i>	Cero	x		
76	<i>S. cavalla</i>	King Mackerel	x		
77	<i>Lutjanus mahogony</i>	Mahogony Snapper	x		x
78	<i>Haemulon aurolineatum</i>	Tomtate			x
79	<i>Odontoscion dentax</i>	Reef Croaker		x	x
80	<i>Equetus acuminatus</i>	Cubbyu		x	x
81	<i>Pseudopeneus maculatus</i>	Spotted Goatfish			x
82	<i>Gerres cinereus</i> (T)	Yellowfin mojarra		x	x
83	<i>Bothus lunatus</i>	Peacock Flounder			x

Table 3 (con't.)		Class III (con't.)	FR	AP	BR
84	<i>Scorpaena plumieri</i>	Spotted Scorpionfish		x	
85	<i>S. grandicornis</i>	Grass Scorpionfish		x	
86	<i>Chaetodon capistratus</i>	Foureye Butterflyfish	x	x	x
87	<i>C. striatus</i>	Banded Butterfly	x		x
88	<i>Bodianus rufus</i>	Spanish Hogfish	x		
89	<i>Hemipteronotus novacula</i>	Pearly Razorfish		x	
90	<i>Sparisoma aurofrenatum</i>	Redband Parrotfish	x		x
91	<i>Lactophryis triqueter</i>	Smooth Trunkfish	x		x
92	<i>Sphaeroides greelyi</i>	Caribbean Puffer			x
93	<i>S. spengleri</i>	Bandtail Puffer			x
94	<i>Diodon hystrix</i>	Porcupinefish	x		x

## Class IV

95	<i>Dasyatis americana</i>	Stingray
96	<i>Gymnothorax moringa</i>	Spotted Moray
97	<i>G. vicinus</i>	Purplemouth Moray
98	<i>Apogon maculatus</i>	Flamefish
99	<i>Dactylopterus volitans</i>	Flying Gurnard
100	<i>Scarus vetula</i>	Queen Parrotfish

## Class V

101	<i>Trachinotus falcatus</i>	Permit
102	<i>Caranx hippos</i>	Crevalle Jack
103	<i>Pempheris poeyi</i>	Shortfin Sweeper
104	<i>Pomacanthus paru</i>	French Angelfish
105	<i>Eupomacentrus mellis</i>	Honey Gregory
106	<i>Halichoeres garnoti</i>	Yellowhead Wrasse

## Lagoon, Sand, Grass

## Near the Reef

107	<i>Ophichthus ophis</i>	Spotted Snake Eel
108	<i>Myrichthys oculatus</i>	Goldspotted Snake Eel
109	<i>Hippocampus reidi</i>	Slender Seahorse
110	<i>Mugil curema</i>	Mullet
111	<i>Hypoplectrus nigricans</i>	Black Hamlet
112	<i>Monocanthus ciliatus</i>	Fringed Filefish
113	<i>M. tuckeri</i>	Slender Filefish
114	<i>Antennarius multiocellatus</i>	Longlure Frogfish

## Cryptic within carbonate pavement

115	<i>Stathmonotus</i> spp.
116	<i>Enneanectes pectoralis</i>



	A. palmata / A. palmata / coralline-Millepora / fleshy algal pavement														
	A. palmata			A. palmata / coralline-Millepora			fleshy algal pavement								
	Fajou (G)	Middle Reef (A)	Fishtail Cay (A)	Union Island (Gr)	Palm Island (Gr)	World's End (Gr)	Horseshoe Reef (Gr)	St. Marie (G)	St. Barts	Goyave (G)	Nevis	Ramville Island (M)	Vauclin Point (M)	Lezard Island (M)	
<u>Scarus vetula</u>	::	::	::	:::	:::	:::	:::	:::	:::	::		(.)	(.)		
<u>Sparisoma viride</u>	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	
<u>Halichoeres garnoti</u>	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	
<u>Chromis cyanea</u>	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	
<u>Holacanthus tricolor</u>		::		:::	:::		:::								
<u>H. ciliaris</u>				:::	:::		:::								
<u>Scarus taeniopterus</u>							:::								
<u>S. coelestinus</u>							:::	::	:::						
<u>S. guacamaia</u>							:::	::	:::						
<u>Hypoplectrus chlorosus</u>	(.)						:::	.							
<u>Pomacanthus paru</u>							:::								
<u>Sparisoma rubripinne</u>	::	::	::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	:::	
<u>Halichoeres poeyi</u>	:::			:::	:::		:::	:::	:::	:::	:::	:::	:::	:::	
<u>Sparisoma radians</u>							:::	:::	:::	:::	:::	:::	:::	:::	
<u>Doratonotus megalepis</u>															
<u>Alphestes afer</u>															
<u>Abudefduf taurus</u>															

KEY  
(G) Gaudeloupe  
(A) Antigua  
(Gr) Grenadines  
(M) Martinique

		<u>no/hr</u>
:::	Abundant (large % of biomass)	50
:::	Abundant (small % of biomass)	50
::	Always Seen	10-50
:::	Frequently Seen	2- 9
::	Occasional	1
::	Rare	1

Table 4. Fish species contrasting most in relative abundance on different reef types. Parentheses indicate the presence of a species on small patches of A. palmata near or surrounded by coralline-Millepora pavement.