CORAL REEF AND ASSOCIATED INVERTEBRATE COMMUNITIES (MAINLY MOLLUSCAN) AROUND MAHÉ, SEYCHELLES

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[Plates 13 to 17, and 2 folding maps]

CONTENTS

The Seychelles Bank is an area of approximately 31 000 km^2 of shoal water with an average depth between 44 and 65 m. The granitic island of Mahé is situated centrally on the Bank, it is 27 km long, 6 to 8 km wide and rises to a height of 900 m above sea level. The climate is oceanic with two distinct seasons; from April until October the strong South-East Trades blow with an average speed of 8 to 10 knots and from November until March the area is under the influence of the north-west monsoon, when calms are frequent and the average wind speed is 4·5 knots. The average temperature is 26·8 °C and the average rainfall at sea level is 2500 mm. The near-shore sea-water temperature varies between 27·5 and 32 °C but in tidal pools values up to 40·7 °C were recorded, with a daily range of about 8 °C. Salinities in water with open circulation were close to that of normal sea-water but on reef flats after heavy rain values as low as 5·6 ‰ were recorded. Tides are mixed semidiurnal, with a maximum range of 1·8 m. Sites exposed to the dominant S. E. Trades experience the highest degree of wave action. Fringing coral reefs are developed around the island, on the eastern side they are generally wide and more or less continuous, but on the western side they are confined to narrow bay reefs. Submarine topography, wind direction and strength have influenced the development and resultant shape of the reefs.

The most obvious feature of the flora and fauna occurring on and in the fringing reef is that there is a zonation parallel to the shore. This zonation may be related to that occurring upon rocky intertidal shores throughout the world: most of the reef lies in the sublittoral zone but with projections upwards into the eulittoral and littoral fringe zones. The upper limit of abundant coral corresponds with the appearance of *Laminaria* in temperate regions. A number of distinct communities of organisms can be recognized forming and inhabiting these zones. The area above high-water mark but with maritime influence is the supralittoral zone and around Mahé is colonized by salt-resistant plants such as *Ipomoea*, *Scaevola*, *Cocos* and *Calophyllum*. In creeks and sheltered areas mangrove patches occur, commonly *Rhizophora* and *Avicennia* and inhabited by many crabs such as *Uca*, *Cardisoma* and *Scylla*, and the gastropod *Terebralia*. Where the shores are rocky, either granite or beachrock they are colonized by a typical rocky shore biota; in the littoral fringe blue green algae and *Littorina* are common, below in the eulittoral zone green algae, barnacles, limpets, several species of *Nerita*, *Isognomon* and oysters occur. The area between the tide marks on sandy beaches is inhabited by the crabs *Ocypode* and *Coenobita* and the burrowing bivalves *Donax* and *Atactodea*.

On the reef flat proper, communities are almost completely sublittoral and only partly emersed at lowest spring tides. In sheltered areas around Port Victoria, where the once extensive mangrove swamps have now been cleared, the remaining sediment is blackened, has a high organic content and smells of hydrogen sulphide; the overlying water is turbid with generally reduced salinities. The area is inhabited by a large population of 'fiddler' crabs (*Uca*), green algae and the burrowing bivalves *Gafrarium*, *Quidnipagus* and *Psammotea*. On reef flats which are wide enough beds of marine angiosperms are developed which extend up to 300 m seawards from the base of the beach. They are mainly formed by the genera *Thalassia*, *Cymodocea* and *Syringodium* which by means of rhizome and root systems accumulate and fix sediment. These 'grass' beds support a large population of holothurians and burrowing bivalves, principally *Codakia*, *Quidnipagus*, *Tellinella* and *Gafrarium*. On windward reefs immediately seawards of the grass beds are open sandy areas which interdigitate with lower ridges of loosely bound calcareous algal cobbles and coral fragments arranged at right angles to the algal ridge with which they are in continuity. Brown algae such as *Sargassum* and *Turbinaria* are abundant and attached to hard substrates; *Halimeda* is common in the sandy areas. A great number of species of burrowing gastropods and bivalves inhabit the sandy areas, the fauna on the cobble ridges is very similar to that occurring on the algal ridge.

The algal ridge is well developed only on windward reefs, it consists of a low ridge at the seaward edge of the reef flat made up of a cavernous growth of calcareous red algae such as *Lithophyllum* and *Porolithon*. This substrate is clothed in *Sargassum*, *Turbinaria* and many other algae. The associated fauna shows an extraordinary diversity with many species of gastropods, particularly *Cypraea*, *Conus*, *Triphora*, *Turbo* and *Trochus*. Many crabs, echinoids, ascidians, sponges and cemented foraminifera are present.

The extreme seaward edges of the reef flat, the reef front and the reef edge are the only environments where corals are the dominant organism in the community. The reef edge marks the seaward extent of the reef flat and slopes shallowly seawards from the algal ridge to the change in slope at the reef front and is the area where the waves break. The reef front is generally steep but

around Mahé is only about 20 m high, descending to the shallow base platform outside the reefs. Two distinct reef edge and front communities can be recognized, the *Acropora–Millepora–Stylophora* community characteristic of windward edges with good water circulation and dominated by branching corals, and the *Porites–Favia–Leptoria* community is characteristic of reef edges in sheltered areas with massive, rounded, growth forms.

An abundant molluscan fauna has been dredged from areas outside the reefs, but sufficient information is not yet available to warrant a division into communities.

Introduction

This account of the marine organic communities around Mahé, the principal island of the Seychelles Group, is a contribution to research on the sedimentation and fauna of the Seychelles Bank being carried out from King's College, London. The work forms part of the International Indian Ocean Expedition.

This report seeks to define the extent and relations of the communities associated with the fringing reefs around Mahé; emphasis is placed on those organisms secreting calcareous skeletons because of their sedimentological and palaeoecological importance.

Field work was carried out from March to July 1963 and from October 1964 to January 1965, thereby enabling observations to be made in both seasons.

The fauna and flora are not well known and a large proportion of time was spent in the identification of the collections; except in a few instances the author is responsible for the identifications cited.

Location

The Seychelles Bank is an area of approximately 31 000 km^2 of shoal water with an average depth of 44 to 65 m. It extends from 3° 4′ S to the limit of its probable southernmost extension at Coetivy Island, 7° 15′ S; however, the major part of the Bank only extends as far as 5° 30′ S. The longitudinal extent is from 54 to 57° E.

There are two groups of islands, a granitic and a coralline group. The former, 32 in number, occupy a more or less central position on the Bank; they are the most densely populated and include Mahé, the largest of the granite islands. Mahé is 27 km long and 6 to 8 km wide at the widest points and is of generally high relief, the highest point being 900 m above sea level. The eastern side of the island and isolated bays on the western side are fringed by coral reefs.

Only two coralline islands lie on the Bank, these are Bird and Denis Islands on the northern rim; both are small, only about 2 to 3 km long and low-lying at about 1 to 2 m above the high spring tide level. They have been formed by the accretion of coral sands and reef in association with the frequent changes in sea level during the Post-Glacial period.

The southern edge of the Bank projects southwards as a narrow tongue and may possibly extend as far as Coetivy Island, 240 km from Mahé; this is a large elongate island about 10 km in length. The small island of Platte lies approximately due south of Mahé on a small shallow Bank rising from surrounding depths of about 3000 m.

Previous work

Most of the previous work on the marine fauna and flora of the Seychelles area has consisted of the documentation and listing of specimens collected by various expeditions.

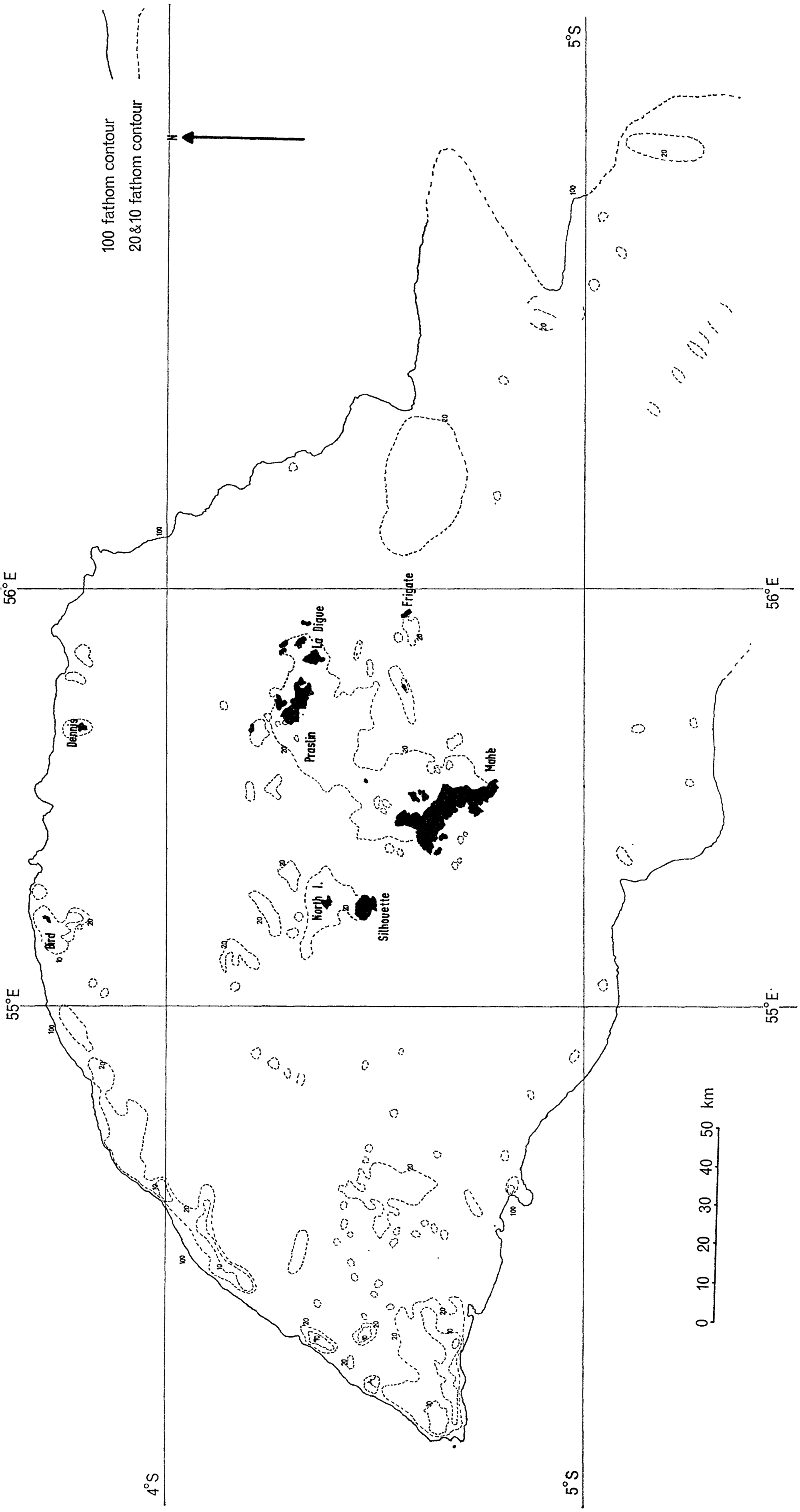
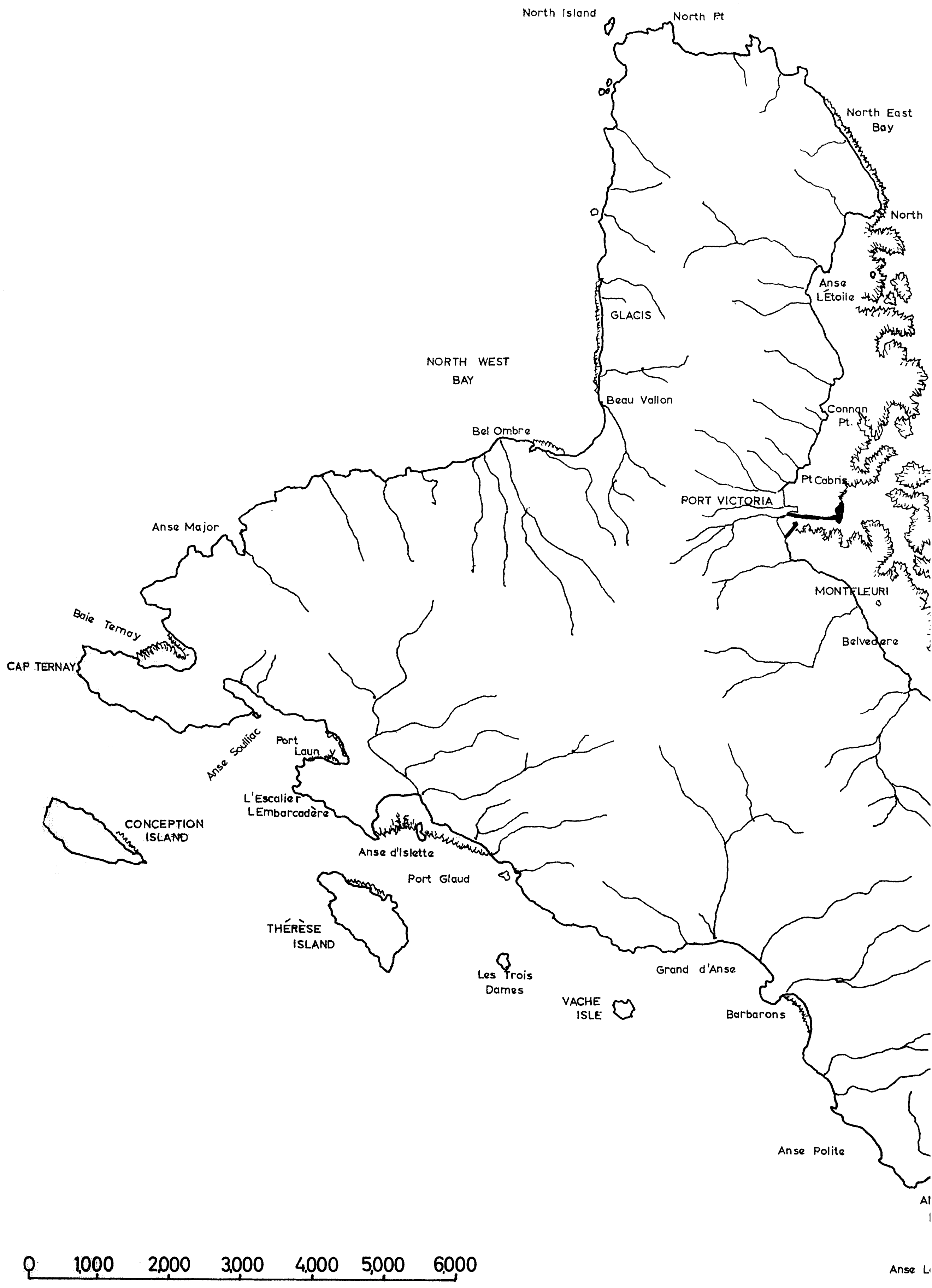


FIGURE 1. The Seychelles Bank.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GLACIS
NORTH WEST BAY
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Connan Pt.
Bel Ombre
Pt Cabris
PORT VICTORIA
Anse Major
MONTFLEURI
Baie Ternay
Belvedere
CAP TERNAY
Anse Souillac
Port Laun
L'Escalier
L'Embarcadère
CONCEPTION ISLAND
Anse d'Islette
Port Glaud
THÉRÈSE ISLAND
Les Trois Dames
Grand d'Anse
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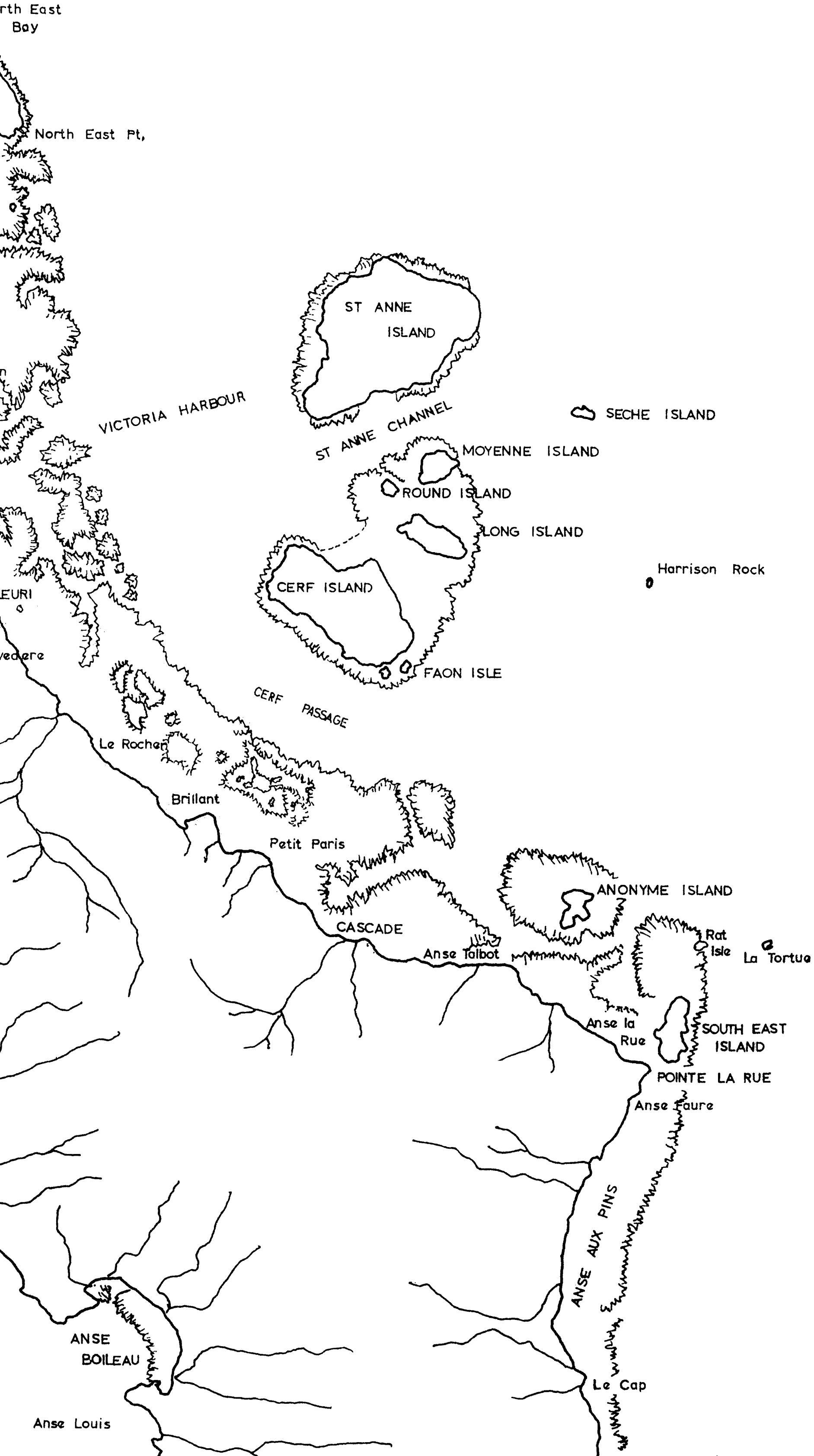
North East Bay
North East Pt,
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ST ANNE ISLAND
ST ANNE CHANNEL
SECHE ISLAND
MOYENNE ISLAND
ROUND ISLAND
LONG ISLAND
Harrison Rock
CERF ISLAND
FAON ISLE
CERF PASSAGE
Le Rocher
Brillant
Petit Paris
ANONYME ISLAND
Rat Isle
La Tortue
CASCADE
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Le Cap
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Anse Louis

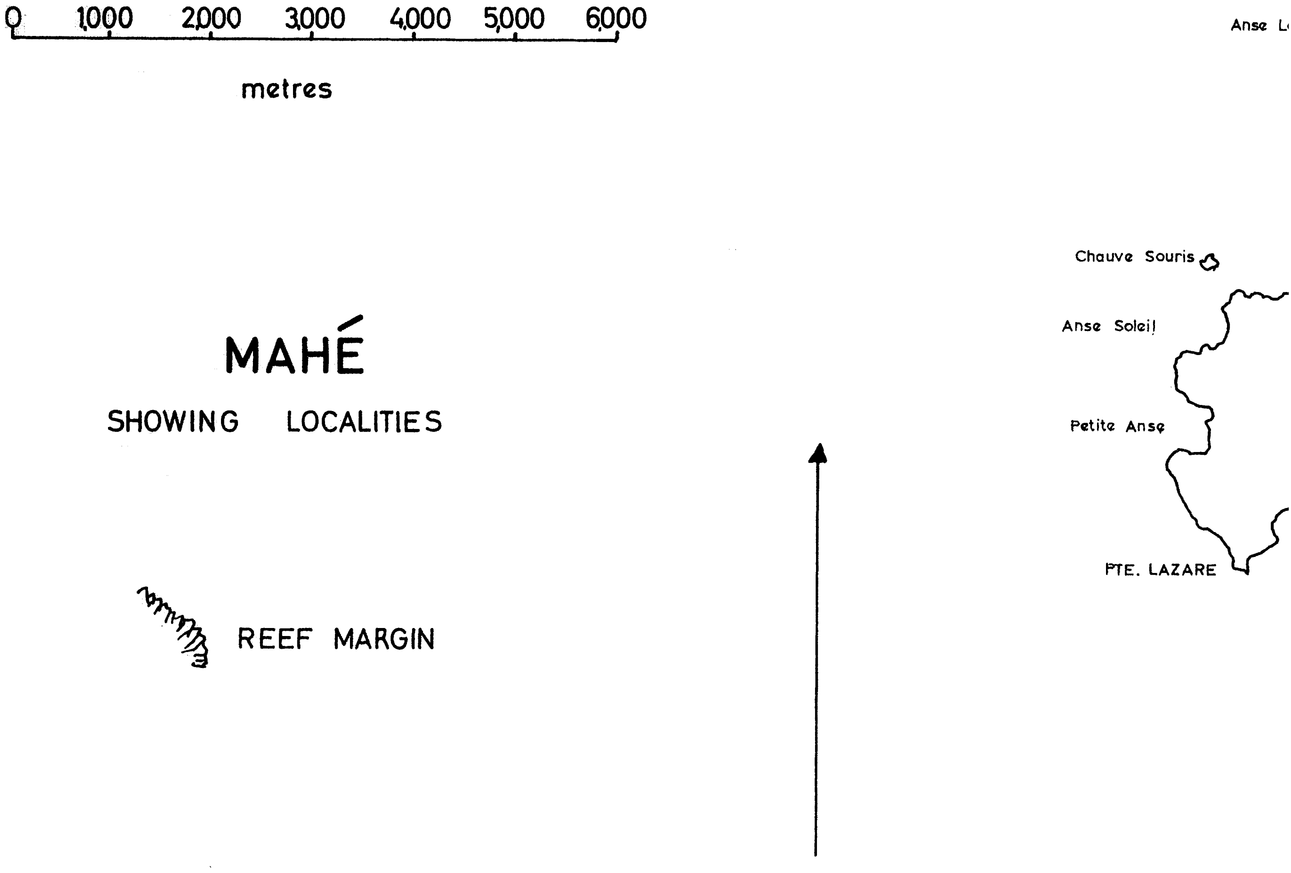

FIGURE 2. Sketch map of Mahé showing localities menti

es mentioned in the text.

(*Facing p.* 132)

During the French occupation of the islands from 1770 to 1814, a few specimens, mostly molluscs and corals, found their way to the Paris Museum and into various taxonomic works. Early visitors to the islands published descriptive accounts but included little information on the reefs and the marine fauna.

A French naturalist Dufo (1840) spent some time on the islands making observations on the living habits of some marine and land molluscs; unfortunately, some of his observations are not accurate. A few marine molluscs were described by Nevill (1875) incidental to descriptions of land molluscs. Lienard (1877), in a catalogue of the molluscan fauna of Mauritius and its dependencies, included a few records for the Seychelles.

The first large expedition to visit the islands was the Möbius Expedition of 1875 which visited Mauritius, the Mascarenes and the Seychelles where it stayed for about a month. The results of the expedition were published in a report (Möbius, Richters & von Martens 1880), describing some of the Foraminifera, Crustacea and Mollusca collected. *H.M.S. Alert* made a short stay at the Seychelles in 1882 and made notable additions to the molluscan and decapod crustacean faunal lists (Smith 1884; Miers 1884). A short list of the marine Mollusca collected by three visiting French naturalists was published by Dautzenberg (1893).

The Deutschen Tiefsee Expedition (1898–9) made a short call at Port Victoria and a few molluscs were collected and listed in von Martens (1903) and Thiele & Jaeckel (1931).

The most important contribution to our knowledge of the Seychelles fauna and flora was made by the Percy Sladen Expedition of 1905 led by J. S. Gardiner in the *Sealark*. This expedition visited the Chagos group, Mauritius, the Mascarenes, the Amirantes and most of the Seychelles islands. About a month was spent on the islands of Mahé and Praslin, but the collections of marine organisms at this late stage in the expedition were not as extensive as earlier, and more emphasis seems to have been placed on terrestrial collections. Nevertheless, important collections were made, and the results published in a series of reports from 1907 to 1936 and summarized by Gardiner (1936).

From 1936 until 1947 a substantial contribution to the knowledge of Seychelles Mollusca was made by the collections of Colonel H. C. Winckworth. The collections were sent to his conchologist brother R. Winckworth for identification and a short list was published in Winckworth (1940). A second more comprehensive list was compiled, but not published; this and the collection are now in the British Museum (Natural History).

A short account of some Seychelles bivalves in the Oslo Museum, collected from beaches around Mahé in 1932–3, was published by Rost & Soot-Ryen (1955).

In 1954, J. C. Smith visited the Seychelles to investigate the fish fauna and he increased the number of recorded species from 300 to 880, listed and illustrated in Smith (1963). A small expedition from Yale University visited the islands in 1959 and reports on the stomatopod Crustacea (Manning 1960) and the spawning and larval development of *Conus* (Kohn 1961 *a*) have so far appeared.

During the International Indian Ocean Expedition various research ships have called at the Seychelles and small marine collections were made.

Climate

The climate of the Seychelles is essentially oceanic with only local orographic effects; small-scale sea breezes are frequent. Two distinct seasons are evident; from April to October the area is under the influence of the S.E. Trades and from November to March is affected by the southerly spread of the N.W. Monsoon system. Conditions are variable in the transition months.

The air temperature is very equable throughout the year, the mean annual figure being 26·8 °C, the maximum 31·5 °C and the lowest 20 °C. The mean daily range is approximately 3·2 °C.

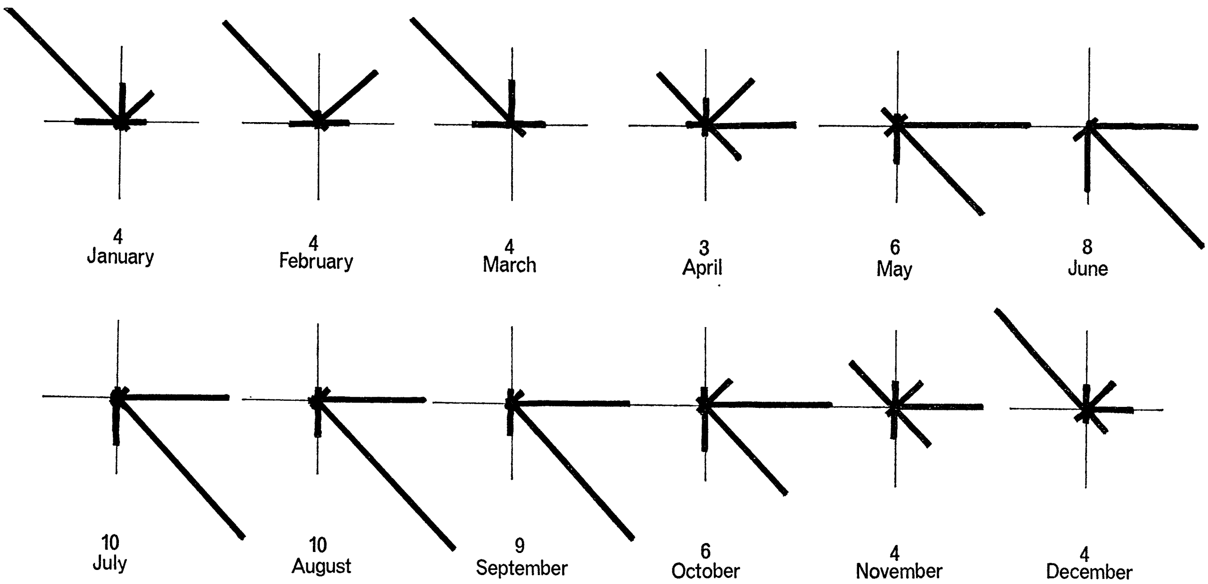

Figure 3. Mean monthly variation in wind direction and speed. Speed in knots. 1 cm = 10 % of observations.

The average rainfall is about 2500 mm at sea level, but on the higher ground the fall reaches 5000 mm. Most rain falls between November and March, December and January having 346 and 406 mm respectively, whilst July and August, the driest months, have average falls of 78 and 56 mm.

From April to October the Seychelles are influenced by the S.E. Trades wind system which has moved northwards with the sun. They blow continually and strongly with an average speed of 8 knots and a maximum of 10 knots in August. In July and August 80 % of observations show winds from the south-east or east. Between mid-November and March the islands lie within the N.W. Monsoon influence; these winds are rather light and inconstant in direction and the frequency of observations from this direction is less than 40 %. The average wind speed for this season is about 4·5 knots, calms are frequent. The Seychelles are well north of the regular path of cyclones and severe storms are rare. The direction and strength of the wind with its resulting wind-generated waves is an important factor in controlling the shape and zonation of the reefs.

Sea-water conditions

Temperature

In the equatorial shallow water areas where the temperature is high and equable throughout the year with small seasonal changes, it has no broad-scale limiting effects on the distribution of organisms. On a local scale in marginal shallow water areas temperatures may be high enough to approach the lethal limits for poikilothermic marine animals, therefore affecting local distribution patterns. The thermal death point for marine animals is usually 30 to 35 °C, although for most intertidal animals the lethal figure is about the same as that of land animals, 42 to 45 °C (Gunter 1957).

In the open Indian Ocean the differences between the sea and air temperature is small, at all seasons varying throughout the year by about 1 to 2 °C, the sea being warmer than the air for most of the year. From many measurements around Mahé it was found that in water in open circulation the surface temperature varied from about 27·5 to 32 °C; the higher figures were recorded in March, April and May, figures for October and November were generally lower. Close inshore at low tide, higher temperatures approaching the lethal range for marine animals were obtained. At Anse aux Pins in tidal pools a few centimetres deep, on the reef flat, figures of 38·5 to 40·7 °C were recorded. Figures of 34 to 37 °C on shoal water of the reef flat were common, at the water margin the daily range in temperature was of the order of 7 to 8 °C.

Salinity

Salinity variation is an important factor controlling the distribution of organisms in some communities.

Salinity measurements were made with a National Institute of Oceanography temperature–salinity bridge. Waters with open circulation had only slight variations in salinity and values obtained were always close to that of normal sea water, 35 ‰, the highest value obtained was 35·5 ‰. Variations of the order obtained were of no apparent biological significance. As a consequence of the high annual rainfall and high relief the run-off of fresh water into the sea from Mahé is large and rapid. Between Anse Étoile and Cascade, where the reef is backed by steep slopes, many streams enter the sea. Here across the landward 300 m of reef flat salinities are always reduced and even at high tide values of 28 to 33 ‰ are obtained. At falling tide, near stream mouths, values close to fresh water are obtained. The water from these streams crosses the reef flat through channels and passes, caused principally by the inhibition of coral growth by this fresh water. After heavy rainstorms a stream of laterite coloured water is seen passing across the reef flat and gradually mixing with sea water out to sea. At Le Cap after heavy rain, water of 5·6 ‰ salinity was flowing across the reef flat a few centimetres above a patch of the coral *Psammocora*. Between Plaisance and Port Victoria many measurements were made of values between 15 and 26 ‰.

Tides

The tides are mixed semi-diurnal type, with a strong inequality between successive highs and lows. A tide-gauge record for December 1964 is shown in figure 4. The greatest range in tidal amplitude occurs in December and the smallest in June and July, when the

S.E. Trades are at full strength. The lowest tides recorded in December were 0·21 m and the highest 2·0 m with a maximum range of 1·8 m, at neap periods the range is 0·9 m. The tides are markedly unequal and the difference between the heights of successive high tides can be as much as 0·8 m.

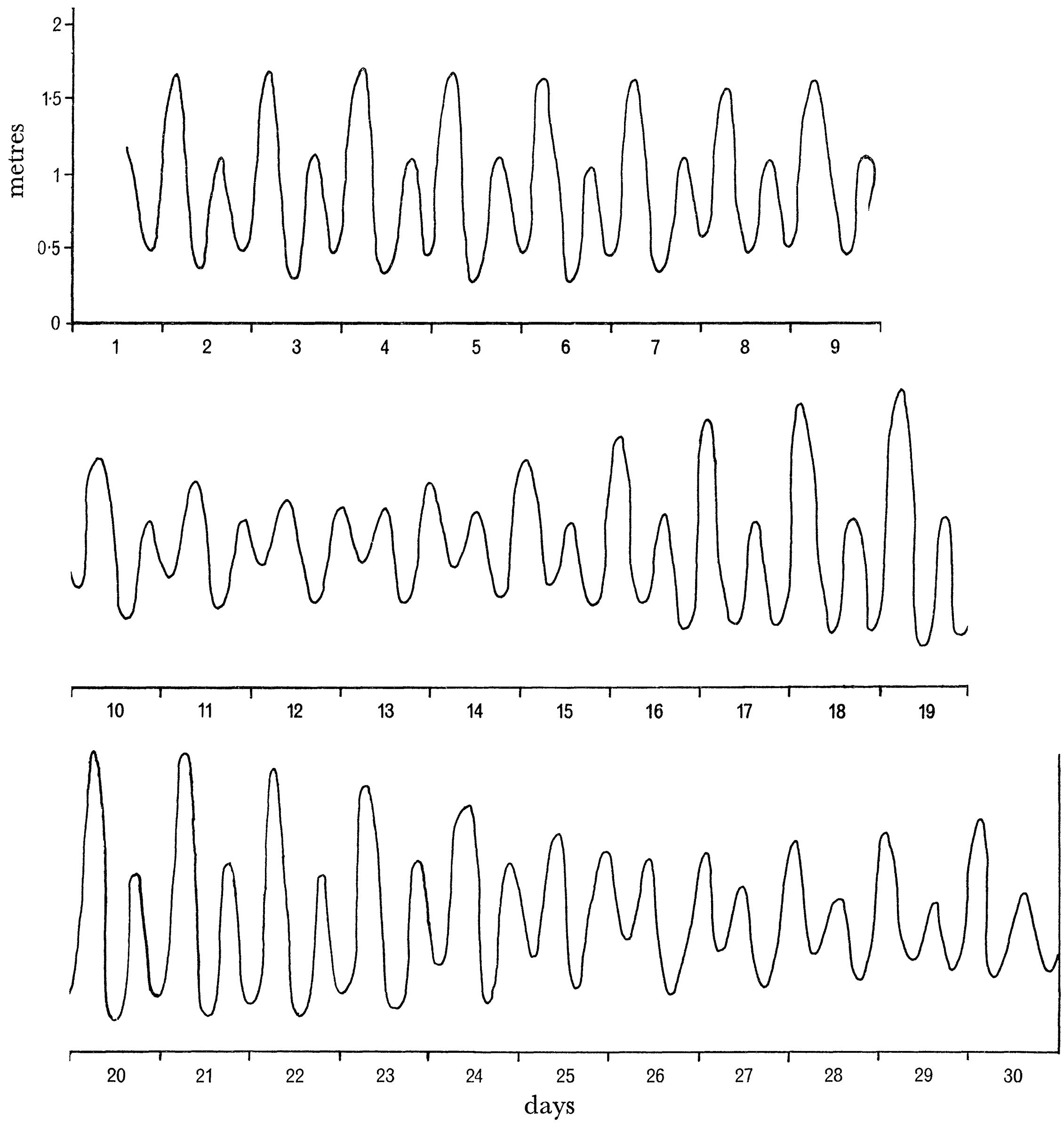

FIGURE 4. Tide gauge record for Port Victoria, Mahé, in December, 1964.

The daily tidal curves for Mahé are complicated by rather strong seiche oscillations. These fluctuations are caused by major oscillations in the tidal basin of the western Indian Ocean, and are particularly noticeable on reef flats at low tide, when small differences in water level will cause relatively large water movements back and forth across the reef flats.

The time of extreme low water is an important ecological factor in the tropics. During the spring tide period from 16 to 22 December the lowest low water occurs at around


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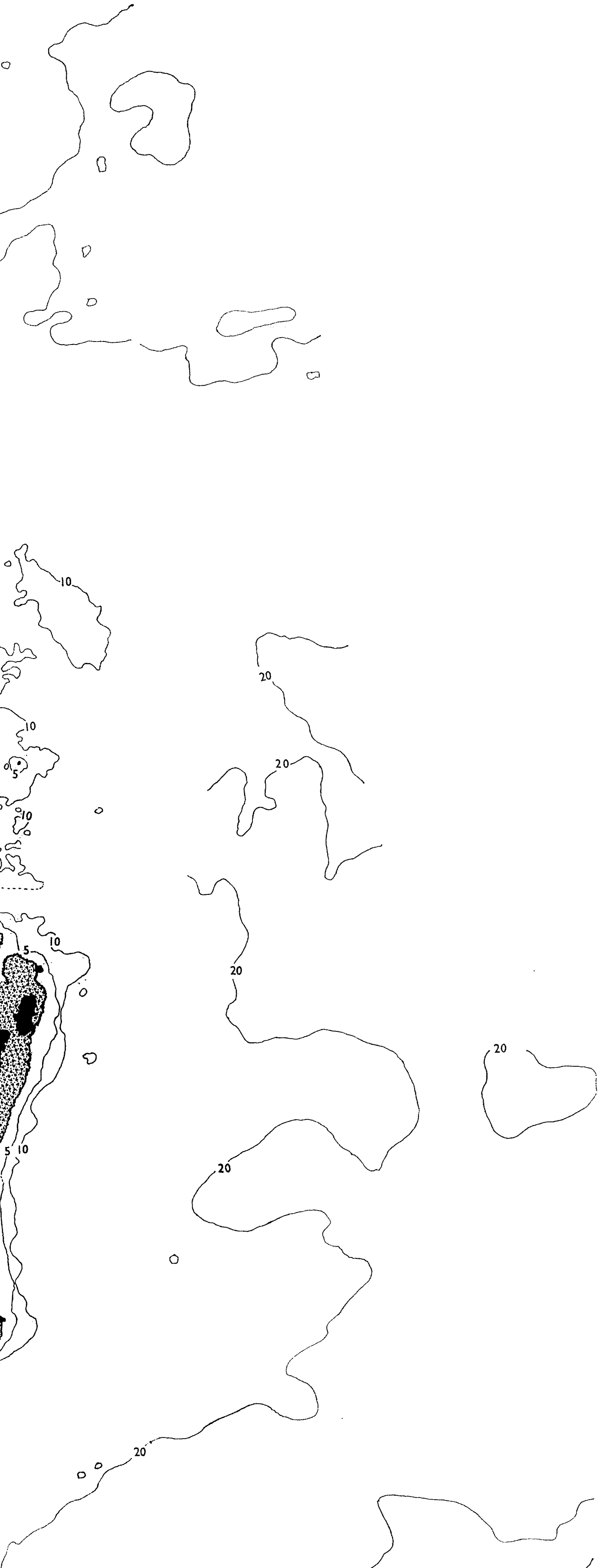
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FIGURE 5. Submarine topography around Mahé.

[M]ahé.

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noon when insolation and temperatures are high. This factor would seem to be important in controlling the distribution of sensitive organisms such as algae and corals in the upper sublittoral zone. The lowest tides of the year also correspond with the time of highest rainfall.

Wave action

The degree of wave action or exposure factor exercises a significant control on the distribution of organisms. Assessments of the exposure factor can as yet only be made in qualitative terms which vary with the experience of the observer. The highest exposure does not approach the severity found around the Atlantic shores of Britain. Therefore the terms very exposed, exposed, sheltered and very sheltered have reference for comparison only on the shores of Mahé.

The whole coast from Anonyme southwards, the eastern side of the Cerf Island group and North East Bay face the S.E. Trades and conditions in July and August are very exposed. The area from Anonyme to North East Point is sheltered from the full force of the S.E. Trades by Pointe la Rue headland and the Cerf Group of Islands; conditions are sheltered for most of the year and only occasionally do reef edges have breakers of any size. The shores behind the reefs in this area were once fringed by mangrove swamps.

On the western side of the islands situations and exposures are variable; Grand'Anse, Barbarons, Anse Corail, Anse Bazacar, Petit Police and Police Bays are exposed for most of the year. Anse Boileau, Anse à la Mouche and Baie Lazare are sheltered or only partially exposed for most of the year. Baie Ternay, Anse Soulliac and Port Launay are relatively calm and sheltered at all seasons.

pH *measurements*

Values of pH vary according to whatever method of measurement is employed, and therefore no great significance should be placed upon the figures obtained, other than as readings on a meter. They may possibly be useful as a comparison between environments in any one area. In the sublittoral communities around Mahé differences in meter readings were obtained which appear to reflect habitat differences.

In sea water in open circulation the meter readings varied between 7·8 and 8·2, in restricted environments such as reef flats low tide values are generally higher and may be as high as 8·8 in shallow isolated pools on *Thalassia* flats. During a single day on Anse aux Pins values of pH increased from 7·7 at 07.00 h to 8·8 at 13.00 h falling to 8·2 at 18.00 h.

On stable sandy bottoms the upper few centimetres of sediment are light coloured, oxidized and give meter readings approximately the same as that of the sea water above it. Beneath the upper layer the sediment is frequently blackened and smells strongly of hydrogen sulphide; pH readings are reduced and may be as low as 7·1, varying according to the degree of blackening. The lowest values occur where wave action is low, salinities reduced and the organic content of the sediment high as between Anonyme and North East Point. Where the sediment is rippled and in motion the pH reduction is slight.

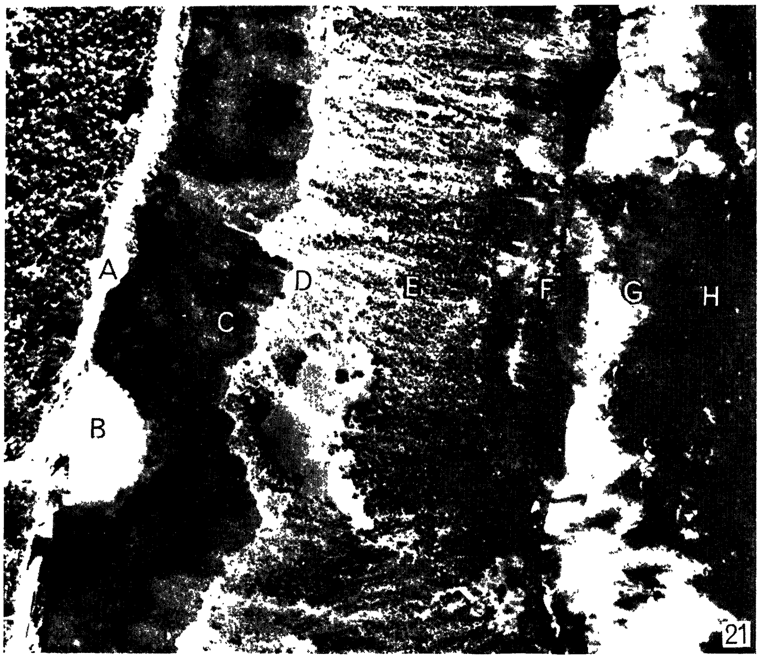
Physiography of the reefs

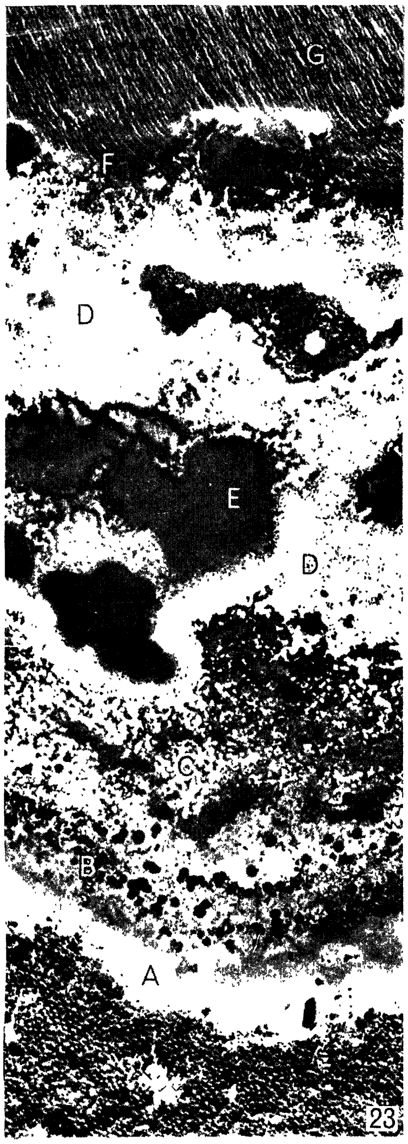
The reef as a structural unit is the result of a complex interaction of biological and physical processes, formed by the accretion and degradation of calcium carbonate in various environments. Similar environmental processes, such as wave action, which affect the distribution of organisms also affect the physical character of the sediments and the reef structure.

The basic structure of the fringing reef around Mahé is a hard platform formed by the gradual constructive advancement of corals and calcareous algae on the seaward reef edge and front. This is gradually filled in, to a greater or lesser extent, and planed off to a uniform level. This reef-platform is complicated because of the frequent changes in sea level during the Post-Glacial period (Lewis & Taylor 1966, p. 279). On windward reefs around Mahé the reef front only extends down to a maximum depth of 20 m where it flattens out gradually to the general level of the Seychelles Bank, with living coral only profuse to a depth of 10 to 15 m. At about wave-base level there is a change in slope upwards towards the shore, the reef edge, and area of high wave action. The reef edge and reef front are often dissected by small-scale spur and groove formations. Immediately landward of the reef edge is the algal ridge, which stands about 0·5 m above the general reef flat level, and is formed by the active growth of calcareous algae. Transitional from the ridge there is a series of ridges of algal and dead coral cobbles extending landward normal to the reef edge. Between these ridges, which gradually terminate towards the shore, are areas of rippled sand. Where the reefs are sufficiently wide, and the substrate suitable, beds of marine angiosperms growing upon layers of poorly sorted sands are developed. Immediately landward of these there is a narrow belt of rippled sand and then the beach. Opposite streams there is often a break in the reef edge forming a reef pass resulting from the inhibition of coral growth by the passage of low salinity water and sediment. This ideal basic pattern is modified or confused by the influence of different local environmental conditions.

The eastern side of Mahé has a virtually continuous fringing reef approximately 27 km long. The reef extends from the north of North-East Bay to Anse Marie Louise in the south, interrupted only by the granite headlands of Cap Macons, Pointe au Sel and Pointe la Rue. Anse Forbans reef in the south is narrow, not more than 150 m wide; exposed to the S.E. Trades it consists of a reef edge with spur and grooves, a strong algal ridge, low cobble ridges, a veneer of rippled sand and no grass beds. Anse Royale, a windward reef (figure 25, plate 14) is about 4·5 km long and at the widest point about 1 km wide, but at the southern and northern ends it narrows down to less than 100 to 150 m. There is a deep wide reef pass in the middle of the bay, grass beds form only small patches and a narrow fringe. Northwards is Anse aux Pins reef, (figures 21, 24, plates 13 & 14) 6 km long and 0·75 km across at the widest point, the reef edge is spurred and grooved and the algal ridge and cobble ridges are well developed. The grass beds are thick and conspicuous and zonation is well marked.

From South East Island to North East Point the reef is unbroken for a length of 12 km; it has an average width of 1·25 km but is over 2 km wide at Cascade. North of Port Victoria the reef edge is irregular and dissected, at Port Victoria and Montfleuri there are wide reef channels and the edge is broken and reduced to a series of coral knolls. From Montfleuri southwards the edge is more distinct but the reef encloses many deeper pools. Off Cascade (figure 22, plate 13) there is a large embayment of deep water open to the sea about 1·8 km across and 18 m deep. Its development is associated with the large streams entering the sea at Cascade Village. There are many small coral knolls rising to sea level but producing no continuous reef margin.





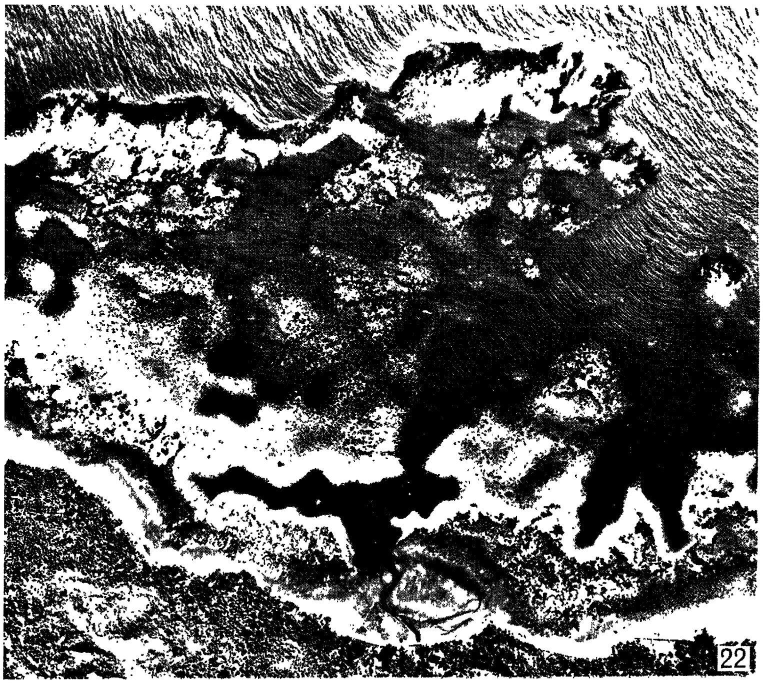


FIGURE 21. Aerial view of the reef flat at Anse aux Pins Village with reef zones indicated. A = Beach; B = delta spread from incoming stream; C = *Thalassia* beds with well marked seaward edges; D = fairly open sand; E = cobble ridges normal to the reef edge with interdigitating sands; F = algal ridge; G = Reef edge with strong surf; H = Reef front.

FIGURE 22. Aerial view of the reef flat at Cascade showing the large embayment, channels and pools associated with an incoming freshwater stream.

FIGURE 23. Enlarged aerial view of the sheltered reef flat near Brillant showing zonation. A = *Uca/Gafrarium tumidum* community, ex-mangrove fringes; B = belt of the marine angiosperm *Enhalus acoroides* (black patches) in surrounding Thalassia; C = *Thalassia* beds; D = open sands with occasional coral colonies and *Sargăssum* covered masses; E = deeper enclosed pools lined with *Porites*; F = poorly developed algal ridge and reef edge with little surf; G = Cerf Passage.

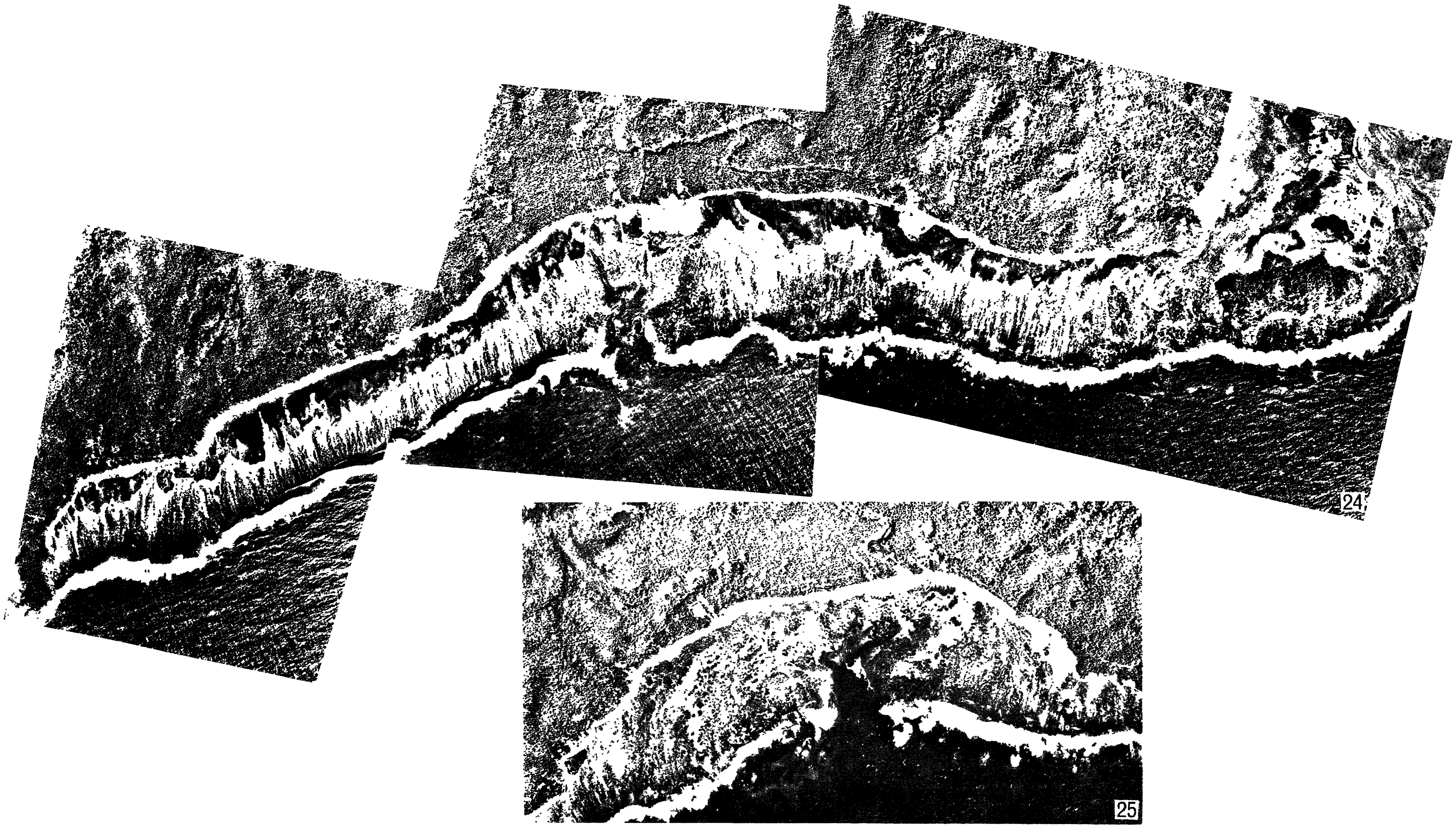
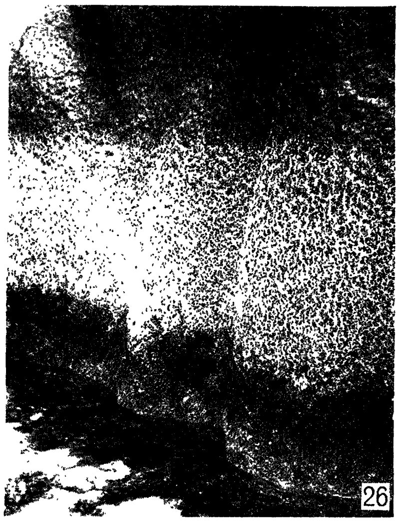
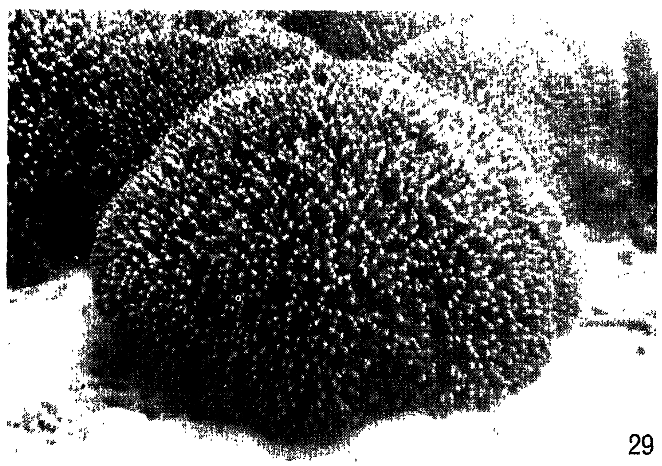


FIGURE 24. Aerial view of the entire windward fringing reef at Anse aux Pins, showing the attenuation of zones at each end, the cobble ridges alined normal to the reef edge and the relation of the reef pass to incoming streams. Length of reef = 5·6 km.

FIGURE 25. Aerial view of Anse Royale reef. Note the large deep pass opposite a stream mouth, the *Thalassia* beds restricted to small patches, the incipient spur and groove formation off the reef front and the arcuate arrangement of the cobble ridges around the reef pass.





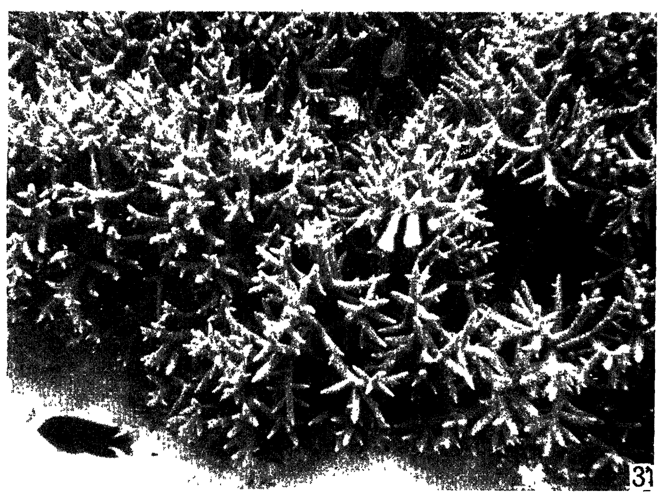


FIGURE 26. Barnacle zone (*Tetrachthalamus oblitteratus*) on granite shore at Pointe au Sel with green algae and *Sargassum* below.

FIGURE 27. Underwater view of beds of the marine angiosperm *Syringodium isoetifolium* with mounds of burrowing crustacea. Anse la Rue. Water depth 3 m.

FIGURE 28. Band of the bivalve *Isognomon dentifer* in byssally attached groups in the upper part of the eulittoral zone at Glacis.

FIGURE 29. Hemispherical colonies of *Porites nigrescens* (1 m high) on reef flat at Anse aux Pins. Water depth 2 m.

FIGURE 30. Clusters of *Littorina undulata* on granite surface at Pointe la Rue.

FIGURE 31. Underwater view of *Acropora pharaonis* on reef flat at Anse aux Pins on sandy bottom.

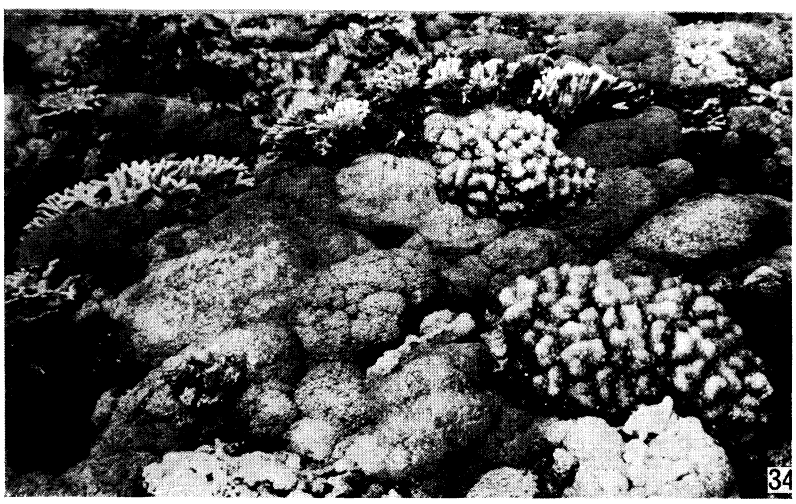
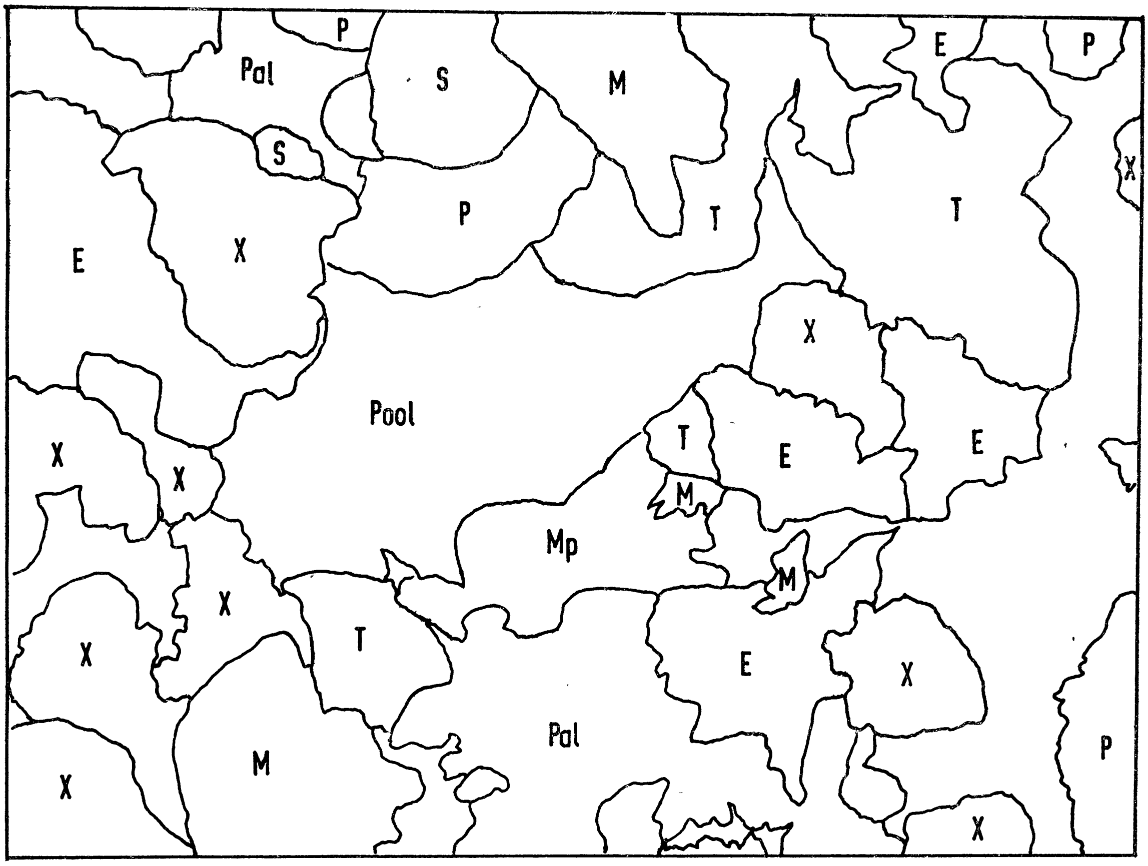


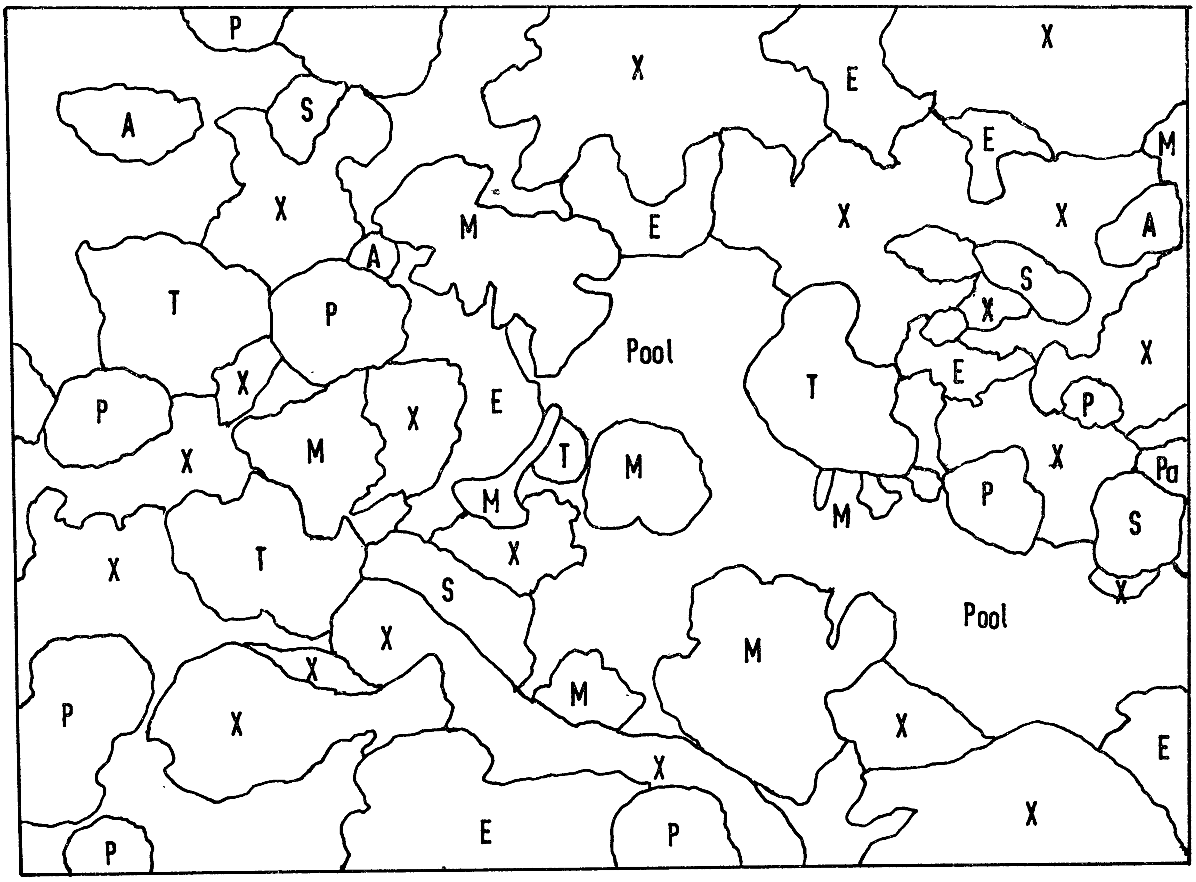
FIGURE 32. Supralittoral vegetation on an exposed shore at Anse Bazacar showing the outpost creeper *Ipomoea pescaprae* backed by *Scaevola* shrubs and *Cocos*.

FIGURE 33. Reef edge at lowest spring tides on a calm day off the northern end of Anse aux Pins reef.

FIGURE 34. Reef edge at Anse Faure emersed at low spring tides showing masses of *Xenia*, *Pocillopora danae* and *Millepora platyphylla*.

Plate 17 (Overlay)





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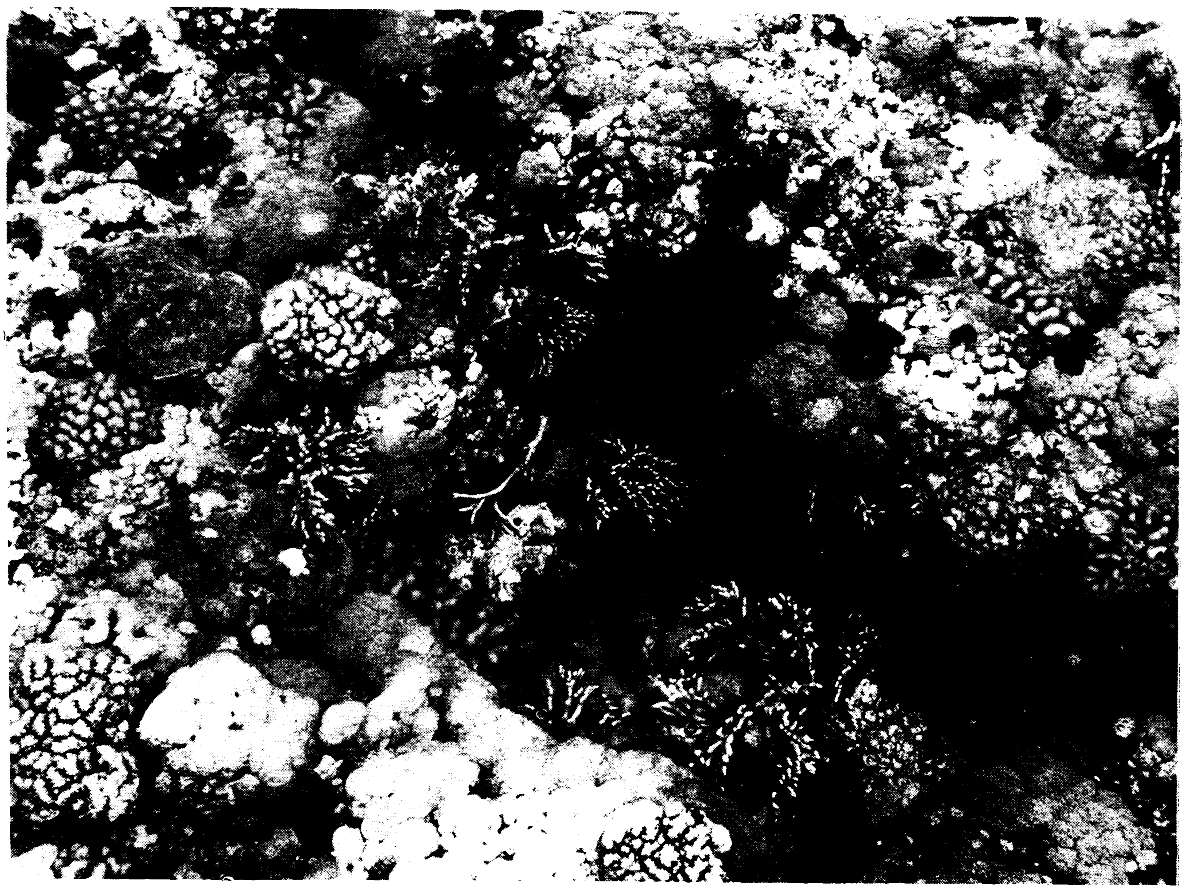

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FIGURE 35. Coral fauna surrounding an enclosed pool on reef edge at northern end of Anse aux Pins reef.

FIGURE 36. Coral fauna surrounding a deeper pool on reef edge at northern end of Anse aux Pins. Key: *A* = *Acropora digitifera*; *E* = encrusting zoanthid; *M* = *Millepora platyphylla*; *Mp.* = plates of *Montipora*; *Pa* = *Palythoa*; *Pal* = *Palythoa*; *P* = *Pocillopora danae*; *S* = *Stylophora*; *T* = *Tubipora musica*; *X* = *Xenia*.

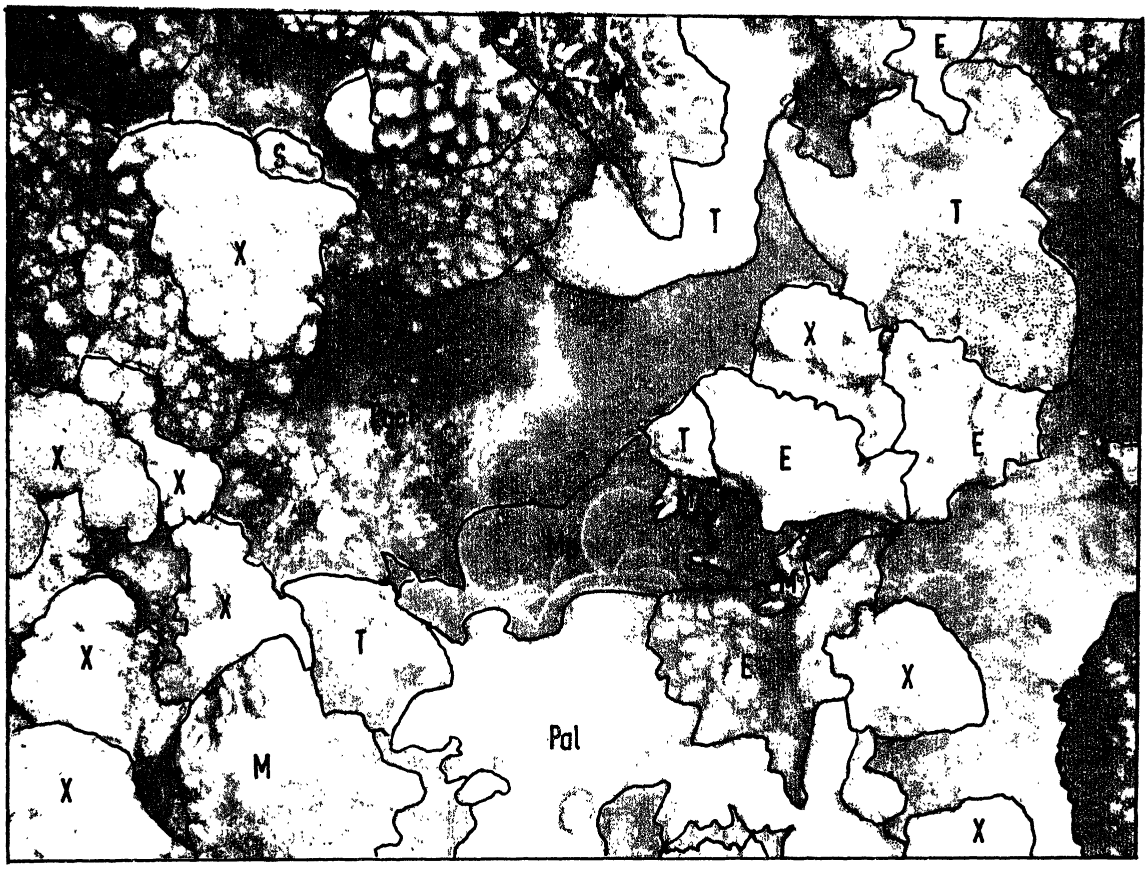

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FIGURE 35. Coral fauna surrounding an enclosed pool on reef edge at northern end of Anse aux Pins reef.

FIGURE 36. Coral fauna surrounding a deeper pool on reef edge at northern end of Anse aux Pins. Key: *A* = *Acropora digitifera*; *E* = encrusting zoanthid; *M* = *Millepora platyphylla*; *Mp.* = plates of *Montipora*; *Pa* = *Palythoa*; *Pal* = *Palythoa*; *P* = *Pocillopora danae*; *S* = *Stylophora*;

The reefs around the Cerf group of islands show a solid and distinct edge with spurs and grooves on the eastern side but on the sheltered western side the reef shows a gradual transition into deeper water with numerous small coral patches.

On the western side of Mahé reefs are poorly developed and are confined to a series of bay reefs. There are narrow platforms at Petit Police, Anse Bazacar, Anse Corail and Barbarons all exposed to the S.E. Trades and usually with high wave action for most of the year. These platforms are only about 20 to 30 m wide. At Anse à la Mouche, a bay about 2 km across, fringing reefs are developed around the south and north sides with a reefless area in the middle corresponding to the entry of a stream, the southern reef has a dissected margin with the marine angiosperm beds extending across to the edge. The northern side has an edge which is rather more continuous but not a strong feature, there is no algal ridge and the marine angiosperm beds again extend across most of the flats. This northern edge is exposed to wave action on some days of the year. The reef at Anse Boileau is about 1·75 km long, sheltered at the south but partially exposed to the S.E. Trades at the northern end. Three streams entering the sea have caused three delta spreads of sand on the reef flat. The Port Glaud-Anse d'Islette reef is 1·75 km long, faces the S.E. Trades and has a strong reef edge; an algal ridge and cobble ridges normal to the reef edge are developed. The large stream entering the sea forms a large delta and a wide reef pass at the northern end. The other small bays have small sheltered reefs. The edge at Baie Ternay is exposed during the N.W. Monsoon. Off Glacis there is a narrow fringing reef about 1 km long and 150 m wide which faces the north-west winds and has developed miniature spur and groove formations, an algal ridge and a narrow marine angiosperm bed.

Relation of reefs to physical conditions

Two main factors have influenced the development of the structural features of the reefs around Mahé, the nature of the submarine topography and the wind direction and velocity.

Darwin (1842, p. 49) said 'we must conclude that the dimensions and structure of fringing reefs depend entirely on the greater or lesser inclination of the submarine slope.' This conclusion seems particularly true around Mahé; the base level of Seychelles Bank around the Island is a maximum of 70 m but usually nearer 20 m close to the Island. Where the reefs are narrowest, as at North-East Bay, the bottom shelves off steeply into deeper water. Where there are wide bays and the submarine slopes are more gentle the reefs are correspondingly wider, as at Anse aux Pins and Anse Royale. North of South-East Island the 18 m contour extends outwards to encircle the Cerf–St Anne Island group forming a broad shallow water area fronting this part of Mahé. Here the reefs are widest but in fact occupy a sheltered position from the full force of the S.E. Trade winds. This suggests that a suitably shallow bottom is an important factor in the growth of wide reefs. In the Cascade area at the wide embayment where the water is calm and shallow there is no real reef edge but coral knolls are common. Darwin (p. 49) states: '. . . where the sea is very shallow . . . the reefs lose their fringing character and appear as separate and irregular patches.' This is also seen in the southern end of Cerf Passage where many coral knolls rise from the bottom of the channel. Immediately south of the lighthouse in Port Victoria Harbour the reef edge is discontinuous and consists of a series of elongate reef patches.

The winds, currents and associated swell are important in the shaping of the reefs. Although the winds affecting Mahé show seasonal variations the S.E. Trades are dominant in strength and consistency. The winds produce waves, swell and a current which moves in a generally west to north-west direction. Even when the S.E. Trades are not blowing there is a strong swell originating farther south in the Indian Ocean. Consequently, the great percentage of the coast on the eastern side of the island is fringed by reefs, whereas on the western side the reefs are small bay reefs. Reef edges and algal ridges, which on the eastern side are strong structures, are generally diminished on the western side. Cobble ridges normal to the reef edge are only developed on windward reefs.

Most of the Seychelles Islands lie out of the regular path of cyclones and heavy storms are infrequent. Destructional forces by greater than normal wave action are therefore small. Boulder tracts such as occur at Low Isles on the Great Barrier Reef (Manton & Stephenson 1935) are not developed. Large coral blocks cast upon the reef edge and algal ridge are infrequent; a few large boulders occur on Anse aux Pins reef especially immediately north of Pointe aux Sel. Large boulders are present on the beach at Petit Police and Anse Bazacar where wave action is high for most of the year.

Zonation

The most obvious feature of the fauna and flora of a coral reef is that it is zoned. This zonation forms the basis for the division and description of the communities of reefs around Mahé considered in this work.

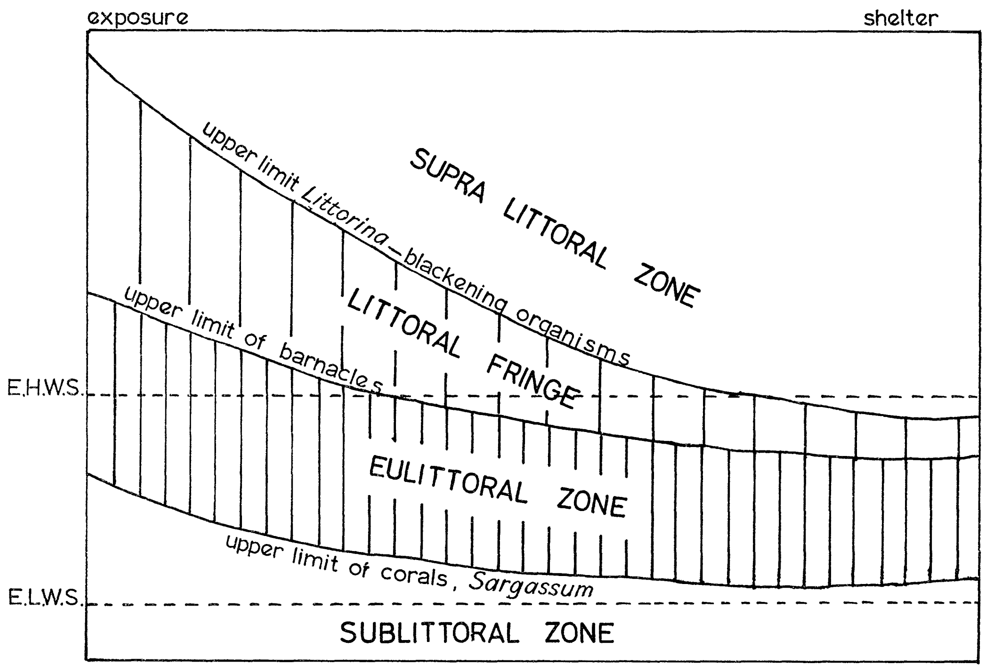

Figure 6. Scheme and terminology of zonation (adapted from Lewis 1964).

The zonation of organisms upon a rocky shore is a phenomenon recognized all over the world (Stephenson & Stephenson 1949; Southward 1958; Lewis 1964, p. 44). It results from the universal occurrence of similar processes at the air-water interface: diffusion, convection and mass action (Doty 1957).

In this work the terminology used in the description of zonation is that used by Lewis (1964) and depends upon the fact that certain types of organism characterize approximately the same levels on rocky shores. Physical characters are rejected for zonal definition, largely because of the difficulties in measurement of factors other than tides and also the lack of complete correspondence of biological divisions with tidal levels. Moreover, the organisms themselves reflect variations in physical factors more closely than can be measured.

The shore consists of three main biological zones, the littoral fringe which corresponds to the littorinid/blackening organism zone, the eulittoral zone which is characterized by barnacles, and limpets and the sublittoral zone extending below the upper limit of laminarian algae or corals. A further term, the supralittoral, is used in this work for the lower edge of the maritime terrestrial region directly influenced by the sea.

Relation of reefs to the zonal scheme

Once the hard platform of the reef is established, it behaves as a rather complex rocky shore. Stephenson & Stephenson (1949) first suggested that zone of maximum coral growth corresponded to the laminarian beds of the temperate sublittoral zone. Doty & Morrison (1954) described the zonation of the reefs of Raroia in terms of rocky shores

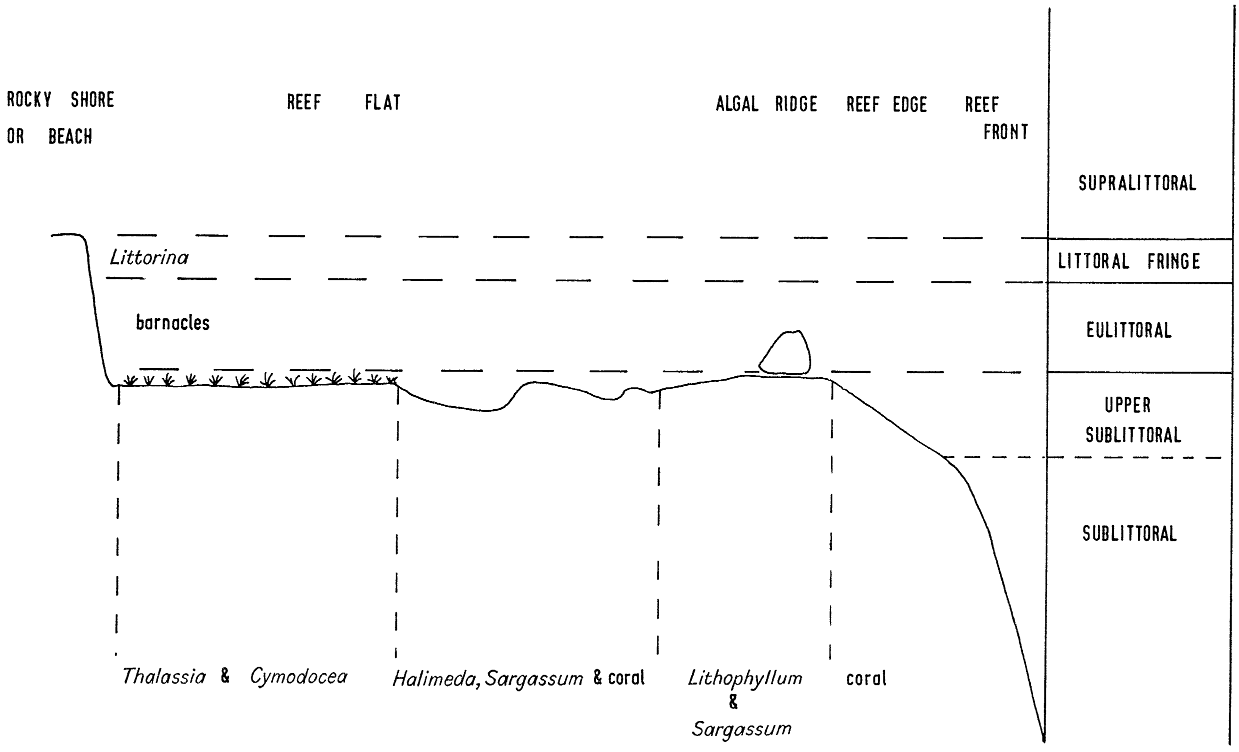

Figure 7. Diagrammatic representation of structural areas of the reef and the relation of the reef to the zonal scheme (not to scale).

zonation, and the same approach was used by Endean, Stephenson & Kenny (1956) for islands off the Queensland coast. Doty (1957) stated: 'The reef flats of coral atolls may be considered as specially developed sublittoral fringe pools of the constantly varying surface level type.' The reef surface offers innumerable microhabitats and microclimates. As opposed to the normal virtually completely epizoic nature of the rocky coast communities, those of a coral reef can have extensive infaunas as well. The diversity of life on coral reefs has tended to obscure the relations to a universal zonation scheme, and made the analysis of the various zonal communities more complex.

Figure 7 shows the diagrammatic relation of a windward reef to the zonal scheme and it can be seen that the greater part of the reef lies within the sublittoral zone. Granite, or superficial beach rock on the shore behind the reefs, shows the littoral fringe and eulittoral zones; where boulders are cast up on the algal ridge they are occasionally large enough to project upwards into the eulittoral zone and have a fauna of barnacles and limpets. Wide areas of the reef flats are virtually emersed at low spring tides, and the lowering of the water level restricts circulation, resulting in increased insolation effects and fluctuation of oxygen and carbon dioxide concentrations in the remaining water of the reef flat, which thus behaves, as suggested by Doty (1957) as a rock pool.

The supralittoral and mangrove environments

Beach vegetation

The coastal vegetation of the granitic Seychelles has recently been described by Sauer (1967). The natural zonation of the vegetation has been greatly disturbed by human activities on the heavily populated shores.

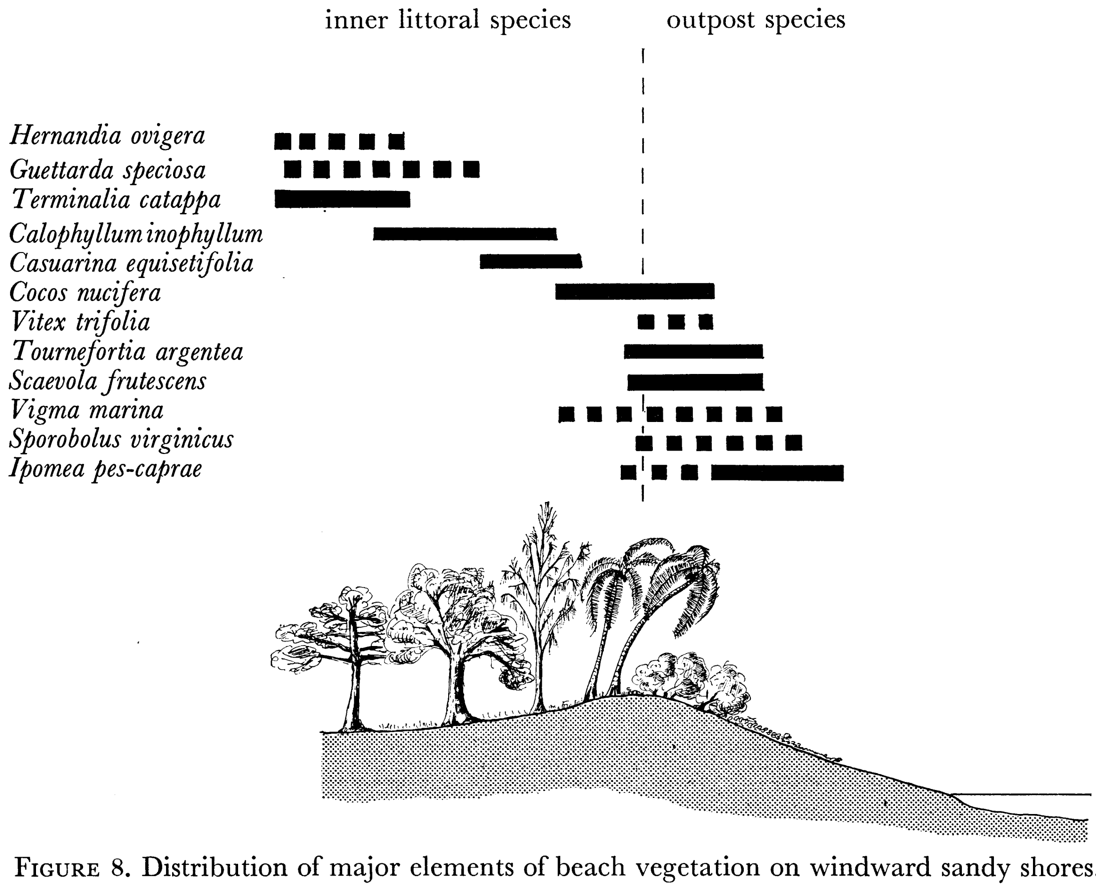

FIGURE 8. Distribution of major elements of beach vegetation on windward sandy shores.

On windward shores, where there is a well-developed beach and sometimes a 'plateau' area of vegetated sand behind, as at Anse aux Pins and Anse Royale, a characteristic vegetation pattern is developed. From the beach crest and extending down the beach slope are the creeper *Ipomea pescaprae*, the vetch *Vigna marina* and the grass *Sporobolus virginicus*. All of these low-level plants grow extremely rapidly and are able to recolonize areas very quickly, down the beach during periods of calm and neap tides, only to be ripped up again during spring tides or rough seas.

On the beach crest there is usually a dense thicket of the shrub *Scaevola frutescens*, forming a solid barrier to the seaward front; the roots and bases are washed at the highest spring tides.

The berm of the beach is inhabited by the ubiquitous *Cocos nucifera*, often overhanging the lower beach. When the first settlers arrived the coconut palm formed a single line of trees at the top of the beach, as a result of water-borne dispersal, but it has now been planted extensively over the whole island. Other common elements in the inner littoral belt are *Casuarina equisetifolia*, *Terminalia catappa* and *Hernandia ovigera*. The more massive and spreading *Calophyllum inophyllum* is important between Pointe la Rue and Cascade, and at Anse Boileau.

In quiet sheltered localities the vegetation belts may be telescoped so that the inner littoral species overhang the outpost species, or the latter may be absent altogether. At Anse la Rue *Calophyllum* overhangs the water edge, and *Ipomea* and *Scaevola* are virtually absent. On very exposed, wind- and spray-swept coasts, such as Anse Bazacar, Police Bay, Anse Forbans and Barbarons the outpost belt is expanded, and the *Scaevola* thicket is broader and more dense than on less exposed coasts.

The supralittoral vegetation is inhabited by the crabs *Coenobita rugosus*, *Ocypode ceratopthalma*, and the occasional *Birgus latro*. The numbers of the latter species have been severely reduced by human predation. The ellobiid gastropod *Melampus castaneus* occurs beneath dead vegetation at the top of the beach.

Mangroves

Where there are quiet water conditions, reduced salinities and a suitable substrate, mangrove swamps are developed. Along the coast from Anse Talbot to North East Point, where most of the inner reef flat is sheltered, and many streams enter the sea from the steep granite slopes behind, early arrivals on the Island recorded the presence of a thick mangrove swamp (Jeffrey 1962). These swamps were inhabited by crocodiles, long since eliminated. The swamps have now been cleared to make way for human occupation on this, the most densely populated part of the Island. However, small remanié patches survive at Brilliant, Petit Paris and Anse Etoile.

The former extent of the swamp can be seen by the extent of the relict sediments on the reef flat (now inhabited by the *Uca/Gafrarium* community, see below). The sands retain some of their mangrove swamp characteristics, much quartz, organic debris, crustacean debris and blackened grains. At the mouths of some of the streams entering the sea on windward reefs, there is a fringe of mangroves as at Anse aux Pins Village or Baie Lazare. On the western side of the Island, at Anse d'Islette, a large swamp has developed around a large stream crossing the broad low-lying 'plateau' area; it is separated from the sea by sandy beaches.

The distribution of the various mangrove genera within the swamps is broadly similar to that described by Davis (1940) in Florida. On the seaward edges of the mangrove fringes, *Rhizophora* and *Bruguiera* are dominant, *Ceriops* and *Sonneratia* usually occur behind the seaward front. *Avicennia* is very characteristic of the higher drier sandy bars within the swamps, and *Lumnitzera* to the landward edges of the swamps. The fern, *Acrostichum aurium*, is common on the higher sandy areas of the swamps. Often this arrangement of species is reversed or complicated. The swamps at d'Islette show complicated patterns around tidal creeks. Sauer (1963) concludes that the distributions of species are correlated with combinations of water level changes, salinity and sediment factors, but the critical ecological conditions are subtle and largely unknown.

The faunal assemblage from the mangrove swamps and fringes is highly characteristic, and all the species are able to tolerate reduced salinities. Decapod Crustacea dominate the swamps in numbers of individuals. The 'fiddler crab' *Uca annulipes* is the most abundant; it is a detritus feeding scavenger and restricted to areas immersed by tides. On the higher sandy portions of the swamps, which are often emersed for long periods, *Cardisoma carnifex* is common. Its burrows, which may be more than a metre deep, reach down to the water table. Both species are active during the low-tide period. The carnivorous swimming crab *Scylla serrata* inhabits the estuaries, and at low tide shelters beneath crevices and rocks. The swiftly moving scavenger *Sesarma longipes* and *Metopograpsus messor* are common around rocks and boulders.

In the estuaries the 'mudskipper' fish, *Periopthalmus sobrinus*, is common. It is active on emersed rocks and mud at low tide, and feeds upon crabs, molluscs and insects. The large gastropod *Terebralia palustris* is often present in large numbers in the muddy creeks and often spreads on to the reef flats at the mouths of streams. This species is able to tolerate changes in salinity from normal sea water to almost fresh water. At low tide it grazes upon the green algal coatings of the sediment surface, but at high tide it is inactive. Local densities of up to approximately $12/m^2$ were recorded. Higher up the streams, where the water salinity is very low, *Theodoxus* is common, feeding upon green algae on the stream bottoms. On the seaward faces of the mangrove fringes *Littorina scabra* and *L. undulata* are found on the prop roots, trunks and branches of the mangroves, the latter occupying the higher positions. *Crassostrea cucullata* is common cemented to the lower prop roots and trunks of the mangroves. In the swamp at d'Islette, approximately 0·8 km from the sea, the bivalves *Gafrarium tumidum* and *Ctena divergens*, both suspension feeders, and *Quidnipagus palatam*, a deposit feeder, are found. Although living out of the main freshwater flow, they must, nevertheless, be able to tolerate much reduced salinities. Normally these three species inhabit sands of the reef flats in marine conditions.

The beach: (the Donax–Ocypode community)

All reefs, except those between Anse Talbot and North East Point, are backed by a beach, the width of which depends partly on the degree of exposure. Sheltered shores have low narrow beaches, as at Anse la Rue, whilst exposed beaches are generally steeper and wider. The beaches are formed mainly of detrital carbonate grains with locally greater or less concentrations of land-derived quartz.

The beach at Grand'Anse, not fronted by a reef, is exposed to heavy surf for most of the year; other beaches show seasonal variation in the amount of wave action. Many beaches, such as North East Bay, Petit Police, Bel Ombre and Anse aux Couches, possess a line of beach rock at the base and mid beach. The sand behind the rock exposure is usually devoid of life except for the crab *Ocypode*.

The fauna of the beaches is understandably sparse in the number of species present but locally populations may be quite large. The macrofauna of the beaches consists normally of several bivalves, crabs and a gastropod.

Species of *Ocypode* are characteristic inhabitants of tropical beaches throughout the world. The species found on Mahé, *O. ceratopthalma* inhabits a non-branching curved sloping burrow about half a metre in length. Active excavation of the burrows and scavenging of beach detritus takes place at low tide. On several occasions at incoming tide, large numbers of these crabs were seen descending the beach and entering the sea.

The bivalves present in this community are *Atactodea glabrata*, *Donax cuneatus* and *D. faba*. They show rather variable distribution and abundance. *A. glabrata*, a small suspension-feeding mactrid, is the most common, occurring on beaches such as Anse aux Pins, Anse Royale, the Cerf Island group and Glacis. The two species of *Donax* are more restricted to beaches not fronted by a reef, that is, where beach circulation is greater, such as Grand'Anse, Beau Vallon and Port Launay. In *D. faba* and *D. cuneatus* the siphons are short; both feed primarily on suspended matter, an adaptation for life in beach sand where organic detritus is low. *D. cuneatus* migrates up and down the beach with the tides in a process similar to that of *D. semigranosus* described by Mori (*in* Hedgpeth 1957). It is exposed, carried down the beach by the swash and reburrows lower down the beach, the process being reversed on the incoming tide. This may be a mechanism by which feeding may take place at the level with maximum suspended matter (i.e. the wave breaking edge) at all stages of the tide. *Atactodea glabrata* is not visibly active at low tide. Both *Donax* and *Atactodea* supplement the diets of the local population and densities are correspondingly decreased near areas of human habitation.

The opisthobranch gastropod *Umbraculum umbraculum* with a small patelliform shell and large foot and gills is occasionally found buried in the sand at the base of the beach.

The littoral fringe and eulittoral zones

The higher zones of the rocky shore environment are rather restricted in extent, confined to headlands between sandy bays, beach-rock exposures within bays, and the bouldered shore from Cascade to North East Point. The western side of the island has less bays and the rocky shore is more dominant, than on the eastern side.

Sometimes headlands may be a jumble of granite boulders, as around North Point, or they may be solid granite slopes, as at Pointe la Rue, Cap Ternay and Pointe au Sel. The granite surfaces are usually smooth with few crevices for the shelter of organisms; on very exposed situations, such as the tip of the Pointe au Sel Headland, grooving of the granite normal to the direction of the waves is developed. Where the coast is bouldered there are many microhabitats, shady or sunny, damp or dry, sheltered or exposed. The rather impervious nature of the granite surface does not retain surface moisture for long on exposure to the sun. Beach-rock surfaces are varied in microhabitats; solution weathering on the higher portions has caused pitting and the lower surfaces have been worn smooth by wave action. The porous nature of the rock retains its moisture longer than the granite surfaces. Fine developments of beach-rock are seen at Anse Bazacar and Petit Police, where the landward portion is high and pitted, whereas the seaward side is undercut. More usually the beachrock exposures are low and gently dipping towards the sea, terminating at about low spring tide level.

The littoral fringe: the Littorina*–blackening organisms community*

The littoral fringe extends from the top of the upper limit of barnacles to the top of the upper limit of marine organisms and corresponds with the extent of the *Littorina*–blackening organisms community (Lewis 1964, p. 52). The width of the zone varies with wave action and is largely independent of tidal range.

Around Mahé, lichens and other blackening organisms, such as blue green algae, are not as conspicuous as around the shores of Europe; they tend to occur on the seaward faces of boulders. The paucity may be caused by the high insolation on the bare rock surfaces, or the unsuitable nature of granite as a substrate. Blue green algae frequently blacken the higher portions of beach rock exposures.

Species of *Littorina* are characteristic of this zone throughout the world (Stephenson & Stephenson 1949). Around Mahé, *L. scabra* and *L. undulata* are present. The latter is the more common, occurring mainly on sheltered shores, often on open surfaces or gathered in groups in small depressions on the granite surface but under shady, damp, overhangs it is more evenly distributed. In very sheltered conditions it occurs up to 3 m above high spring tide level, but always in shady situations. *L. scabra* is the more common lower in the zone and on more exposed shores. Local populations of both species show great variation in size and colour markings. Both are grazers upon blue green algar coating the rock surfaces. *Planaxis sulcatus*, a small gastropod, occupies a similar niche to *Littorina*. It usually occurs in a belt immediately above the barnacle line and has a localized distribution. The thick shelled *Nerita plicata* often ranges up from the eulittoral zone. It usually occurs on open rock surfaces, frequently near fresh water seeps where there are growths of *Enteromorpha*.

The crabs *Metopograpsus messor* and *Grapsus strigosus* range throughout the littoral zone but are more common in the littoral fringe. Both are extremely fast moving and well camouflaged. *M. messor* is more frequently found among the boulders between Cascade and North East Point.

The eulittoral zone

Barnacles are recognized as the most characteristic and dominant organism of the eulittoral (midlittoral of the Stephensons) zone throughout the world (Stephenson & Stephenson 1949, Lewis 1964, p. 72).

The upper limit of this zone is taken as the upper limit of abundant barnacles. Around Europe and temperate shores the lower limit is taken at the upper limit of abundant laminarians, but around Mahé the first appearance of corals and *Sargassum* is used. The width of this zone can be correlated with tidal range although severe exposure will widen it significantly.

The barnacle line around Mahé is somewhat spasmodic but where it occurs is definite and conspicuous. The dominant barnacle *Tetrachthalamus oblitteratus* belongs to a newly described genus (Newman 1967; Southward 1967) which shows a restricted distribution in the Indian Ocean, suggesting that it is a biological relict. It is usually abundant in a zone about 60 cm wide but occurs less plentifully throughout the zone; in very sheltered situations the population is sparse. The large barnacle *Tetraclita squamosa* is present lower in the zone, but is not so tolerant of prolonged emersion.

The lower limit of the eulittoral, equated with the upper limit corals, is more difficult to delineate in the field as corals only occasionally occur in this habitat; however, the first appearance of the brown algae *Sargassum* and *Turbinaria* can be taken as equivalent.

Even in an area as small as Mahé there are a great many variations in the fauna and flora of this zone. A demonstration of these variations can be seen in the change in composition of the community passing from very sheltered to exposed conditions around the north side of Pointe au Sel. The habitat changes gradually around the point from very sheltered conditions with scattered boulders on sand (passing outwards into a solid granite shore with some boulders and sheltered conditions) to the intersection of the Anse aux Pins reef edge with the headland and lastly the seaward headland of Pointe au Sel with extreme exposure (for Mahé).

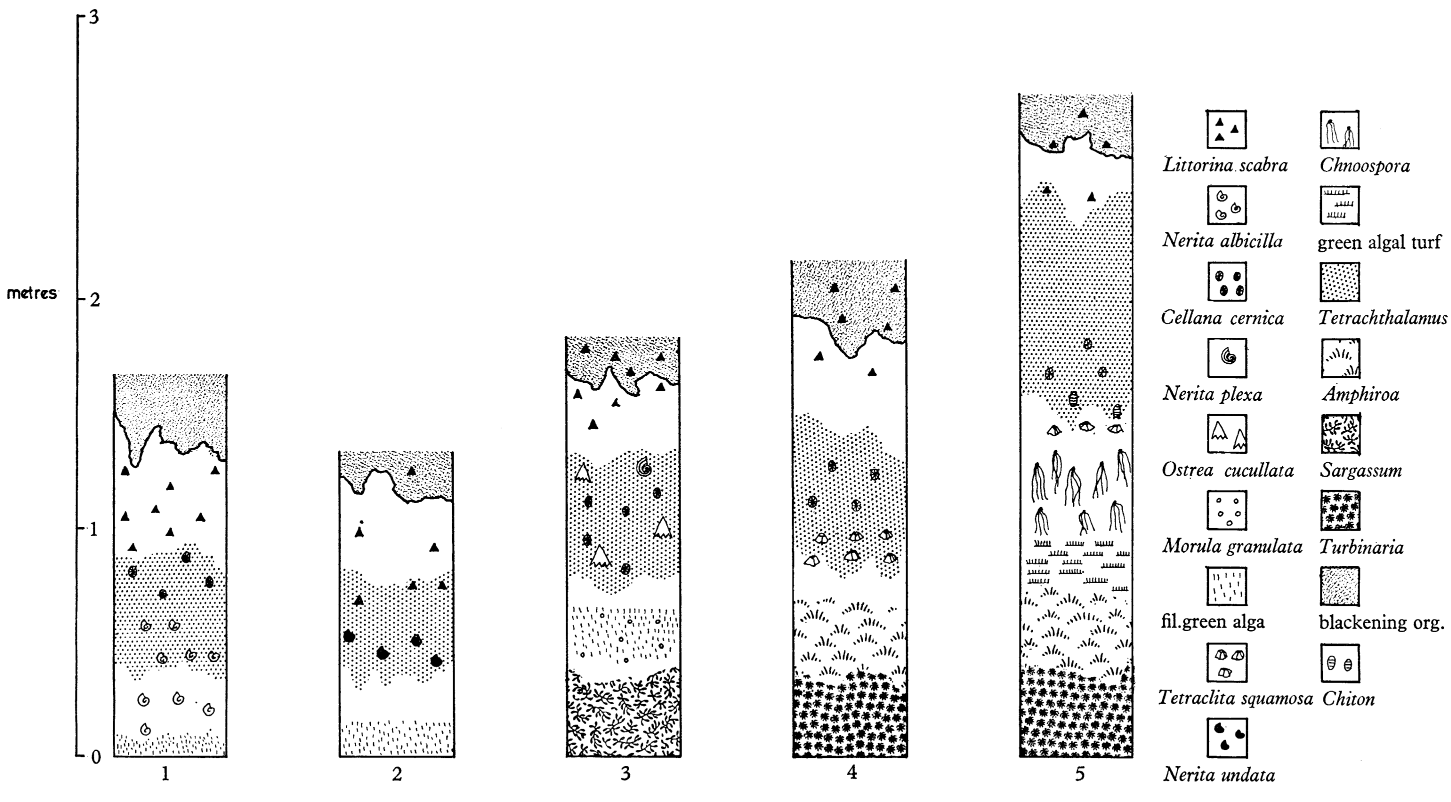

FIGURE 9. Distribution of intertidal organisms at sites on north side of Pointe au Sel.

At site 1 (figure 9) on the inshore sheltered boulders the total littoral zone is narrow, about 1·25 m in the shade, but narrower where exposed to the sun. *Littorina undulata* is common on open surfaces but *Nerita albicilla* is always confined to low shady damp positions. *Tetrachthalamus* is sparse and the limpet *Cellana cernica* is present towards the top of the belt on open surfaces. At site 2, a boulder surface facing the sun for most of the day, the biota is very sparse, consisting only of *L. undulata*, sparse barnacles, *Nerita undata* confined to cracks and a band of green filamentous green algae at the base of the rocks.

At site 3, a vertical seaward granite face, the littoral zone is nearly 2 m wide and zonation of organisms is very well marked. The barnacle zone is wide and well defined, below it is a belt of filamentous green algae and immediately below this in the sublittoral zone is the top of the *Sargassum* belt (figure 26, plate 15). Above the barnacle belt *Littorina undulata* and *L. scabra* are common, within the belt the limpet *Cellana cernica* is common, and cemented to the granite is the oyster *Crassostrea cucullata*. The barnacle-feeding gastropod *Morula granulata* is found at low tide, amongst the green algae, and among *Sargassum* two other prosobranchs, *Drupa ricinus* and *Nassa sertum*, occur. Between sites 3 and 4 the large barnacle *Tetraclita squamosa* appears at first occupying damp shady overhangs, but seawards, as emersion time becomes less, it occurs on the open surfaces. Site 4 is situated at the intersection of the reef edge and headland and conditions are exposed for most of the year. This situation is notable for the appearance below the barnacle line of the encrusting calcareous alga *Lithophyllum* and cushions of closely packed branches of another calcareous alga, *Amphiroa*. Below the *Amphiroa* the brown alga *Turbinaria* has replaced *Sargassum*, the shorter stubby growths are more resistant to wave action. A band of *Tetraclita* occurs at the base of the '*Tetrachthalamus*' belt. *Cellana cernica* is flattened, coated with *Lithophyllum* and occupies small depressions on the rock surfaces. At the seaward tip of the headland is site 5 with very exposed conditions throughout the year where the granite surface slopes at about 40° into the sea and is dissected by runnels up which waves surge. Zonation is broad and the littoral zone is 3 to 5 m wide. Five conspicuous belts are seen, the barnacle belt, a belt of short thongs of *Chnoospora*, a narrow belt of short algal turf, a wide belt of *Amphiroa* cushions with *Lithophyllum* encrusted rock surface and then *Turbinaria*. In a few sheltered overhangs *Tetraclita squamosa* and the chiton *Acanthopleura* occur. The prosobranchs *Purpura rudolphi*, *Drupa ricinus*, *Cellana cernica* and *Drupa morum* are also present.

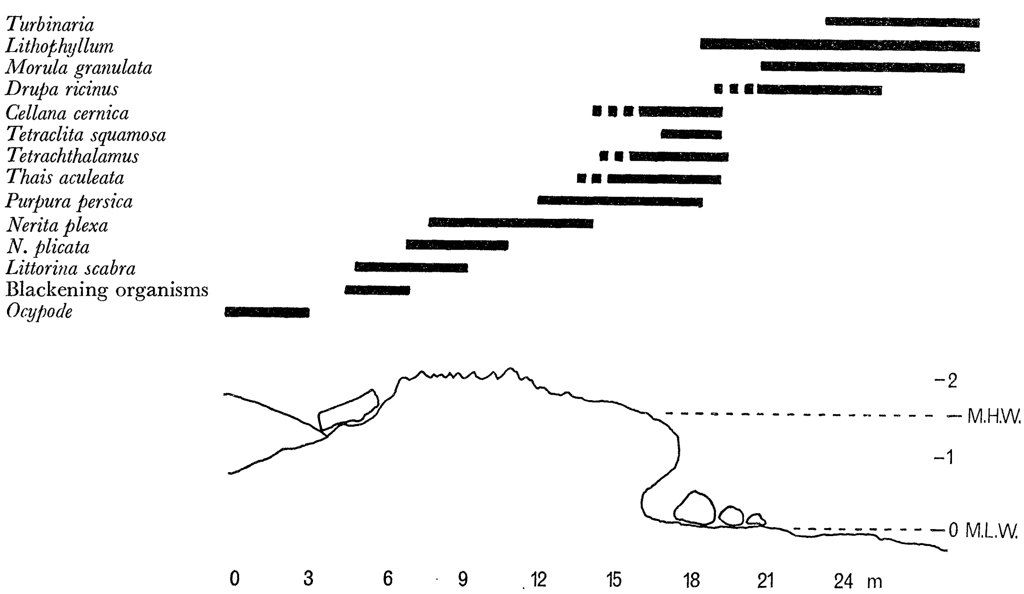

FIGURE 10. Zonation of organisms on beach rock at Petit Police.

An interesting zonation pattern is seen on high beach rock at Petit Police. On the highest portions *Littorina scabra* occurs with the thick shelled *Nerita textilis* in the littoral fringe. The large heavily rugose *N. plicata* is common in the eulittoral zone and the lower littoral fringe. On the face of the small cliff are *Tetrachthalamus*, *Tetraclita squamosa*, the limpets *Cellana cernica* and the carnivorous *Purpura rudolphi*. *Tetraclita* occurs in the undercut overhang and below this on the flat platform the predatory gastropods *Morula granulata*, *Drupa ricinus* and *Conus ebraeus* are abundant.

The normal pattern for beach rock on sheltered to moderately exposed shores is shown in figure 11. Groups of *Littorina undulata* occur on the higher pitted areas which are coated in blue green algae. Barnacles are generally absent but on the lower portions *Nerita albicilla* and *Cerithium morum* occur in more damp, shaded crevices and beneath loose blocks.

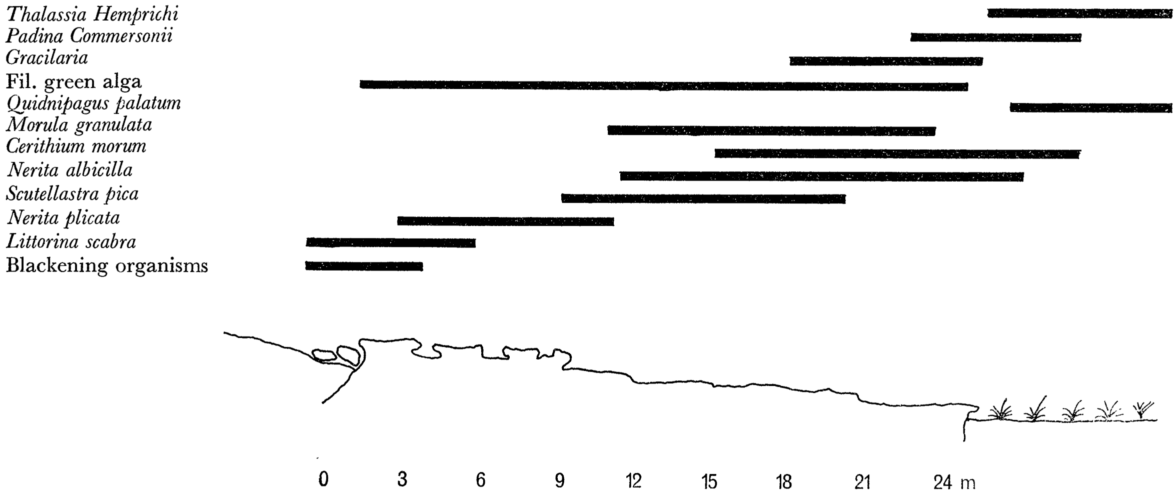

FIGURE 11. Zonation of organisms on beach rock at Anse aux Couches.

On the algal ridge, cast-up blocks occasionally project into the eulittoral zone; between Le Cap and Pointe au Sel some of these blocks have a fauna of the barnacle *Tetraclita squamosa* and the limpet *Cellana cernica*. On the very large blocks at Pointe au Sel the green algae *Enteromorpha* and *Ulva* colonise the extreme upper surface which is frequently exposed to fresh rain water.

Discussion

The ranges of some intertidal organisms on rocky shores around Mahé are shown in figure 12. It is seen that certain levels are important for the appearance and disappearance of organisms. The M.L.W.S. to E.L.W.S. level is important as macroscopic algae do not usually flourish above these points. Barnacles, limpets and most neritids disappear at or about the M.L.W.N. level, which is usually the upper range limit of these forms. *Littorina* does not usually range far below H.W.N.

Six sympatric species of *Nerita* inhabit the narrow littoral zone around Mahé. All are algal grazers, but on closer inspection they are seen to have slightly different habits and distributions. *N. plicata* usually occurs high on the shore and frequently near freshwater seepages exposed to strong sunlight and often not covered by high neap tides. *N. textilis*, the largest species, thick-shelled and heavily rugose, is usually restricted to exposed shores in the high eulittoral. The most common species *N. albicilla* is usually confined to the lower eulittoral in damp and shady situations; it frequently ranges down into the sub-littoral. *N. polita* appears to spend the high tide period in the sand at the base of the rocks and on falling tide emerges and moves up the rocks to a mid-littoral position. Individuals often retain a coating of sand over the shell which may act as a protection against excessive insolation. Two relatively uncommon species are *N. undata* and *N. debilis*, the former occurs at inshore sites and at Pointe au Sel and Takamaka, whilst the latter occurs only at the north end of Takamaka; both inhabit shaded, damp positions in the mid-eulittoral zone.

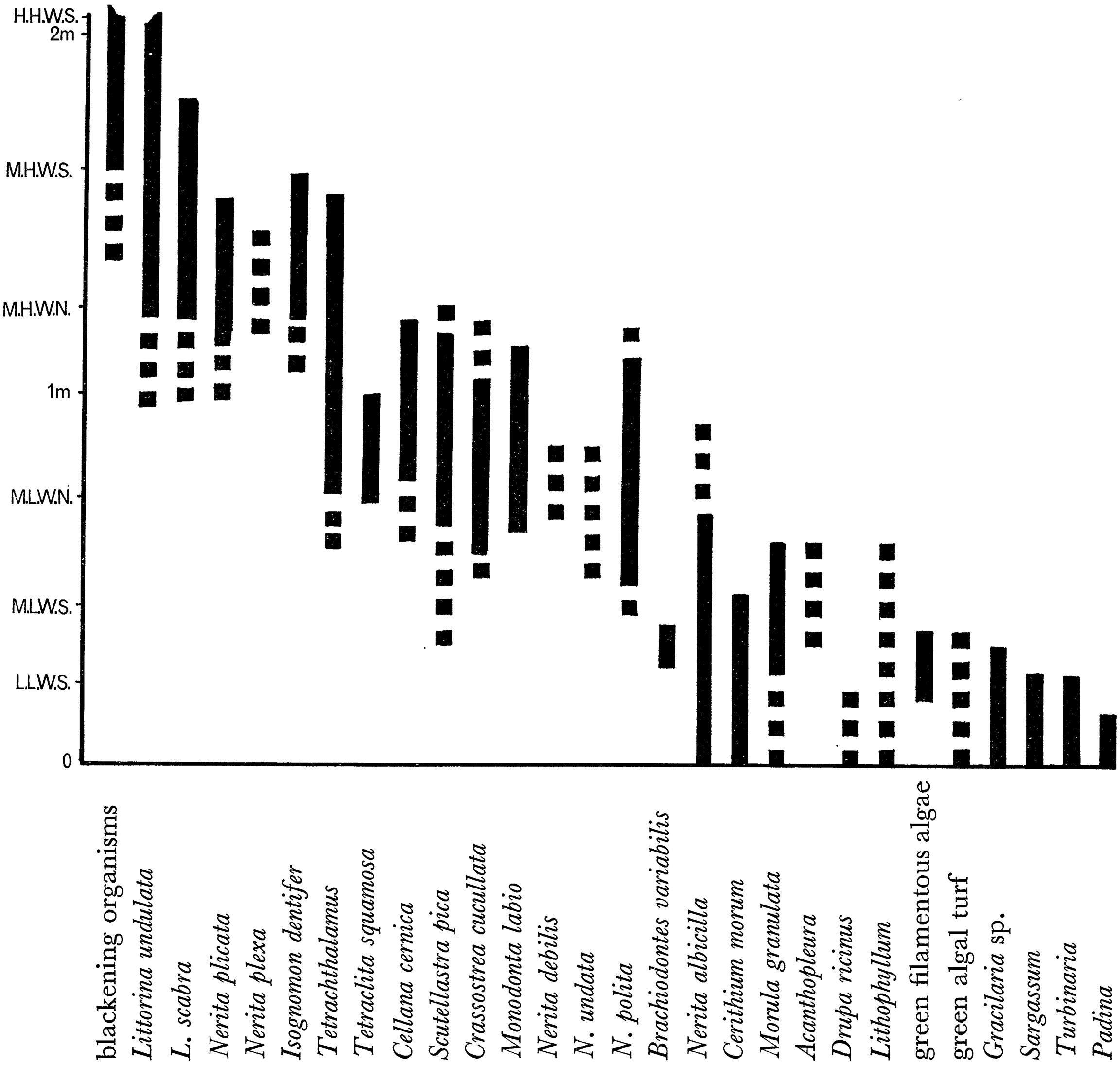

FIGURE 12. Intertidal distribution of organisms on shores other than very exposed.

EX-MANGROVE FRINGES: THE *UCA ANNULIPES–GAFRARIUM TUMIDUM* COMMUNITY

Between Anse Talbot and North East Point the area from the boulder shore line to the landward edge of the grass beds is occupied by a distinctive community, the most abundant members of which are a crab *Uca annulipes* and a bivalve *Gafrarium tumidum*. This is the former site of mangrove swamps which once fringed this part of the Island. The belt now extends to a maximum width of about 350 m near the mouths of streams but generally forms a fringe from 80 to 199 m wide. Between Le Rocher and Port Victoria, which is very sheltered and where many streams enter the sea, the belt is uniformly wide at about 300 m.

The sediment of this fringe shows special characters; there is much quartz present, with weathered felspar, and the carbonate constituents are much lower than in other environments and consist mainly of crustacean and molluscan debris. The surface 2 to 3 cm of the sediment is medium brown in colour, but immediately below is blackened and smells strongly of hydrogen sulphide; pH readings as low as 7·1 were obtained. The blackening is most intense close inshore and decreases towards the outer edge of the fringe, where pH values closer to that of normal sea water are obtained. Peat layers and lenses are common beneath the surface and the sediment as a whole is rich in organic debris. Close inshore the sediment is very soft. This section was once a dense mangrove fringe populated with crocodiles; remnants of the mangroves can be seen at Petit Paris and Brillant. Within living memory the mangroves were more extensive and have been cleared for human occupation. Occasional mangrove hypocotyls take root on the flats some distance from the shore but never survive for long. The sediment of the present-day fringe has retained some of the mangrove swamp characteristics.

Salinities over this area are generally reduced, even at high tide, and in the proximity of stream mouths values are very low. After heavy rain, masses of fresh water can be seen moving across the reef flat and into reef channels. Wave action along the reef edge fringing this section of the coast is slight and this habitat on the landward edge of the reef flat is very sheltered in comparison with the equivalent position on windward reefs. The water over this community is always turbid; much of the suspended matter is fine sediment stirred up by tidal movements, but a significant proportion consists of detritus brought down by the streams and effluvia from the human settlement on this, the most densely populated part of the Island.

At low spring tides the *Uca-Gafrarium tumidum* community fringe is almost completely emersed for considerable periods of time; even at neap tides when a much smaller area is emersed, the water over the flats is only a few centimetres deep. At high tides the water depth is not usually more than 1·5 m. The seaward edge of this community passes transitionally into the *Thalassia* beds with no sharp demarcation line as seen on windward reefs.

Algae and marine angiosperms

The most important plant in this community is the marine angiosperm *Halophila ovata*, a low growing, creeping form spreading by adventitious rooting of the stems. Although inconspicuous, it is always present, except close inshore. It is the most tolerant of long emersion times, high insolation and turbities. The larger angiosperm *Enhalus acoroides* forms patches about 5 to 10 m across at the junction of this community with the *Thalassia* beds. Although absent from windward reefs, *Enhalus* forms these patches between Cascade and North East Point (see figure 22, plate 13).

Near shore and particularly near streams the green alga *Enteromorpha* occurs as an epilithic coating on the sediment surface. *Padina commersoni* is most common near the granite boulders near shore but can form patches across the flats. In the outer 10 m of the community there is a more abundant algal flora. Intertwined, unattached, epilithic masses of green algae are common, each colony occupying an area of about half a square metre. These algae support vast numbers of the gastropod *Cerithium morum*. Low clumps of *Gracilaria*, about 40 cm in diameter, occur in great abundance between the Short and Long piers in Port Victoria Harbour.

Clumps of *Halimeda opuntia* are common towards the outer edges of the community and the larger, leaved, single stemmed *H. macroloba* is locally common. Both are important sediment contributors. Much of the coarser sediment is covered by a fine, green, filamentous alga.

Crustacea

The rock crab, *Metopograpsus messor*, shelters in, and between, the granite boulders close to the shore, becoming very active at low tide. *Epixanthus frontalis* is found at the base of the rocks beneath overhangs and *Ocypode ceratopthalma*, a species more usual on sandy beaches, was found on the mudflats at Cascade.

From the shore, and extending about 100 to 120 m across the reef flat, is a dense population of the fiddler-crab *Uca annulipes* which is the most abundant macro-invertebrate. The density of this population decreases seawards but averages about 3 to $4/m^2$. The crabs are very active at low water as deposit feeders and scavengers but as the tide advances begin to block the entrances to their own burrows. These are 15 cm deep; those of males and females being separate. The male of *U. annulipes* has one very large chela (either right or left) which is coloured bright orange or red: the chelae of the females are more or less equal.

As the *Uca annulipes* population decreases seawards it is replaced at about 100 to 120 m from the shore by a smaller, inconspicuous, burrowing crab *Macrophthalmus parvimanus*; this is elongate, brown and at low water inhabits shallow pools. *Calappa hepatica* is common towards the seaward edge and ranges into the *Thalassia* beds.

Near shore the carnivorous swimming crab *Thalamita crenata* is common; it is active at high tide but at low water confines itself to shallow pools, or burrows beneath the sediment surface. The burrowing prawn *Alpheus rapax* is characteristic at this level where it occupies burrows, 15 to 20 cm deep, lined with coarse sediment and organic debris.

Hermit crabs are abundant and usually inhabit the shells of *Cerithium morum* which are readily available. *Dardanus deformis* inhabits the shells of *Terebralia palustris* and the large land pulmonate *Achatina*, and lives close inshore near the mouths of streams.

Molluscan fauna

This stable sand environment, with water high in suspended detritus, has a restricted fauna because of prolonged emersion, reduced salinities, and strongly reducing conditions immediately below the surface of the sediment. The fauna of 24 species of which prosobranchs and bivalves form 50 % each, is dominated in numbers of three species of bivalve and one prosobranch. Some 80 % of the bivalve species are suspension feeders and although the sediment is rich in organic detritus, deposit feeders are limited by reducing conditions below the surface. The prosobranchs both in species and individuals are algal feeders and scavengers; predators such as *Natica* are rare.

The characteristic and most abundant bivalve is *Gafrarium tumidum* which is almost restricted to this community, only being found elsewhere at the landward edge of *Thalassia* beds near streams. It is a shallow burrower so that almost all the shell lies within the upper, oxidized layer of sediment, indeed the posterior may often protrude above the sediment. A suspension feeder, the siphons are very short and the tentacle ring around the siphons is well developed and may act as a straining mechanism. Densities of the population are discussed below. A related species, *G. pectinatum*, appears to prefer more normal salinities than *G. tumidum* and occurs towards the outer edge of the community but never in densities of more than 1 or 2 per m^2.

Psammotea radiata is a deep burrowing deposit feeder; it is elongate and thin shelled with a thick periostracum, and lives in a vertical position, posterior uppermost, at about 15 cm below the surface. It has long divided siphons. The sediment immediately surrounding these and the shell is light colour, suggesting oxidizing conditions, immediately around the animal. *P. radiata* is found up to 120 m from the shore but is most abundant from 20 to 80 m. Another deposit feeder, *Quidnipagus palatam*, is common. It burrows and lies on the left side. Although as abundant as in the *Thalassia* beds, individuals in this community tend to be smaller. It ranges between 60 and 260 m from the shore with the maximum density always seawards of the maximum density of *Psammotea radiata*.

At the outer edge of the fringe, where it is transitional to the *Thalassia* beds, the large arcid *Anadara antiquata* is found. This is a shallow burrower when adult but juveniles were found byssally attached to *Halimeda* clumps, other seaweeds and isolated corals. *Crassostrea cucullata* occurs attached to rocks and stranded vegetation.

The prosobranch *Cerithium morum* is extremely common in this community. It lives on sediment surfaces, feeding on the green algal coatings. This species is very variable in shell shape, ornament and size. The scavengers *Nassarius albescens* and *N. arcularis* are again abundant occurring in densities of 4 to $5/m^2$. The clumps of green algae provide shelter for many individuals of *Pyrene azora* and *Cerithium rostratum*. The predator *Natica marochiensis* is present but uncommon.

A series of quadrat traverses was made, to estimate the abundance and distribution of bivalves in this community, normal to the shore at Port Victoria, Montfleuri, Brillant and Cascade; 64 quadrats were made, all 20 m apart. The distribution of bivalves shown in figure 15 for Montfleuri is typical. *Gafrarium tumidum* is the most abundant, reaching a maximum density of $113/m^2$ at 160 m from the shore, *Quidnipagus palatam* reaches a maximum density of $45/m^2$ at 180 m and *Psammotea radiata* is present from 60 to 140 m. with a maximum density of $14/m^2$. This pattern is repeated in the other traverses, *G. tumidum* reaching a maximum density of $180/m^2$ at Cascade, *Q. palatam* $75/m^2$ at Petit Paris, and *P. radiata* $80/m^2$ at 90 m from the shore at Cascade. At all traverses it was found that the bivalves have an average density of $44/m^2$ and that *G. tumidum* forms 80 % of the population. The distribution curves also show that the greatest densities occur in the shoreward parts of the habitat decreasing considerably seawards. Further, both deposit and suspension feeders are more abundant near shore, suggesting that this is the region in which the greatest amount of suspended organic matter and organic detritus in the sediment occurs. Most of this detritus is land derived.

Other fauna

Other faunal constituents are rather restricted. The algal colonies support populations of small amphipods. Brown sponges are locally abundant towards the outer edge of the fringe. Sediment burrowing polychaetes include *Eurythöe* and *eunicids* sipunculids also occur. Echinoderms are notably absent.

THE MARINE GRASS BEDS: THE *THALASSIA–CODAKIA–HOLOTHURIA* COMMUNITY

The beds of marine angiosperms form one of the most distinctive communities, with well-marked physiographic and organic limits.

On windward reefs the angiosperm beds extend from immediately seaward of the base of the beach, where there is often a belt of rippled sand about 5 to 10 m wide, which, except for scattered growth of *Padina*, is barren. There is then a 'step' of about 20 cm on to the grass beds which have a dissected and irregular landward edge. The grass beds are variable both in width, from a few metres to 200 to 300 m, and in the amount of grass cover. The beds are fairly uniformly level, approximately the same depth is covered to about 2 to 5 m at high tide at the landward and seaward edges; irregularities in the surface are caused by pitting and megaripples fixed by grass growth. There is another 'step' down off the seaward edge of the beds.

The marine angiosperms with extensive root and rhizome systems are able to fix sediment in a very stable position. Ginsburg & Lowenstam (1958) pointed out that *Thalassia* beds influence sedimentation in two ways: by protecting the sediments from waves and currents and also by encouraging sedimentation by the slowing down of water currents, causing deposition of the suspended load of particles; it is in this habitat that reef flat sediments reach their maximum thickness of more than a metre. The broad leaves of the grass are coated with epiphytic algae which trap sediment in the filamentous growths. The sediments of the grass beds are usually poorly sorted and contain much coarse debris with median diameters ranging from 0·3 to 1·2 mm and with sorting coefficients from 0·87 to 1·6 mm. At the extremities of bay reefs, where the beds are narrow, the angiosperms frequently grow out over coarse cobble debris with little finer grade sand. Study of aerial photographs taken in 1959 show little alteration in the outline of the seaward edge of the angiosperm beds.

Narrow, windward reefs, such as Anse Forbans, North East Bay, Petit Police, Anse Bazacar, and the southern part of the d'Islette reef do not support grass beds; strong wave action and the initially thin sediment do not encourage settlement and development. At Anse Royale there is only a narrow fringe of grass developed in the middle of the bay and, except for two small patches, none is developed at the extremities of the bay where wave action is higher. At Anse à la Mouche the grass has spread out almost to the sheltered reef edge, and a similar condition exists at Anse Boileau. Close inshore at Glacis the grass beds grow on thick sand but seaward they spread over coarse cobbles. At Anse aux Pins, where the beds show the best development, they vary in width from 200 m, in the middle of the bay, to a few metres at each end. Around the Cert group of islands angiosperm beds are not developed on the eastern and south-eastern windward sides, but are present as a narrow fringe around the west side of Cerf Island, and as broad beds between the islands.

Between Anse la Rue and North East Point the grass beds are rather different in character; they reach a width of about 300 m, but there is no step at the landward and seaward edges and there is a transition region rather than a boundary from the environments on each side. From Anse Talbot northwards the grass beds are extended seawards by the development of the *Uca–Gafrarium tumidum* community on the sites of the old mangrove swamps.

Six species of marine angiosperms contribute to the formation of the grass beds. Around Mahé the most important is *Thalassia hemprichii*. *Syringodium isoetifolium*, an erect cylindrical leafed form, is locally common around Anonyme, South East Island and Anse Royale. It shows an irregular distribution with *Thalassia* but appears to prefer slightly deeper water areas. *Cymodocea rotundata* is a narrow-leafed form which occurs at Glacis, or on the outer edge of the beds at Le Cap. *Halophila ovata* is a low creeping form with oval-shaped leaves, and is more common north of Anse Talbot, where it is a very abundant but inconspicuous background element in all the grass beds. It often colonizes the higher portions of the beds which are emersed for long periods at low tide and from which *Thalassia* may be absent. It is more tolerant to emersion and desiccation than *Thalassia*. From Cascade northwards the landward margin of the grass bed is characterized by *Enhalus acoroides* which has strap-like leaves up to a metre long; it occurs in patches from 5 to 10 m. across (see aerial photographs, figure 22, plate 13). Most of these patches occur between Petit Paris and Port Victoria but occasionally patches are seen north of Port Victoria, particularly at Pointe Connan.

Cymodocea ciliata was not found around Mahé but it is the major element in the grass bed flora of the coralline islands of Platte and Coetivy where it forms a very dense cover, and extends into water 40 m deep. This species is also the dominant form on the reefs of the East African coast at Mombasa and Dar es Salaam.

The leaves of the grasses, particularly *Thalassia*, *Enhalus* and *Cymodocea ciliata*, provide a suitable substrate for many small epiphytic algae of which only the more important genera have been identified: *Ceramium* and *Polysiphonia* are very common and occur as densely branching tufts. *Acrochaetium* is common as a network of filaments along the surface of the leaves and is very important in the trapping of sediment. The red calcareous alga *Melobesia* occurs as flat circular encrustations and is exceedingly common, sometimes covering almost the whole leaf surface. Humm (1964) considers that after death and disintegration this alga should be regarded as an important contributor to the finest sediments. The leaves often have such a coating of epiphytes that they appear to be covered with a thick brown fur; growth of angiosperms must be affected if such a large amount of the photosynthetic surface is non-functional. These epiphytes are important in trapping sediment grains ranging in size from 0·05 to 0·5 mm.

Other algae are never abundant although at Anse à la Mouche small hemispherical heads of the green branching *Valonia* are common. Colonies of *Gracilaria* and occasionally *Halimeda opuntia* occur. Any coral cobble or rock lump inevitably has a strand of *Sargassum* attached.

Beds of marine angiosperms in Florida have been shown to be highly productive, with an evolution of 34 g O_2/m^2 from *Thalassia* bed per day (Odum 1957). Phillips (1960) also found in Florida that there was a standing crop of *Thalassia* leaves of 2897 lb. dry weight per acre and moreover (Pomeroy 1960) states that the inclusion of rhizomes and roots would more than double this figure.

The thick stable sediment of the grass beds provides an excellent habitat for burrowing organisms and supports an extensive infaunal population. The leaves of grasses also form a protective habitat for the epifauna. The fall and decay of *Thalassia* leaves produce a higher 'organic detritus' content in sediment available for deposit feeders than in any other habitat around Mahé. Newell (1965) has found that so-called detritus feeders digest mainly the bacterial coating and micro-organisms around the sediment grains and organic debris, but reject the organic compounds in the faeces. Nevertheless, an area with a large amount of dead-plant debris will be a favourable habitat for both detritus and suspension feeding organisms. Environments to the seaward of the grass beds are characterized by very clear water, not apparently rich in suspended detritus. It seems from qualitative observations that most of the detrital food for this the *Thalassia* beds is generated within the community itself. This, however, needs quantitative proof.

Molluscan fauna

In the marine grass beds the molluscan assemblage is 55 % prosobranch and 45 % bivalve species. The thick stable sediment substrate is favourable for burrowing bivalves which in terms of members of individuals are the most important factor in the molluscan population. Of these bivalves 75 % are suspension feeders and 15 % deposit feeders, but the distinction between deposit and suspension feeders in this habitat is neither sharp nor important. The prosobranch fauna is dominantly epifaunal: 30 % are algal feeders, 35 % are predators, feeding mainly upon bivalves or worms, and 15 % are faunal grazers.

Epifauna

The tiny neritid *Smaragdia rangiana* lives amongst, and grazes upon, the epiphytic algae coating the surface of the *Thalassia* leaves. It is locally very abundant, usually closer to the shore where the epiphytic coatings are more dense. *Phasianella aethiopica*, another algal grazer, is common in the *Cymodocea* beds around Platte Island but except at Anse Bougainville is uncommon around Mahé.

Four species of *Cerithium* are present, all of them algal detritus or algal feeders. *C. rostratum* lives amongst the epiphytic algae and upon angiosperm leaves particularly *Enhalus*. *Cerithium morum* is present in large numbers amongst epilithic green algae on the sediment surface on green beds north of Cascade. *Rhinoclavis asperum* is common on windward reefs and is often found partially buried beneath the sediment surface at low tide during the day.

On the landward margin of the grass beds on windward reefs *Strombus gibberulus* is very common; it is a very active feeding on detritus and algae, capable of making strong leaping motions when disturbed, using long pointed operculum as a lever. Although found usually in the grass beds on the reef flats, it appears to be abundant in an offshore grass bed in the middle of Beau Vallon Bay. A smaller species, *Strombus mutabilis*, is less common, but found all over the grass beds.

Nassarius arcularis and *N. albescens*, both scavengers, are common on the surface of the sediment and are active at low tide during the daytime. If bivalve carrion is placed on the sediment, nessarids approach from several metres around and begin devouring it. If the carrion is placed on an emersed patch of sand the response is much slower. *N. arcularis* appears restricted to inshore and grass bed communities, whereas *N. albescens* is present in all communities except those of the rocky shore and reef edge.

The cypraeids *Cypraea annulus* and *C. moneta* are very characteristic of the grass beds and often occur in great numbers. They live on the leaves of the grass, the surface of the sediment or under dead coral lumps and blocks washed on to the beds. The larger *C. tigris* was once very common but the population has been severely depleted by human collecting.

The large *Conus litteratus* is locally common, particularly at Anse aux Pins Village, Anse à la Mouche and around Long Island. It has a thick heavy periostracum and is usually heavily colonized by green and calcareous algae and therefore well camouflaged. During daytime and at low tide it lies with the aperture buried in the sand; *C. betulinus*, a large species, was found only at Anse aux Pins and Anse à la Mouche. *C. tessulatus* and *C. flavidus* occasionally stray in from more seaward communities. Beneath coral blocks on the landward edge of the beds the neritid *Nerita albicilla*, which ranges down from the eulittoral zone, is frequent. The molluscivorous predators *Drupa ochrostoma* and *D. margariticola* are also found beneath these blocks. *Natica marochiensis*, although infaunal, is considered here as it is the only infaunal gastropod in this community. It is a predator on the smaller bivalves, particularly near the beach where it feeds upon *Atactodea glabrata*. The large opisthobranch *Dolabella auricularia* is common on the grass bed surface particularly at Le Cap; it exudes a purple dye when disturbed.

Bivalves are uncommon in the epifauna; the oyster *Pycnodonte numisma* is occasionally attached beneath dead coral blocks. The venerid *Gafrarium dispar*, although usually a shallow burrower, is occasionally found byssally attached to the bases of *Thalassia* stems or beneath coral blocks. Small colonies of *Modiolus auriculatus* are present, e.g. at Glacis where a band of *Modiolus* occurs at the seaward edge of the grass beds.

Molluscan infauna

In contrast the infauna is almost bivalve, only *Natica* and stray *Terebra* represent the gastropods.

On the landward edge of the grass beds up to 30 m from the shore *Pinna muricata* is common, living vertically buried in the sediment, with only the gaping posterior valve edges protruding. It is anchored into the sand by a tangle of byssus threads and is well hidden by the surrounding grass, generally living in situations which are emersed at low tides. Detritus in suspension is rich here, water being constantly swashed back and forth by the tides.

The bivalve fauna of the *Thalassia* beds is dominated by the lucinoid bivalves *Codakia punctata*, *C. tigerina*, *Ctena divergens* and *Anodontia edentula*. All of these species have a strong pointed foot which is used in the construction of a U-shaped cylindrical burrow, open to the surface and in all but *C. divergens* about 15 to 20 cm deep. This burrow is mucus lined for support and is periodically cleared of debris by the foot. The burrow is a permanent living position and this stable sand environment is eminently suitable for occupation by lucinoids. Allen (1958) has discussed fully the mode of life of the Lucinacea. These bivalves feed by setting up currents of water into the burrow; the posterior inhalent current is very weak and little or no food enters posteriorly.

Several species of venerids, suspension feeders, are present but never common; *Pitar obliquata* with short-fused siphons lives immediately below the surface of the sand sometimes with the posterior end protruding; it occurs at most localities, but is not usually found with a density of more than 1 or $2/m^2$. *Gafrarium dispar* is more common in the next seaward community where it occurs as a shallow burrower or byssally attached to the base of *Thalassia* stems. *G. pectinatam* and *G. tumidum* occur close inshore near where streams enter the grass beds or where the sediments are severely blackened; both are very much more common in the *Uca-G. tumidum* community.

The most abundant deposit feeder present in the *Thalassia* beds is *Quidnipagus palatam*, a large tellinid, with a coarsely ridged shell and long siphons. It lives horizontally on the left side with the curved posterior end of the valves from which the siphons emerge pointing uppermost. Holme (1961) describes a similar attitude for the British *Tellina squalida* and suggests that the horizontal position may increase the ease of horizontal migrations and allow a fuller exploitation of the sediment. *Q. palatam* is most abundant close inshore about 30 to 40 m from the base of the beach. *Tellinella staurella* is a fast burrower with a flattened shell and long siphons. It usually occurs on the seaward edge of the grass beds in numbers not more than 1 or $2/m^2$.

Two smaller deposit feeders, *Scissulina dispar* and *Leptomya rostrata*, are common at Anse la Rue and Anse Talbot where the sediment tends to be finer than on Anse aux Pins reef.

Sediment samples were examined for small molluscan species; most of the constituents were juveniles of species discussed above. However, *Pinguitellina robusta*, *Cadella semen* and *Parvicardium sueziense*, all small species, are common in most samples; the last species is much more common in *Thalassia* bed sediments north of Pointe la Rue. *Acar plicata* is frequently found in sediments of the grass beds, but it has probably been washed in from the more seaward communities where it was observed byssally attached to dead coral and algae.

Densities of bivalves in the *Thalassia* beds were estimated by square metre quadrats at a number of localities on Anse aux Pins reef and localities north of Point la Rue (in all, 70 quadrats were dug). A typical distribution pattern in shown in figure 13 for Anse la Rue.

The average density of bivalves in traverses on Anse aux Pins reef is $20/m^2$ and at Anse la Rue and Anse Talbot it is $34/m^2$. On Anse aux Pins the greatest density occurs close inshore decreasing outwards, but at the other localities densities show a more even spread across the beds or there may be an increase in numbers away from the shore. *Leptomya* and *Scissulina* are present north of Pointe la Rue but are absent on Anse aux Pins. The densities of bivalve populations recorded around Mahé are very low when compared with those often found around British shores such as $4000/m^2$ for *Tellina tenuis* and $3000/m^2$ for *Macoma balthica* (Yonge 1949). It has been shown that the productivity of *Thalassia* beds is probably high; a large amount of dead plant material can be seen in and on the sediment and it would be expected that the beds are rich in food for bivalves. However, Newell (1965, p. 41) states: 'In coarse deposits, breakdown of autotrophs is slow owing to the small population of micro-organisms and the population of deposit feeders is also small. In fine deposits, however, the organic debris is decomposed more rapidly owing to the presence of an abundant population of micro-organisms providing a source of food for a population of deposit feeders whose density is hence closely related to the grade of deposit.' On Anse aux Pins reef most of the grass-bed sediments are relatively coarse grained and even though they are rich in organic detritus this may not be in a state available as food. It is significant that densities are higher at Anse la Rue and Anse Talbot where the sediment

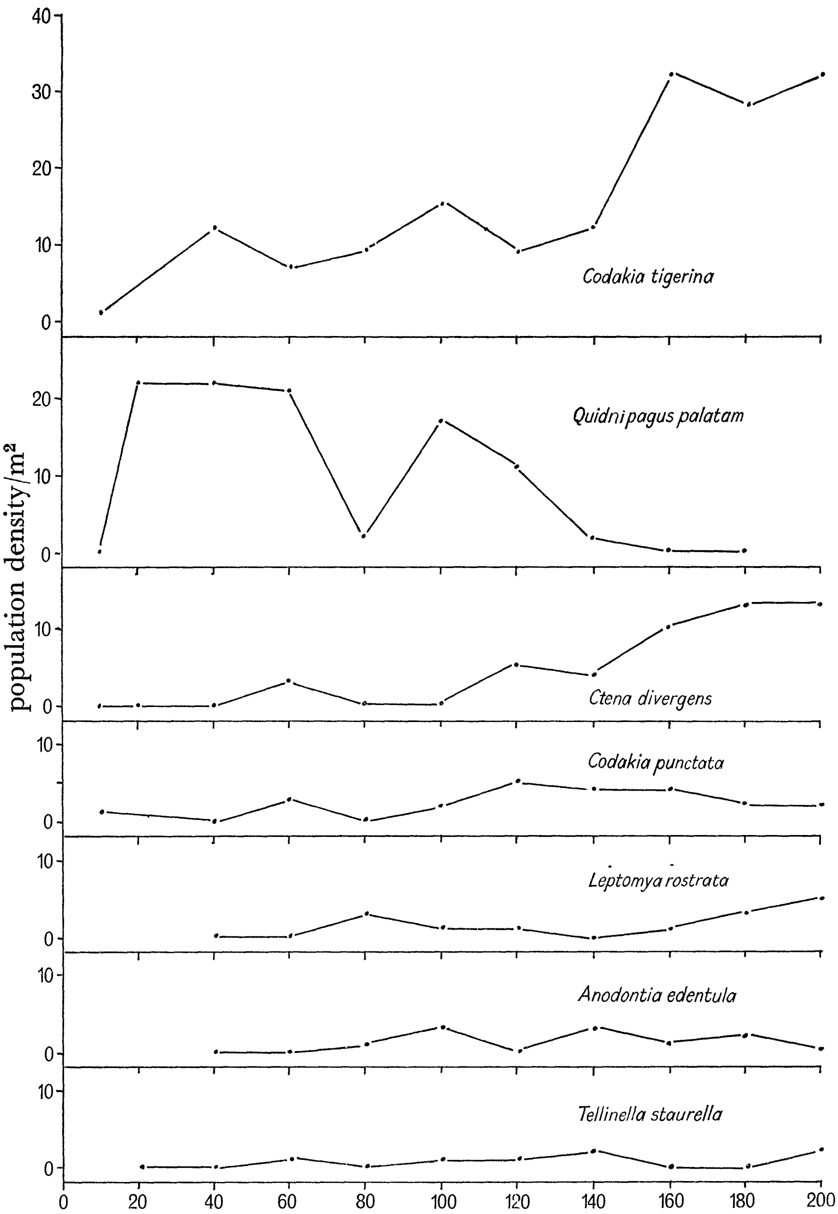

FIGURE 13. Distribution of bivalves in *Thalassia* beds at Anse la Rue.

is finer in grade. Certain smaller deposit feeders may be limited in the size of deposit intake by the size of the siphonal opening. The most abundant deposit feeder *Quidnipagus palatam* is always most abundant close to the shore where available food is highest. It is of interest that the greatest density of deposit-feeding holothurians occurs in approximately the same position.

The lucinoid bivalves are the most important element in the bivalve population of the beds; Allen (1958) states, '. . . the Lucinacea live in environments where the food supply is so low that all available particulate food must be accepted, thus sorting mechanisms are necessarily poorly developed', and later concludes that they have successfully adapted themselves to conditions where food is at a minimum and the oxygen content of the substrate is low.

The available evidence suggests that although the *Thalassia* beds are relatively rich in organic detritus from dead plants the coarse nature of the sediment is not favourable to a large population of decay micro-organisms on which the deposit feeders and probably suspension feeders depend.

Echinoderms

One of the most conspicuous features of the grass beds is the abundance of holothurians. Several species are represented, by far the most common being *Holothuria atra*; less common are *Actinopyga* sp., *Stichopus chloronotus* and *S. variegatus*. At Anse aux Pins village a traverse

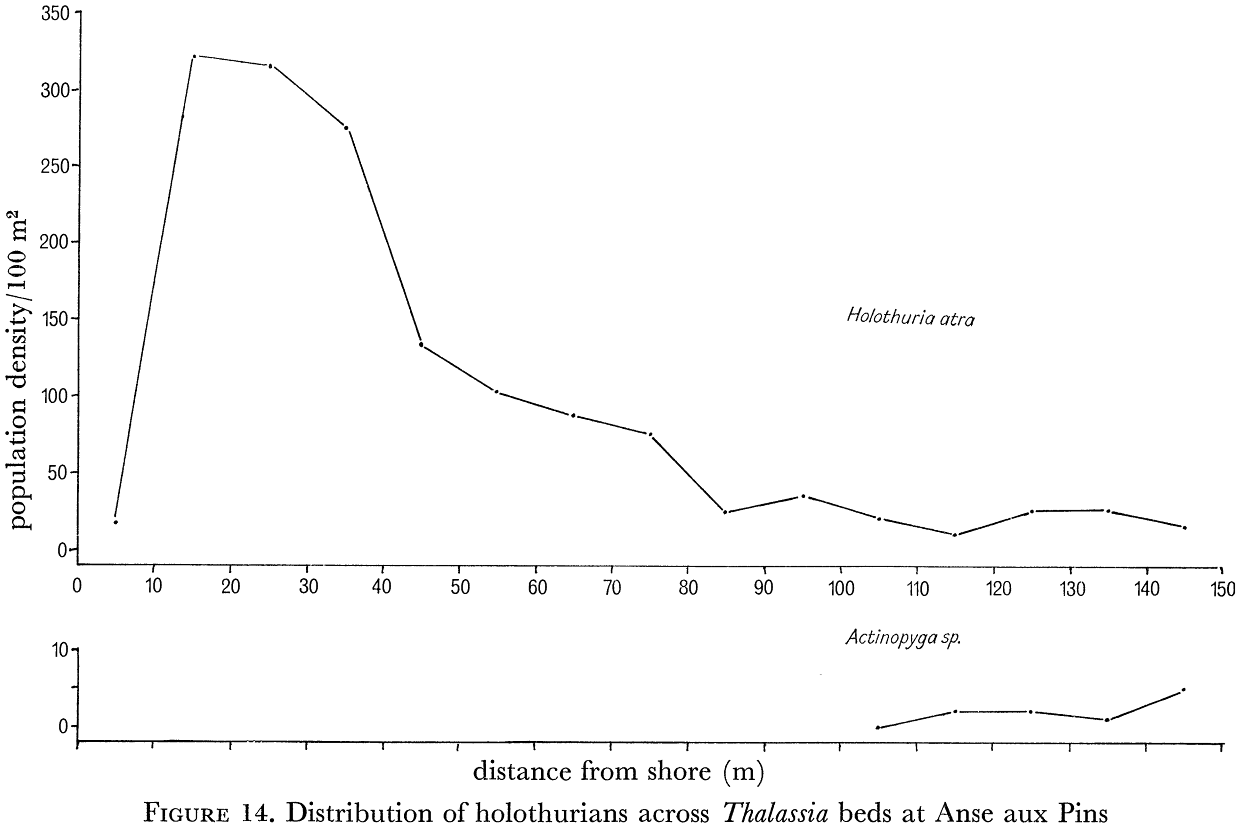

FIGURE 14. Distribution of holothurians across *Thalassia* beds at Anse aux Pins

was made across the beds to determine the density of the holothurian population. Numbers were counted within 100 m² quadrats. The highest density of 320/m² was found between 10 and 20 m from the shore rapidly falling to 100/m² at 50 to 60 m and then falling to 18/m² at 100 m. Most of the population consists of *H. atra* but on the seaward edge of the beds *Actinopyga* appears. Holothurians being deposit feeders should be most common where organic debris is at its highest, i.e. betwen 10 and 40 m from the base of the beach. Most of the holothurians live in an unsheltered position on the surface of the

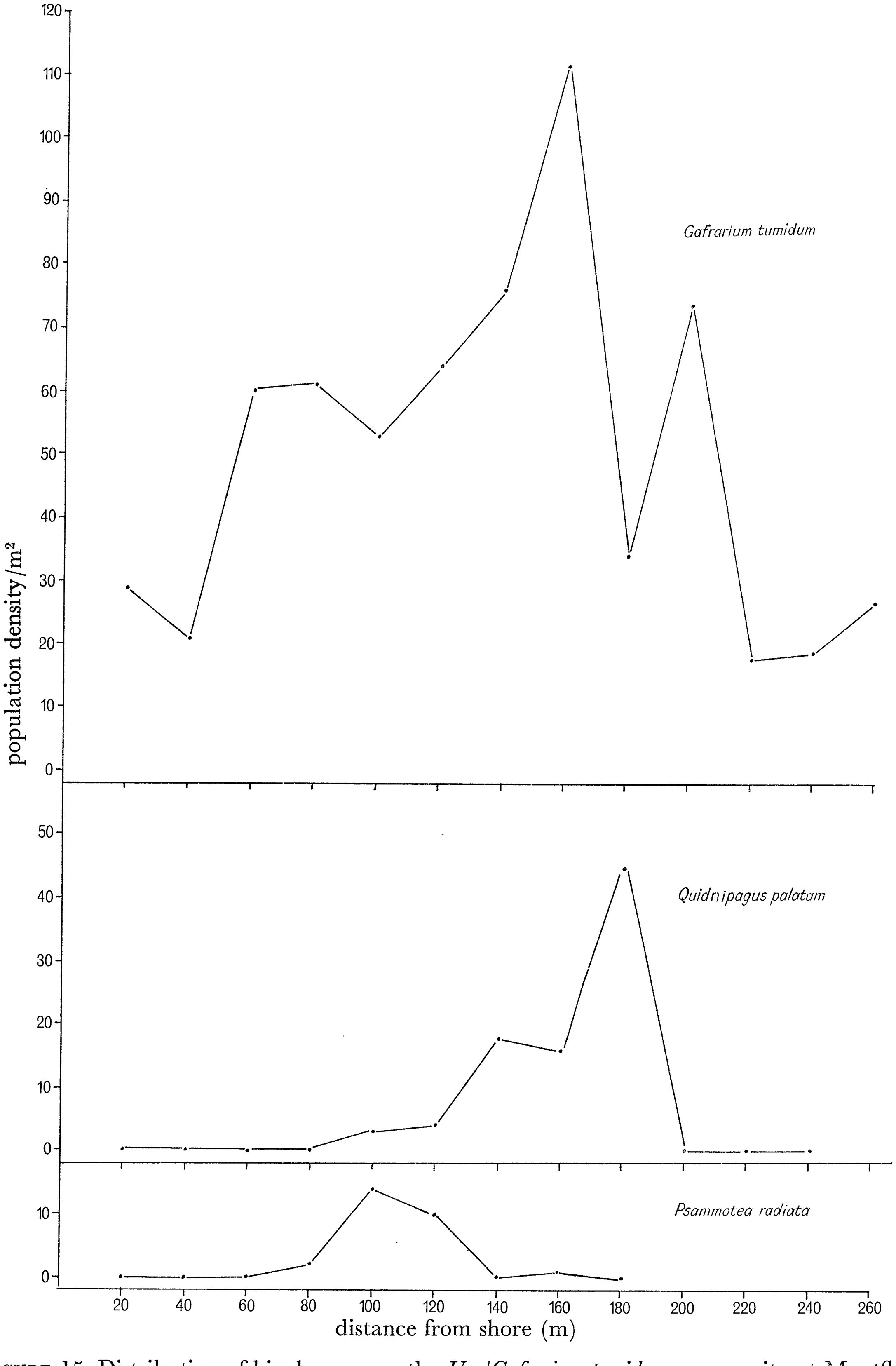

FIGURE 15. Distribution of bivalves across the *Uca/Gafrarium tumidum* community at Montfleuri.

sediment, although there is a tendency to congregate in shallow pools left at low tide. *Actinopyga* often covers itself with *Thalassia* leaves, as a protection from insolation or predators.

The asteroid *Linckia multifora* is common on open grass surfaces with densities of about 4 to $5/100\ m^2$. It is very variable in colour from yellow to bright blue, and it frequently is parasitized by the ectoparasitic prosobranch *Thyca crystallina*. The gastropod is depressed, cap-shaped and lives attached to the arm of *Linckia* (not usually in the ambulacral groove as stated by Morton 1963, p. 178). The foot is reduced and the mouth region enlarged to a disk-like sucker. The proboscis is about three times as long as the body and it is inserted into the skin between the calcareous plate of *Linckia*. *Thyca* usually has the same blue coloration as *Linckia*. Other asteroids, *Protoreaster linckii* and *Culcita schmideliana*, are uncommon but appear restricted to the grass beds.

The ophiuroids, *Ophiocoma scolopendrina* and *O. brevipes*, are abundant beneath dead coral blocks and in the bases of living coral colonies. *O. erinaceus* and *Ophioplocus imbricatus* are less common but more abundant in other communities.

Two echinoids, *Toxoneustes pileolus* and *Tripneustes gratilla*, are present in most sheltered water sandy bottom communities but are especially common on the seaward edge of the grass beds. Although they live on the open surface of the beds, they frequently cover the tests with coral debris, bivalve shells, *Thalassia* leaves and *Sargassum* fronds which are held in place by the tube feet. This may be camouflage or protection against insolation. Both species have pedicellaria with poison glands around the teeth to paralyse any potential predator; nevertheless, dead tests are common, frequently with a small hole in the side drilled by predatory gastropods *Cassis* or *Cymatium*. Fish are probably the most serious predator. At Anse à la Mouche, Glacis and Anse Royale the small *Echinometra matthai* is abundant beneath coral blocks. The cavities are often circular, deep and appear to have been excavated.

Corals

The coral fauna of the grass beds is poor in numbers of species and in abundance; there is a lack of firm hard substrate for the settlement and development of coral planulae; areas of the beds are completely emersed at low spring tides and the corals are therefore subject to insolation, desiccation and rain water. The more rapidly growing angiosperms must be serious competitors for space. Nevertheless, a few species of corals are able to tolerate these conditions and form quite extensive patches. *Pavona frondifera*, *Psammocora contigua* and *Porites lutea* form the major constituent of three patches on Anse aux Pins reef. These patches are about 25 m long and 10 m wide in situations that are never uncovered even by the lowest spring tides. The two former species both exhibit a growth form of low platy, compact branches forming a pavement, the level of which is controlled by low tide level. All of these patches occur close inshore in close proximity to stream mouths; at Le Cap after heavy rain, water flowing only a few centimetres above a *Psammocora* patch gave a salinity of 5·6 ‰. Both species also occur as small isolated colonies, a few centimetres in diameter, widespread in the beds. Small nodular and ball-shaped (10 cm) colonies of *Porites* living loose or attached to small detrital fragments are abundant. *Pocillopora damicornis* is abundant as small colonies.

Crustacea

The shrimp *Alpheus rapax* and the stomatopod *Pseudosquilla ciliata* are common, inhabiting burrows lined with organic debris such as *Thalassia* leaves. A commensal bivalve *Erycina* sp. lives in the burrow of *Alpheus*. The most abundant crab is *Calappa hepatica*, which rapidly burrows at the approach of danger. *Thalamita admete*, a carnivorous swimming crab, ranges across the beds but at low tide shelters beneath coral blocks. Several other species of crab particularly xanthids shelter beneath dead and living coral.

Throughout the grass beds mounds of sand up to 30 cm high occur, especially common between Anse la Rue and Anse Talbot. The mounds can reach up to 1 m in diameter often with a concave crest through which water issues in gushes during the low tide period. On investigation a burrow system was revealed with a second opening in a depression (usually water filled) about 1 m away. No inhabitants of the burrow were found but it is highly probable that they are of crustacean origin. Similar mounds occur in the Bahamas (Bimini Lagoon, Bathurst, personal communication, and Taylor 1964, p. 419, text-fig. 1), and likewise after a great deal of effort no inhabitants were found.

The sands and cobble-ridges

Immediately seaward of the *Thalassia* beds, on windward reefs, such as Anse Royale and Anse aux Pins (figures 24, 25, plate 14), is an area of open sand-patches which are variable in width. Seawards these sand-patches interdigitate with ridges of loosely bound algal nodules and dead coral cobbles, arranged normal to the algal ridge within which they are transitional.

The sands are generally coarse, clean, white and often strongly rippled, with very little organic detritus. In places there are patches of coarse coral and algal debris and in others the sand may be fine. Narrow windward reefs, such as Anse Forbans, have a thin sand cover, which, when rippled, often show the underlying reef platform in the troughs; the sand is often restricted to small pockets. At the junction of the sand with the *Thalassia* beds there is a step of 15 to 20 cm seawards and the water depth at low tide is 1 to 2 m; seawards, the water becomes shallower and, immediately behind the algal ridge, the low-water level is 0·75 to 0·5 m.

The ridges interdigitating with the sand areas consist of a structure built up of algal and dead coral lumps of cobble size which are loosely cemented together by algal growth. At the landward ends the ridges gradually decreased in height and tail off as cobble patches into the sandy areas. At Anse aux Pins they are about 1 m above the general reef flat surface; dimensions, however, are variable. At Anse aux Pins and Anse Royale, they tend to be steeper on the side facing away from the reef pass, which is the direction of the ebb tide. Immediately around the reef passes the ridges are arcuate, as at Anse Royale, where the reef pass is wide and deep and ridges are only developed at the extremities. Well-developed ridges are only present on windward reefs, and around the southern side of Cerf Island the transition from a ridged reef flat on the windward side, to the ridgeless dissected reef flats of the leeward, can be seen. Once the cobbles and coral lumps are piled up, probably by tidal currents during the Trades season, the surface becomes loosely cemented by algal growth on adjacent algal cobbles. Ridges similar to these are seen in other areas; notably on islands in the Great Barrier Reef (see plates in Gillett & McNeil (1962) and Yonge (1930)).

Along the sheltered reef from Anonyme to North East Point, ridges are not developed and, between the diminutive algal ridge and the seaward edge of the grass beds, there is an area of fairly open sands dissected by deeper coral-lined channels and many pools. These sand areas support many live and dead coral patches but without any obvious distribution pattern; living corals are more abundant around the channel edges. The sand here is much finer than windward reefs, more or less undisturbed, usually not rippled, and is extensively colonized by sabellid polychaetes. The water here is usually turbid in contrast to the clear waters on windward reefs. The sand is generally a grey-white and beneath the top centimetre it is darker grey, indicating more reducing conditions beneath the surface.

Algae

The whole area of the sand patches and cobble ridges is dominated by the dense coverage of *Sargassum* and to a lesser extent *Turbinaria*. Fronds of *Sargassum* develop whereever there is a suitable hard substrate on which to make a holdfast; in the sandy areas it attaches to algal cobbles and dead coral colonies and, except for the highest surfaces of the cobble ridges, it forms an almost complete algal cover. As the algal ridge is approached, and sand areas are reduced or absent, the *Sargassum–Turbinaria* cover is almost 100 %.

The *Sargassum* of the reef flats grows as loose fronds about 1 m long; the pinnae are rather thin and elongate, but nearer the algal ridge the pinnae become thicker and shorter and the fronds more rigid, in response to the increased wave action. *Turbinaria* is rather similar in aspect to *Sargassum* but the branches tend to be more erect, the pinnae thick, and polygonal to triangular in shape. *Sargassum* and *Turbinaria* show an interesting distributional relationship. On cobble ridges *Sargassum* is abundant and dominant around the lower edges which are infrequently emersed, but on the upper surfaces of the ridges which are often emersed *Turbinaria* is dominant and *Sargassum* virtually absent. *Turbinaria*, with thick pinnae is able to resist insolation, desiccation and wave action to a greater extent than *Sargassum*. This dense cover of the reef flat by brown algae is an important ecological factor. They act as primary producers, shade and shelter for organisms, and probably limit the settlement of larvae of sedentary organisms, particularly corals. It is interesting to note that *Sargassum* was unexpectedly absent from the reefs around Bikini (Taylor 1950); there is also no substantial growth of algae other than calcareous forms: intense insolation is suggested as the limiting factor. *Sargassum* is also absent from the Island of Gan in the Maldives (Stoddart 1966). An epiphytic growth of *Jania*, a small calcareous alga, often infests *Sargassum* and *Turbinaria*; complete fronds of *Sargassum* may be smothered by its growth. This epiphyte is more common towards the inner reef flat and is almost absent from the algal ridge.

Coralline red algae of the sand and ridges area are dominantly encrusting. Most of the cobbles consist of rounded nodular growths and the branching forms found on the algal ridge are generally absent. On the cobble ridges the cobbles may have a rounded growth on the outer surface, but the sheltered underside may be papillate. Most of the algal cobbles are formed by the algae encrusting a piece of dead coral or shell; but occasionally a nodule may be found formed entirely by algal growth; these are usually hollow. Only the surface of the cobble ridges consist of living algae; a few centimetres below the surface all is dead. Adjacent cobbles, with algal growths, tend to coalesce where in contact, so that there is a loose cementation of the upper, outer surface. At the landward edges of the ridges algal growth is reduced and they diminish into the sandy areas. From a limited number of thin sections it appears that *Lithophyllum* is the dominant encrusting alga. North of Anonyme the growth of calcareous red algae is reduced and there are often expanses of uncolonized dead coral platform; the absence is explained by the fact that coralline algae can only flourish in areas with a strong circulation of water (Johnson 1963).

The articulate coralline algae *Amphiroa* is abundant on windward reefs, where there is some degree of water movement, although absent from the reef flats from Anonyme to North East Point. It grows as low compact cushions of closely packed segmented branches; the colonies are usually not more than 15 cm high and 30 cm in diameter, loosely attached to the hard substrate or to algal cobbles. On Anse aux Pins reef, in a traverse from the edge of the grass beds, *Amphiroa* appears at about 100 m from the seaward edge of the grass beds, but is here dominated by clumps of *Halimeda*, which occupy a large proportion of the substrate available beneath the *Sargassum* fronds. At 180 m, however, *Halimeda* has been almost completely replaced by *Amphiroa*. On narrow reefs, such as Anse Forbans, circulation is such that *Amphiroa* thrives close to the shore.

The green calcified alga *Halimeda opuntia* (forma *typica*) is abundant, forming dense clumps of segmented branches. The clumps average about 20 cm in diameter but can be as large as 80 to 90 cm, especially near Montfleuri. Usually only the outer segments are living and the inner ones are bleached and corroded. Segments of dead Halimeda colonies are important sediment contributors.

A second species, *Halimeda macroloba*, is restricted to the sheltered area between Cascade and North East Point. The joints are thick, discoidal and less heavily calcified than *H. opuntia*. Segments of *H. macroloba* are not such obvious sediment contributors for they break up into fine carbonate debris.

Padina commersonii is fairly common, attached to cobbles at Anse aux Pins, close inshore at Anse Forbans and very abundant all across the reef in Port Victoria and Anse Etoile. Two species of *Caulerpa* are common, either as epilithic growths on the surface of the sand, or attached to a hard substrate, and widely distributed on windward and sheltered reefs.

In the wider areas of open sands, where the sediment is more stable, as between Cerf and Long Islands, there may be an epilithic coating of filamentous red algae.

Corals

The coral fauna consists of two assemblages, that growing upon the sandy areas and that on the cobble ridges. This is the first habitat outwards from the shore to support a significant growth of coral; many species are found but most are uncommon and only occur as small isolated colonies.

The wide sand area opposite Anse aux Pins Village supports large colonies of *Acropora pharaonis* with the characteristic ramose 'Stagshorn' growth form (figure 31, plate 15). Colonies may be up to 4 m in diameter but never more than 1 m high; the upper surface is usually flattened, dead and encrusted with calcareous algae and *Sargassum*. Only the outer 20 to 30 cm of the coral branches are living. The colonies are never emersed but the limit of upward growth is closely related to low tide level. The most common of the larger reef-flat corals is *Porites nigrescens*; it grows in hemispherical-shaped colonies about 3 to 4 m in diameter and 1 m high, consisting of a compact structure of radially arranged dichotomous branches (figure 24 plate 14). Again only the outer 20 to 30 cm of the colony is living. *P. nigrescens* is more widely distributed on reef flats than *A. pharaonis* but usually as small colonies. At Anse aux Pins Village colonies of these two species occur together.

A very loose association is shown between the fish *Chromis caerula* and *Acropora pharaonis*. The fishes are pale blue and live in small shoals between the branches of the coral; at any sign of danger they retreat deeply into the branching network. Another fish, *Holocentrus seychellensis*, appears associated with colonies of *Porites nigrescens*.

At several localities, Anse aux Pins Village, Baie Ternay, Port Victoria and Petit Cours on Praslin, *Acropora divaricata* grows as laterally flattened, spray-like, branches usually attached to dead coral masses, but at Port Victoria it forms complete, mound-shaped banks.

Colonies of the alcyonacean *Heliopora caerulea* are common in this mid-reef flat, sandy belt; at Anse Faure, Anse aux Couches, Le Cap and Anse aux Pins village it occurs as isolated colonies, about 2 m in diameter, usually flattened and dead on the upper surface. At Anse Bougainville a large area of the reef flat is formed by the lateral growth and coalescence of *Heliopora* colonies. The shallow water level prevents upward growth, but encourages lateral growth, and the subcircular flat-topped platform growths have a living edge of vertical *Heliopora* plates. This occurrence of *Heliopora* around Mahé on the mid-reef flat corresponds in position to the rather better developed *Heliopora* zone on windward reef flats of Bikini where large growths, often 1 to 8 m in diameter, cover the reef flat (Emery, Tracey & Ladd 1954; Wells 1954).

Pocillopora damicornis is extremely common on reef flats, occurring as small bushy growths about 30 cm in diameter and 15 to 20 cm high; branching is irregular and delicate with much minor branching and elongate verrucae. The colonies were originally attached to pieces of dead coral, or other debris, but when older have become more or less loose on the surface of the substrate. Small colonies of *Acropora digitifera*, also about 30 cm in diameter, are common; the growth form is of low, compact, slender branches, often with blue tips. Rounded colonies of *Favia*, *Porites* and *Goniastrea*, free or semi-encrusting, are frequent.

North of Anonyme, on the more sheltered reef flats, the coral population is rather different. The sandy areas of the reef flat are generally covered by a greater depth of water, salinities are frequently reduced and the water is generally turbid. Characteristic are large colonies of massive *Porites*, *Goniastrea*, *Favia* and *Platygyra* whilst *Pocillopora damicornis*, *Acropora digitifera* and *Millepora* are uncommon. Large masses of dead coral, still in position of growth, are coated with *Sargassum* and *Turbinaria*. The coral fauna shows great similarity to that of *Porites* community reef edges described later. Some unusual associations occur, for instance at Port Victoria, where salinities are often very reduced and turbidity is always high, *Pocillopora damicornis*, *Acropora divaricata* and *Galaxea clavus* are found in association, and at Anse Étoile, *Lobophyllia*, *Galaxea* and *Favia* occur together on the reef flat in about 2 m of water.

On the cobble-ridges encrusting corals are dominant. Encrusting nodular *Millepora* grows around cobbles and dead coral surfaces. It is brick-red in colour and the nodular encrustations are usually not more than 20 cm in diameter. The colonies are commonly heavily infested with parasitic barnacles. On the higher, more open parts of the ridges, not covered by *Sargassum*, *Millepora* is common together with encrusting, rounded *Porites lutea*, and flat growths of *Montipora*. Small colonies of *Pocillopora damicornis* are frequent. On the steeper sides of the cobble-ridges, and usually well sheltered by *Sargassum* are encrusting sheets of *Cyphastrea*. In the crevices of the cobble-ridges small attached *Fungia fungites* are common; they are attached by short stalks, about 2 to 3 cm long, with a corallum diameter reaching a maximum of about 5 cm.

Molluscan fauna

The sands and cobble-ridges have two distinct molluscan faunas. The sands which are frequently rippled, shifting and mostly unstable have a fauna of which 75 % of the species are prosobranchs and 27 % are bivalves. About 45 % of the prosobranchs are predators, 25 % algal feeders and the rest are scavengers or parasitic. Most of the gastropods are highly motile and adapted for life in a shifting sand and have specialized diets; common prey organisms are bivalves, polychaetes, including terebellids. About 55 % of the bivalves are deposit feeders and most species show morphological features associated with swift burrowing or maintaining positions in an unstable habitat. Organic detritus for deposit feeders is low, and even though the number of different species is high, the number of individuals is low.

The cobble-ridges have a hard substrate and most of the molluscan fauna is epifaunal and very similar in feeding types to the algal ridge. Gastropods are dominant and constitute 85 % of the species of which 30 % are predators, 20 % algal feeders and 45 % faunal grazers on sessile prey such as encrusting sponges, ascidians and coelenterates. The four bivalves represented are all suspension feeders and live either byssally attached or cemented to the substrate.

The density of the molluscan population of the sandy areas is low compared with the *Thalassia* beds but there is a much greater diversity of species particularly of predatory gastropods. A narrow belt extending for about 2 m seaward of the grass beds is the most densely populated on windward reefs. Much of the detailed collecting of this assemblage was carried out on Anse aux Pins reef.

Bivalves

One of the commonest species at Anse aux Pins is the cardid *Fragum fragum* which is more frequent in the coarser sands. In this species the siphons are short, and do not extend beyond the margins of the valves; the mantle edge around the siphons is fringed with long tentacles which protrude through the plications of the posterior margin of the shell. *Fragum* lives with the posterior end slightly protruding from the surface of the sediment. The plication of the valve margins and the tentacle fringe are adaptations for life in a coarse shifting sand. *F. fragum* has a strong, pointed foot and can move in a series of violent leaps by bending and flexing the foot against the substrate. This progression can be sustained for five or six successive leaps. *Lima fragilis* lives by day beneath dead coral lumps and is capable of short swimming movements; long orange tentacles extend beyond the valve margins. The lucinoids *Codakia punctata* and *C. tigerina* are sometimes found where the sand is finer and more stable. The venerid *Gafrarium dispar*, a suspension feeder with short fused siphons, is found either in shallow burrows or byssally attached to dead corals or reef platform. Other venerids are *Pitar obliquata* and *Timoclea marica*.

Two tellinids are common, both laterally compressed and capable of swift burrowing. *Tellinella crucigera* is thin-shelled, elongate, with the posterior end deflected towards the right; it lies in the sediment on the left valve. *Quadrans gargadia* is laterally compressed and highly polished and was very common at Anse aux Pins village. Other tellinids are *T. staurella*, *Scutarcopagia scobinata*, *Scissulina dispar*, *Pinguitellina robusta* and *Cadella semen*.

Bivalves occurring on the cobble ridges are similar to those of the algal ridge; all are byssally attached or cemented to the substrate. *Cardita variegata* lives byssally attached in cracks and crevices and is common. *Tridacna squamosa* is often found byssally attached and embedded in the upper surface of the cobble ridges. *Pinctada margaritifera* often lives in crevices in the ridges, attached byssally in the vertical position. *Ostrea numisma* is found cemented beneath some coral lumps but is more common on the algal ridge.

Gastropoda

Herbivorous gastropods are represented by *Strombus luhuanus* and *S. gibberulus*, neither very common in this habitat. *Cerithium echinatum* is very common in the sandy areas across all the reef; during daytime it is slightly buried. Individuals frequently have an epibiota of calcareous algae, *Homotrema rubra* and the coprophagous prosobranch *Amalthea conica*. *Rhinoclavis asperum* is usually found in sand close to the edge of grass beds. The large *Cerithium nodulosum* is uncommon; its spire is usually heavily corroded.

Predaceous prosobranchs are common and their diets consist largely of other molluscs or polychaetes. A mollusc-feeding species is *Pleuroploca trapezium*. It lives half buried in the sand at low tide; it is common on Anse aux Pins reef and around Cerf Island often spreading on to the grass beds. It feeds on both gastropods and bivalves, and was several times seen feeding on *Cerithium echinatum* by first rasping the operculum and then inserting its proboscis. On other occasions it was seen feeding off *Gafrarium dispar* and *Anadara antiquata* by chipping the valve margins and then wedging them open. It can also feed upon *Pinna muricata*. Paine (1963) found that the Florida species *P. gigantea* shows a dietal preference for other prosobranchs but 20 % of the diet consists of larger bivalves. He suggests that *Pleuroploca* feeds within the limits of prey size and that each individual consumes one prey-mollusc about once every four days.

The naticid gastropods *Polynices mammilla* and *Natica onca* feed upon the bivalves *Quadrans gargadia*, *Tellinella crucigera* and *Gafrarium dispar* by boring bevelled holes in the shells.

The sandy areas support nine species of *Conus* of which only *C. tessulatus*, *C. coronatus*, *C. arenatus* are common; all these species remain half of totally buried in sand during the daytime and at low tide. The work of Kohn (1959, 1959*a*) has shown that *C. coronatus* feeds upon eunicid and nereid polychaetes, and *C. flavidus*, a species common around Cerf and Long Islands, feeds upon terebellids.

Several species of *Terebra* occur in this sandy area; all are rare or uncommon, with the exception of *T. affinis* and *T. laevigata*, and tend to be localized in distribution. The large species, for instance *T. guttata*, was found only at Anse Boileau, and *T. crenulata* only at Le Cap. They are inactive at low tide, with the spire often protruding from the sediment, corroded and encrusted.

Scavengers are represented by *Oliva erythrostoma* and *O. episcopalis*, both fusiform, highly polished and very active; the smaller species, *O. episcopalis*, is the more common, particularly on Anse aux Pins reef. Both species were observed feeding off carrion, in particular off recently dead tests of the echinoid *Tripneustes*. The ubiquitous *Nassarius albescens* is another scavenger and is abundant on all sandy areas and active at all stages of the tide.

Two species of pyramidellid opisthobranchs *Pyramidella maculosa* and *Pyramidella terebellum* are common sand burrowers. Most members of this family are ectoparasitic but no obvious association was observed between any of the species and a host organism. They are possibly in contact only during feeding. Most probable hosts are ptychoderid polychaetes.

The gastropod fauna of the cobble ridges shows great resemblance of that of the algal ridge discussed below, however some species are more or less restricted to this mid-reef flat hard substrate, *Cypraea helvola* is common and other cypraeas are subordinate but *C. isabella*, *C. carneola* and *C. caurica* may be locally frequent. The molluscivorous *Drupa ochrostoma* and *D. margariticola* and *Latirus polygonus* are frequent and *Vasum turbinellus* is found upon dead coral surfaces from Anonyme to North East Point. *Quoyala monodonta* is found upon colonies of *Porites nigrescens* upon which it feeds; it occupies a horse-shoe-shaped groove on the coral surface similar to that worn by limpets in rocks.

Echinoderms

Holothurians are common, but numbers are much reduced compared with the *Thalassia* community. The dark green, coarsely tubercled *Stichopus chloronotus* is characteristic with *Holothuria atra* subordinate. The smaller species *H. monocaria* and *H. arenicola* are found beneath coral lumps. Also restricted to this community is the large synataptid *Synapta maculata*, often more than 1 m in length. The decline in numbers of deposit-feeding holothurians may be due to the decrease in the organic detritus in the sediment.

The echinoids *Tripneustes gratilla* and *Toxoneustes pileolus* are widespread. Clones of *Stomopneustes variolaris* are sometimes found living unsheltered on the open sand at Anse Baleine. *Echinometra matthai* is common on the cobble ridges, beneath loose blocks and on the dead *Heliopora* patches at Anse Bougainville. It shows great variation in colour, from olive green to purple black. In the sandy areas the burrowing irregular echinoid *Melatia spatagus* is found. It lives in coarse loose sand and does not appear to maintain a respiratory tube. It is particularly common at Anse aux Pins and Baie Ternay.

Ophiuroids are abundant beneath dead coral lumps and on the cobble ridges. *Ophiocoma brevipes*, *O. valenciae* and *O. erinaceus* and *Ophioploca imbricata* are the commonest.

Crustacea

Crabs are an important constituent of the motile cryptofauna, and are commonly found beneath dead coral lumps and amongst the cobbles of the ridges; most of the species found also live on the algal ridge. The xanthids, *Phymodius monticulosus* and *Etisius electra*, are extremely abundant in areas of cobbles, as at Glacis, Anse Baleine and on the cobble ridges of Anse aux Pins. *Actaea tomentosa* wedges itself into crevices in the base of coral colonies and into dead coral blocks. The carnivorous swimming crab *Thalamita admete*, which occurs here, was seen to feed upon other xanthid crabs. The oxyrhynchid crabs

Menaethius monoceros and *Miccippia philrya* are found on the outside surface of cobbles where the dark brownish green carapace is well camouflaged amongst the epilithic algae. The small, fast-moving, anomuran *Petrolisthes lamarcki* is exceedingly common on both the outside and underside of dead coral blocks. Every colony of *Pocillopora* has at least two individuals of *Trapezia cymodoce* living amongst the base of the branches.

Polychaetes

The sand on windward reefs supports a large population of the terebellid p
Ptychodera which are deposit feeders; large quantities of sediment visible througl
wall, pass through these animals. Sabellid worms are abundant, particularl
where the sand is finer, such as North of Anonyme and inshore at Pointe au Se
occurs in the sand beneath cobbles.

The algal ridge

The algal ridge, as a distinct morphological feature, is restricted to windward and partially exposed reefs, and is a characteristic structure of Indo-Pacific reefs, well known from the descriptions of Emery *et al.* (1954), Newell (1956) and Wells (1957). Around Mahé it is situated at the seaward edge of the reef flat and consists of a low ridge 10 to 20 m wide and rises up to 0·5 m above the general reef flat level. Though not comparable in height or extent with those of the large Pacific Atolls, or even with some of the islands of the Maldives group, nevertheless, it forms a distinct topographic feature of windward reefs. This limited development is a consequence of the seasonal variation in wind strength and direction: coralline algae flourish on edges with high wave action and in general, on leeward reefs, the ridge is reduced or absent. The best development of the ridge is seen around the eastern side of Cerf Island, Anse aux Pins, Anse Royale and Anse Forbans. Reefs on the western side of the island, such as Anse à la Mouche and Anse Boileau, show a limited ridge development, Anse d'Islette which is exposed to the S.E. Trades shows a ridge, and Glacis which is exposed to the N.W. Monsoon shows a low narrow ridge.

At high tide the surf breaks on or around the seaward edge of the algal ridge and the water is in constant agitation. During the S.E. Trades season there is a piling up of swell against the reef and the zone of breaking waves is extended landwards. At low tide the ridge is swept by occasional surges from breaking waves so that even though organisms may be emersed for several hours they are constantly kept damp. A large area of the more landward portions of the ridge is coated with a cover of *Sargassum* and *Turbinaria* which conserve moisture and protect the calcareous algae and fauna beneath from desiccation. Johnson (1963) considers that desiccation is an important limiting factor on the distribution of calcareous algae, rather than the direct effects of light itself.

Algae

Many growth forms of calcareous algae are present from flat encrusting sheets to large hemispherical heads. The principal genera forming the ridge are *Lithophyllum* and *Porolithon* with a minor contribution from *Lithothamnion*. It is difficult to relate growth forms with a genus without thin section studies, consequently it is difficult to evaluate the relative importance of each genus. It appears that *Lithophyllum* is the most abundant, widespread and variable of these algae. Growth forms at the point of highest wave action are often hemispherical heads of closely packed branches, whereas farther back from the surf, encrusting fauna, and then free nodules, are dominant. A similar zonation of growth forms was described around Hawaii by Pollock (1928). Often along the reef edge the algae encrust dead coral and the original coral growth forms can often be distinguished, particularly at Anse Faure. The algal heads and encrusted surfaces gradually grow laterally and coalesce to form a cavernous structure with many deep holes, shallow depressions and nodular lumps. The holes can be up to 1 m deep and are often enclosed and roof over by growth of the algae. The floors of the holes are often covered by a pocket of sand.

Cast up on the highest point of the ridge are loose blocks of dead reef rock and coral, usually these are not more than 1 m in diameter but at Pointe au Sel there is a large block of reef rock 3 m long and 1·5 m high. Usually the blocks are loose on the surface but occasionally they have become cemented to the ridge by algal growth. Blocks on less exposed reefs are less frequent and smaller.

Apart from the calcareous algae the ridge is clothed in a dense cover of *Sargassum* and *Turbinaria*; here, as on the reef flats, *Turbinaria ornata* covers the portions of the ridge which remain emersed for longer periods, but it is absent from the higher positions on the larger cast-up blocks. *Sargassum* is more dense on the lower lying and landward parts of the ridge, the branches are shorter and the pinnae thicker than forms in the calmer water of the reef flat cobble ridges. Gradually towards the seaward edge of the ridge the *Sargassum* disappears, closely followed by *Turbinaria*. But here another species of *Turbinaria* appears with short conical growths and thick resistant pinnules, which disappear as the zone of breaking waves is approached,

The branching calcareous *Amphiroa* is common as low cushion growths on the landward side of the ridge but towards the seaward edge the cushions become smaller and occupy more sheltered positions and eventually disappear. On the surface of the coralline algal crust and on the cast-up blocks there is a thick turf of small algae including *Caulerpa racemosa* var. *turbinata*, *Caulerpa* sp., *Struvea*, *Polysiphonia*, *Ceramium*, *Dictyota* and *Laurencia*.

At Bikini *Sargassum* is absent from reef flats (Taylor 1950); it is present at Low Isles and Heron Island on the Great Barrier Reef but is not abundant on the algal ridge (Manton & Stephenson 1935). It is also absent from Gan Island in the Maldives (Stoddart 1966). Perhaps the wave action on the algal ridge around Mahé is sufficiently low to allow the settlement and development of a soft algal cover. It has important consequences for the distribution of the invertebrate fauna.

Corals

Corals are uncommon on the algal ridge and where they occur they are usually small with rounded and encrusting growth forms, hidden from view beneath the *Sargassum* cover. Encrusting *Montipora*, *Cyphastrea* and small nodular heads of *Porites* are common. *Stylocoeniella armata* is one of the most numerous but inconspicuous corals occurring as small encrustations, about 2 to 3 cm in diameter, beneath coral and algal blocks. Small rounded heads of *Hydnophora microconos* are found on the landward side of the ridge. At some sites the coral fauna may be more abundant as at Pointe au Sel where the *Pocillopora danae-meandrina* series is common together with encrusting *Acanthastrea*, small finger growths of *Acropora digitifera* and rounded heads of *Goniastrea pectinata*. The lack of an abundant coral fauna may be explained by the frequent emersion of the ridge at low spring tides, the dominance of *Sargassum* and *Turbinaria* and calcareous algae which occupy and cover large areas of the hard substrate available for the settlement of coral planulae.

Echinoderms

One of the most characteristic organisms of the algal ridge is the black, long-spined echinoid *Diadema setosus*, which can reach a diameter of 30 cm. It lives in holes and depressions in the cavernous ridge and sometimes beneath cast-up dead coral-blocks. In this sheltered niche individuals inhabiting the deeper holes may be restricted in their movements to a particular hole. They feed upon algae from the hard substrate. Juvenile *Diadema* have green and yellow banded spines which gradually change to purple-black with age. The species is extremely light-sensitive and during the daytime remains in a shaded position and, if disturbed, rapidly retreats into the shade. However, *Diadema* in the deeper water, off reef-fronts, lies on open surfaces during the daylight. Despite its formidable appearance it is preyed upon by fish, molluscs and crustacea. Randall, Schroeder & Starck (1964) record that the closely related West Indian species *Diadema antillarum* is preyed upon by 15 species of fishes and by the gastropods *Cymatium* and *Cassis*. *Echinometra matthai* is common on some algal ridges, particularly on more sheltered reefs such as Anse à la Mouche and Glacis, where it occupies circular crevices in the platform of cast-up dead coral-blocks.

A small irregular echinoid, *Echinoneus cyclostomous*, occurs burrowing in the shallow sand-pockets of the algal ridge particularly at Anse aux Pins. Around Frigate Island, however, it can occur beneath cast-up coral-blocks adhering to the hard substrate (R. Blackman, personal communication).

Beneath almost every cast-up block are several individuals of the small holothurian *Afrocucumis africana* which are adherent to the hard substrate by the tube feet. They are invariably associated with the small ectoparasitic gastropod *Eulima*. Other small holothurians are also abundant, *Holothuria monocaria* and *H. cinerascens* occur beneath coral-blocks and *H. arenicola* slightly buried in sand-pockets.

Ophiuroids are extremely common in the cavities of the algal crust and beneath cast-up blocks; *Ophiocoma erinaceus* is the most abundant. *O. brevipes* and *Ophioploca imbricata* also occur. Asteroids are uncommon although *Linckia multifora* and *Asterina burtoni*, an algal grazer, are represented.

The small crinoid *Comanthus parvicirra* appears to be restricted to the algal ridge. It attaches to the substrate by short cirri, which can easily detach, and lives on the under edges of blocks and crevices, feeding upon detritus in suspension.

Molluscs

The algal ridge is a hard substrate, subject to relatively high wave action and with some areas undergoing frequent emersion; consequently, apart from a few borers into the reef platform, the molluscan fauna is entirely epifaunal. Parts of the algal ridge project into the eulittoral zone and some species are common to both here and rocky shores. The bivalve/gastropod ratio is similar to that of rocky shores; 85 % of the species are gastropods and of these 18 % feed upon algae, 38 % are predators, 28 % are faunal grazers and 5 % are faunal grazers and 5 % are scavengers.

The molluscs of the ridge are found in two major situations:

(i) On the open surface of the algal platform and on cast-up blocks, e.g. *Turbo* and *Trochus*.

(ii) Beneath the blocks and in crevices as a 'cryptofauna', e.g. *Cypraea* and *Diodora*.

Species belonging to (i) have thick shells, often heavily encrusted, strongly adherent and frequently with thick opercula. Species occurring as members of the cryptofauna (ii) do not show obvious morphological features which can be correlated with a rough water habitat. The bivalve-fauna is poor, both in numbers of species represented, and in the number of individuals; all are suspension feeders and are either byssally attached or cemented to the substrate. Several genera of prosobranchs have a number of sympatric species occurring together on the ridge, notably *Conus*, *Cypraea*, *Triphora* and *Rissoina*.

Turbo setosus and *T. argyostomus* are characteristic of the algal ridge and rarely found in any other habitat, both have a thick heavy turbinate shell usually encrusted with calcareous algae, and occur in similar niches on the open surface of the ridge sometimes in crevices but rarely beneath cast-up blocks. Both are algal grazers but are inactive at low tide, during the daytime remaining sealed off by the thick operculum. A larger species, *T. marmoratus*, often attains a size of 25 cm but is now very rare around Mahé because of commercial exploitation. Both smaller species of *Turbo* often have a commensal cap-shaped prosobranch *Amalthea conica* attached to the host, in a circular depression near the adapical portion of the aperture; feeding on its host's faecal material. Three species of trochids, *Trochus flammulatus*, *T. maculatus* and *Tectus mauritianus*, are common on exposed surfaces of the rim, the shells stout and conical and usually heavily encrusted with algae. *T. maculatus* is rare on windward reefs but common on leeward reefs from Anonyme to N.E. Point. *Diodora singaporensis* is common beneath blocks and between layers of the algal crust, and frequently found upon sponges on which it feeds.

The carnivorous gastropods *Drupa morum* and *D. ricinus** are both found on the outer surface of the cast-up blocks; *D. morum* feeds upon the large barnacle *Tetraclita squamosa*. *Morula granulata*, a typical member of the rocky shore community, is often present on the ridge; it feeds upon other molluscs and barnacles.

The molluscan cryptofauna is dominated by cypraeids†, all of which live beneath shelter at low tide and during daylight. Fourteen *Cypraea* species were found on the algal ridge but only four are abundant; the rest are uncommon, rare or extremely localized in distribution. *C. histrio* is the most abundant; it occurs on most reefs beneath almost every cast-up block on Anse aux Pins and Anse Royale reef, with up to five specimens per block. *C. lynx* and *C. carneola* are moderately common. The small species *C. fimbriata* inhabits the smallest crevices. *C. caputserpentis* is abundant but prefers the more exposed seaward edge of the rim where several individuals may aggregate in small depressions. Species such

* *D. ricinus*, in Hawaii, feeds upon sponges, holothurians and carrion (Wu 1965).

† There is uncertainty about the diets of Cypraeidae; *Trivia* definitely feeds upon sponges and *Erato* upon colonial acidians (Fretter & Graham 1962). Robertson (unpublished) considers that Cypraeidae are omnivorous, but as they lack a crystalline style they are probably not able to digest plant material. Whereas Morton (1958, p. 92) states 'Tropical cowries are generally grazing herbivors with a style sac, sorting area and gastric caecum living on cropped algae and bottom deposits.' (Kay, personal communication to Morton.)

as *C. kieneri*, *C. teres*, *C. clandestina*, and *C. assellus* are generally uncommon around Mahé.

The ridge on windward reefs is notable for the occurrence of seven species of *Triphora*, all less than 8 mm high. *T. rubrum* and *T. monilifera* are the most abundant followed by *T. aurea*, *T. corrugata*, *T. coetiviensis*, *T. incisa* and *T. complanata*. Several species may occur in close proximity, living on the surface of cast-up blocks. They appear to browse on organic crust on the substrate surface and have been found in association with green and red algae and sponges.

Several species of *Conus* occur on the algal ridge but only two appear restricted to this habitat. All species of *Conus** are active predators. *C. textile* lives partially buried in the sand of the shallow depressions of the ridge, usually beneath cast-up blocks. *C. lividus*, the most common of the ridge species, is usually found beneath dead coral blocks and is infrequently buried in sand. *C. ebraeus* and *C. chaldeus*, which are locally abundant, burrow shallowly in sand pockets. *C. catus* was only collected on Anse Forbans reef.

Bursa granularis, common off Le Cap, feeds partially on the echinoid *Diadema setosus*, drilling a hole about 1 cm in diameter in the side of the test.

Many more species of gastropods occur on the ridge and these are included in the appended lists.

Bivalve species are, not unexpectedly, few. At Anse aux Couches on the landward margin of the ridge clusters of byssally attached *Modiolus auriculatus* are found; these are heavily encrusted with calcareous algae, soft algae such as *Ceramium* and adherent Foraminifera. Cemented beneath most of the cast-up blocks is the oyster *Pycnodonte numisma* in which the cemented valve is moulded to the outline of the block and its shape is extremely variable. The upper valve is nearly always covered in encrustations of the encrusting Foraminifera *Carpentaria raphidodendron* and *Homotrema rubra*. *Cardita variegata* and *Acar plicata* are abundant; the latter is the smallest bivalve of the ridge (about 5 to 8 mm in length). Both species live byssally attached in the crevices of the algal crust and dead coral blocks.

Crustacea

Crabs are more abundant and show more diversity than in any other habitat. Most of them belong to the Xanthidae.

Most of the species are crevice dwellers and probably the commonest is *Actaea tomentosa* which uses the large rugged chelae to seal off the crevice. Other common crevice dwellers are *Etisius electra*, *Phymodius monticulosus*, *P. sculptus* and *Chlorodopsis aereolata*. The larger xanthids, *Carpilius convexus*, *Atergatis roseus* and *Leptodius sanguineus*, are more motile and were often seen moving around at low tide when the ridge was emersed.

Some species live on the outer surface of cast-up blocks such as *Percnon planissimum* which has long legs and long pointed dactyls and is very fast moving. *Menaethius monoceros*, dark green in colour, lives amongst the soft algae and is well camouflaged. The small crab-like anomuran *Petrolisthes lamarckii* is extremely abundant on block surfaces. The carnivorous swimming crabs *Thalamita prymna* and *T. admete* are common and can be up to 10 cm across. They are active at rising tide and at least part of their diet is xanthid crabs. A large

* Kohn (1959, 1959*a*) has found that the known prey of *Conus textile* consists of other gastropods; *C. lividus* feeds upon tubiculous terebellid polychaetes, *C. rattus* upon eunicid polychaetes and *C. catus* upon small fishes.

macruran *Palinurus* inhabits some of the cavernous deep holes on the ridge, usually those which are in contact with the open sea. Pagurids are abundant, inhabiting the shells of *Turbo*, *Trochus*, occasionally *Cypraea* and *Conus*.

Other fauna

The undersides of cast-up blocks and the algal crust are colonized by large numbers of encrusting colonial ascidians, sponges and zoanthids, which are absent from the outer sides. These encrusting organisms form a food supply for the abundant faunal grazing molluscs. Encrusting sheets of polyzoa, particularly *Schizoporella*, are also abundant. The little known encrusting foraminifera *Carpentaria raphidodendron*, which forms spiky growths up to 5 cm high, is exceedingly abundant and is an important filler of spaces in the cavernous ridge structure and is a minor cementing agent. The smaller encrusting foraminifera *Homotrema* and *Sporadotrema*, which form squat bright red growths, are also very abundant. *Polytrema* forms a white encrusting growth. The calcareous hydrozoan *Distichopora violacea* forms small palmate growths into cavities in the ridge. A sertularid hydroid is common on the outside and underside of blocks and crusts. The porous ridge structure is inhabited by eunicid and nereid polychaetes, sipunculids inhabit small holes in cast-up blocks and crust, the proboscis opening to the exterior. The tubes of serpulid worms encrust the undersides of blocks. The large barnacle *Tetraclita squamosa* is common on the larger cast-up blocks which project upwards into the eulittoral zone.

The Foraminifera *Heterostegina* and *Calcarina* are common in the small sand-pockets of the ridge.

Reef edge and reef front communities

The reef edges and reef fronts are the only environments in which corals are dominant organisms in the community. They face seaward and are the sites at which active advancement of the reef takes place. They are eventually encrusted by calcareous algae, filled in by sediment and indurated and eroded to form the reef flat platform.

The reef edge marks the seaward extremity of the reef flat and extends from the algal ridge to the change in slope at the reef front. It slopes shallowly seawards from the algal ridge and is 20 to 40 m wide. The reef front is generally steep and around Mahé is only about 20 m high; it is limited in height because the level of the base platform outside the reefs is only 20 to 25 m, sometimes much less. This shallow base level is rather unusual, for on most windward Indo-Pacific reefs there is a steep seaward slope to depths of 200 m or more (Emery *et al.* 1954; Stoddart 1966). On windward reefs the reef edges and fronts are dissected by grooves and surge channels, seen at their upward extremities at Anse Faure. The seaward extensions can be seen on aerial photographs particularly off S.E. Island. The zone of flourishing coral growth is surprisingly narrow, not much more than 12 to 15 m and often less than 6 m below sea level. Below this there is talus and sporadic coral growth.

Around Mahé there is a wide range of physical conditions operating against reef edges and fronts and in response two distinct coral communities are developed; the *Acropora–Millepora–Stylophora* community characteristic of windward edges and formed dominantly of branching corals and on sheltered edges with restricted circulation the *Porites–Favia–Leptoria* community consisting mainly of massive rounded colonies.

Windward edges: the Acropora *communities*

On windward reefs, wave action is more or less high for most of the year and is an important factor in influencing the distribution of coral species on any one section of the reef; some species live where the waves break, others prefer sheltered overhangs. The depths of reef fronts around Mahé are all well within the optimum range (90 m) for flourishing hermatypic corals. Most of the growth takes place in the upper 15 m. The only depth control that exists is that some species cannot withstand emersion. Temperatures throughout the year are equable within the range 27 to 30 °C which is well within the optimum limits for coral growth (Vaughan & Wells 1943). Salinities on windward reefs facing the open sea are very close to that of normal sea-water and never attain extreme values. However, when corals are emersed at low tide they may be affected by rainfall, an important factor in the distribution of corals on the upper reef edge.

The water on windward edges is usually very clear and its turbidity low. The hard substrate of reef front and edge is considered suitable for the settlement and growth of corals. Dissolved oxygen on edges with good circulation must be high and the removal of biogenous carbon dioxide, considered by Wells (1957) to be an important factor, efficient.

Corals, as sedentary organisms, primarily obtain their food, if it is first brought into close proximity, by currents or under its own motion. They feed mainly upon zooplankton from the open tropical sea. Therefore areas with a good circulation and a rapid turnover of water, should receive the most food. This leaves aside the problem of the role of zooxanthellae in the nutrition of corals (Odum & Odum 1955; Goreau 1961; Yonge 1963). Recently Goreau (*in litt.*) has found that coral polyps may absorb nutrients through the ectoderm.

Upper reef edges are to a greater or lesser extent emersed to the air during periods of low spring tides, and Vaughan (1913) considered that the ability of a coral to withstand exposure to the air is a function of the porosity of the coral skeleton, i.e. the ability ro tetain moisture.

Along most of the windward reef edges the coral is growing only in a narrow zone, at, or about, where the waves break, and is rather inaccessible for observation. The higher portions of the edge are often clothed in *Turbinaria* and *Sargassum*. The coral-fauna dominating the edges from Anse aux Pins reef pass to Pointe au Sel, Anse Royale and Anse Forbans is *Millepora dichotoma*, *M. platyphylla*, *Goniastrea retiformis*, the *Pocillopora danae–meandrina* series, *Acropora digitifera*, *A. humilis*, the alcyonacean *Lobophyton* and the zoanthid *Palythoa*.

The hydrozoan *Millepora dichotoma* occupies the extreme edge of the reef where the waves actually break; its growth form of solid vertical plates and cross-walls offering a strong structure to the waves; in less turbulent situations the plates are thinner and sometimes branching. At low tide *M. dichotoma* is rarely emersed, except between successive waves. *M. platyphylla*, a more delicately branching form, occupies rather more protected situations in this generally turbulent environment. Often the two species occur in close proximity; I do not think they are growth form variants, as suggested by Hickson (1924).

Pocillopora is at its most abundant on reef edges; on reef flats there may be only one species of *Pocillopora*, with a series of growth form variants often referred to as separate species. In the sand and cobble ridges habitat, *P. damicornis* is the typical form; it grows in small clumps of short spiky branches, with long verrucae, usually a buff yellow in colour, sometimes with pink tips to the branches. As the reef edge is approached, and wave action and emersion are higher, the dominant form is *P. danae*, in which the branches are shorter, and have become fused into short ridges, whilst the verrucae are much reduced. In the most exposed situations *P. meandrina* is found, in which the branches are shortened and fused into low meandrina and arcuate ridges, with short verrucae, which are almost absent from the top of the ridges. The *P. danae* and *meandrina* forms are often coloured bright pink or buff-yellow. There is no morphological difference between these forms with different colouration; colonies were seen which had both colours. In Cocos Keeling Wood-Jones (1912) considered that there was only one species of *Pocillopora* and all the forms were growth form variants responding to environmental differences. However, the form *P. eydouxi* from the *Porites* community seems specifically distinct from the *damicornis–meandrina* series.

Acropora digitifera is common on all windward edges as small, erect, branched colonies; it tends to occur on the higher portions of the edge which are subject to longer emersion at low tide. There appears to be a gradation in growth form from the slender, finger-growth, of *A. digitifera* to thicker, stubby fingers. At Le Cap, at a point of high exposure, flat encrusting sheets were found, but in sheltered clefts of the surface, short stunted finger-growths were growing out of the flattened sheet. This suggests that in very rough water *A. digitifera* can be reduced to encrusting sheets.

Goniastrea pectinata is abundant on the extreme edge, as rounded semi-encrusting heads on projections from the platform and is only emersed between waves. It is usually heavily infected by the commensal crab *Cryptochirus coralliodytes*.

The alcyonacean *Tubipora musica* is found on upper reef edges as small rounded encrusting heads. *Heliopora caerulea* occurs on more exposed sites as colonies of radially arranged vertical plates.

Large areas of the reef edge are covered by growths of the soft alcyonaceans *Lobophyton*, *Sarcophyton* and *Xenia* with the zoanthid *Palythoa*. *Lobophyton* occurs at Le Cap and Glacis as a large, low, flattened, fungoid growth, grey in colour and up to 2 to 3 m in length. It stands up above the general reef edge level and is emersed at spring tides. *Xenia* is not common on most edges, but occurs in large quantities at Anse Faure and Anonyme. *Palythoa* forms low-cushion encrustations, with a leathery texture; even at the lowest spring tides it is not usually emersed.

On the most exposed windward reefs there is a belt at the change in slope of the reef edge and reef front, which is inaccessible for observations because of heavy wave action; this corresponds with the 'Mare incognitum', of Wells (1957). At Anse aux Pins, Anse Royale and Anse Forbans there are suggestions of spur and groove formations both in the field and on aerial photographs. The higher portions of the spurs have a fauna of *Millepora dichotoma*, *Pocillopora meandrina* and *Goniastrea pectinata*. Encrusting *Montipora* tends to occur as sheets lining the sides of the upper landward portions of the grooves.

From limited observations below 3 to 4 m, and by comparison with less exposed reefs, there is a zone about 5 m wide of *Acropora pharaonis* in 'stagshorn' growth form in densely branching masses, with the outer branches extended towards the oncoming currents.

Below *A. pharoanis* there is a belt of delicately branching spray growths of *A. divaricata* and large flattened bracket growths of *A. irregularis*. Below this is an area of debris often with clumps of the very delicately branching *Seriatopora caliendrum*, many free living *Fungia fungites* and often heads of *Porites*, *Platygyra daedaela* and *Favia*, commonly less than 1 m across. *Acropora palifera* is common as short, vertical, club-shaped branches and *A. humilis* as stubby finger growths. Platy growths of *Montipora* were seen on a semi-sheltered edge at Pointe Connan; encrusting *Montipora* and *M. verrucosa* are very common. *Pocillopora* is common and, off Anonyme, the dead portions of the *A. pharaonis* belt were covered in *Xenia*.

The *Acropora* reef-knolls in the outer part of the Cascade embayment, which rise steeply from a bottom at 16 to 18 m, are almost entirely constructed of *A. pharaonis*. There is a similar *Acropora* bank off the north-west end of Cerf Island, but this rises from only 7 or 8 m. These knolls rise to within 0·5 m of low tide level and the shallow upper surface is largely dead and encrusted by calcareous algae. However, small colonies of *Stylophora*, *Pocillopora* and *Acropora digitifera* are present. Below this are the zones of *A. pharaonis*, *A. divaricata* and *A. irregularis*, the zone of flourishing coral growth on these semi-sheltered reefs extends downwards only to approximately 15 m. Rounded *Porites* and *Favia* colonies again occur on the lower slopes. On the undersides of the dead *A. pharaonis* branches an orange gorgonacean and the blue hydrocoralline *Distichophora violacea* are common.

The relatively delicate growths of branching *Acropora* such as *A. irregularis*, which although they live in an area of high circulation, are sheltered by depth from the force of the breaking waves a few metres above. At Bikini, von Arx (1954) found that the wind-induced onshore currents were partially directed downwards on hitting the reef edge. These currents are probably an important source of food supply to the corals of the reef front.

A detailed study of coral distribution of the higher reef edge was made at the northern end of Anse aux Pins reef. Here coral growth is profuse and it is one of the few places where the higher part of the edge is not dominated by *Sargassum*. The edge consists of a hard platform crossed by many narrow reef channels which appear to correspond with the small-scale grooves of 'spur and groove' formation on the reef front. These channels are up to 3 m wide and often on the landward side of the edge they have been partially sealed off and remain as pools partially roofed over by algal and coral growth; these pools are 1 to 2 m deep becoming shallower landwards. Channels in contact with the sea have either a smooth bottom or are floored by coarse coral and algal lumps.

The isolated pools usually have a sediment covered bottom. On this section of the reef edge which shows great variations in the detailed distributions of corals, a series of distribution maps was made on the scale 5 cm = 1 m in order to determine the relations of the coral species to habitat conditions and to each other. Part of one of these traverse maps is shown in figure 16 passing from the landward junction of the *Sargassum* of the algal ridge into an area dominated by the soft corals *Palythoa*, *Xenia* and *Lobophyton*.

Scleractinian corals are subordinate and represented by small colonies of *Acropora digitifera*, *Pocillopora danae* and some *Stylophora*. The soft corals are confined to the lower portions of the edge and usually remain covered by water, even at the lowest tides. Gradually, as more exposed situations are approached, the soft corals, especially *Xenia*, diminish in importance; the encrusting *Palythoa* is the only soft coral to survive into areas of higher exposure. The channel crossed in the traverse is poor in coral growth except for flat encrusting colonies of *Montipora* and occasional *Stylophora*. The colonies of *A. digitifera* occupy the highest portion of the platform, as low patches of finger growths about 30 to 40 cm in diameter. They remain emersed at low spring tides for considerable periods of time, often remaining 2 or 3 h exposed to the effects of insolation and precipitation. On Murray Island Mayor (1918) found *Acropora* to be one of the few species able to withstand drying experiments. Colonies of *P. danae* are usually partially upstanding but are washed between successive waves. Mayor found that *P. bulbosa* is easily killed by emersion.

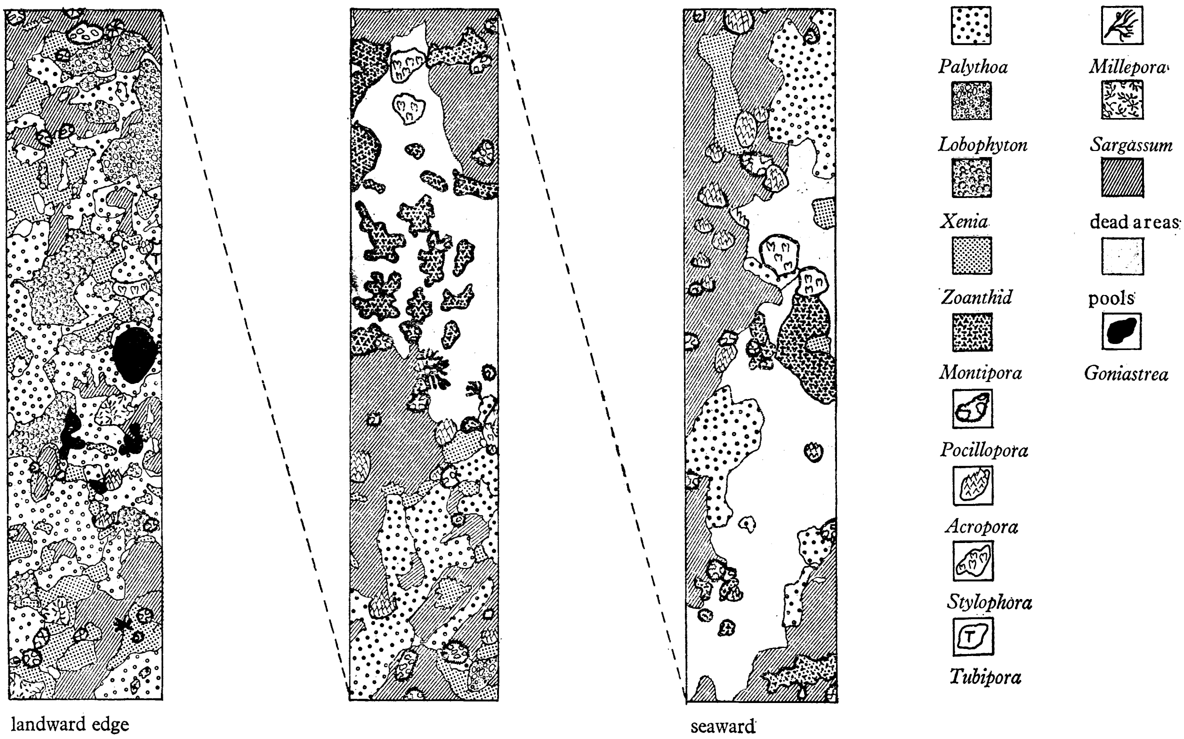

FIGURE 16. Map of coral population on reef edge at northern end of Anse aux Pins reef (Anse Faure). Scale 5 cm = 1 m.

The grooves and channels of this edge show an interesting fauna. Channels in contact with the sea are largely bare of coral, except for flat encrusting growths of *Montipora* on the sides and floor, and short stubby *Stylophora* and *Pocillopora danae* on the upper margins. The termination of the channel is often headed by a colony of *Millepora dichotoma* or *M. platyphylla*. Current action from wave-surge in these channels is high and presumably branching corals and soft corals are not able to survive.

The closed and semi-closed pools have a prolific fauna of great variety shown in figures 35, 36, plate 17. Here the alcyonacean *Tubipora musica* is common as semi-encrusting rounded heads about 15 cm in diameter; the grey–green polyps are expanded during the day but where at low tide part of the colony projects above the water line the polyps are retracted. *Stylophora, Pocillopora danae, Millepora platyphylla, Xenia* and *Palythoa* are all abundant around the pool edges. In figure 36 fragile circular platy growths of *Montipora* are seen deep in the pool. The small encrusting coral *Stylocoeniella armata*, about 4 to 5 cm in diameter, is very common and lives on the underside of dead and living coral colonies.

As a result of the reef traverses it was shown that the variations in coral distribution are closely associated with the small-scale topography of the surface. These changes cause differences in the duration of emersion and exposure to wave action. The position of a coral on the reef edge is a function of its ability to tolerate changes in these and associated conditions. *Acropora digitifera* has a very porous skeleton and can tolerate emersion for long periods but is detrimentally affected by rainfall. On one occasion heavy rain fell during low spring tide, streams of mucus began dripping from the coral, soon after there was the characteristic smell of dying coral and on return the next day many of the colonies were partially bleached white. *Stylophora*, *Millepora*, *Montipora*, *Goniastrea* and *Tubipora* are rarely emersed. *Pocillopora* is often emersed but always frequently washed by waves. *Xenia* and *Palythoa* are at least covered by very shallow water. *Millepora*, *Goniastrea* and *Pocillopora* inhabit the most exposed areas, whereas the other species prefer more sheltered situations.

On the portions of the upper reef edge which are not usually emersed and where zoanthids and alcyonaceans are dominant, slow rate of growth compared with soft corals would seem an important factor in controlling scleractinian coral distribution. Soft corals are faster growing than scleractinians and usually occupy all the available area within their range of tolerance. Scleractinians are not abundant except for the higher areas where soft corals are excluded. On most reef edges, apart from the area under discussion, *Sargassum* is important and is probably an important ecological control in preventing coral planulae from settling.

Associated organisms

(1) *Echinoderms*: *Diadema setosus* is extremely abundant on all *Acropora* community edges and fronts; on areas of the reef subject to emersion it shelters under overhangs or in the cavernous platform, but in deeper water lives on open, unsheltered surfaces. On the *Acropora* reef knolls of the Cascade area *Prionocidaris verticillata* is frequent amongst the tangle of dead stagshorn branches; the jagged spines grip the rough surfaces of the coral well. The ophiuroid *Ophiocoma erinaceus* is abundant and widespread. Asteroids are not common but *Mithrodia clavigera*, *Nardoa variolaris* and *Ophidaster hemprichi* are found. The small crinoid *Comanthus parvicirra* occurs on the underside of dead *Acropora* branches.

(2) *Molluscs*. The higher parts of reef edges have a molluscan fauna similar to that of the algal ridge but neither so abundant nor diverse. *Turbo setosus* and *T. argyrostromus* are again most common with *Trochus flammulatus* and from Anonyme northwards *T. maculatus*. *Cypraea caputserpentis* occurs in small groups gathered into small rounded crevices, in the roughest water. On two occasions, individuals of *Lambis crocata* were found on algal cobbles at the bottom of surge channels on the reef edge, one was upturned, washed in by wave action. *Acar plicata* is abundant but inconspicuous, wedged into tiny cracks and crevices on the underside of dead coral and platform. On reef fronts, reef knolls and patches, the fauna is more abundant. *C. histrio* occurs beneath dead coral and *C. scurra* is usually found in pairs, in the middle of *Acropora pharaonis* colonies. Most characteristic of the reef knolls is *Bursa rubeta*, a large species usually living on the dead upper surface of the patches; it feeds partly upon *Diadema setosus*. *Conus vexillum* is frequent and *Conus tendeneus* rare.

The bivalve *Barbatia fusca* is common on *Acropora pharaonis* patches, occurring byssally attached to the underside of dead coral branches, with a small parasitic pinnotherid crab often found living within its mantle cavity. *Barbatia helblingii* occurs attached to, and wedged between, coral branches, often with a severe distorted shell. The pectinids, *Gloriapallium pallium* and *Chlamys dringi* live attached within branching coral. *Tridacna squamosa* is sometimes found embedded in the solid reef structure, as off the edge at Glacis, but generally the branching growths of *Acropora* edges are an unsuitable habitat for it. *Pinctada margaritifera* and *Trapezium oblongum* are also byssate reef-front associated species.

(3) *Crustacea*. Crabs are much less common on reef edges and fronts than on the algal ridge, the species mostly being the same in both habitats. The corals *Stylophora* and *Pocillopora* are commonly infected by the parasitic crab *Haplocarcinus marsupialis* and *Goniastrea* is infested by *Cryptochirus coralliodytes*. The large crayfish *Galathea spinosirostris* occurs deeper on reef fronts.

Sheltered edges: the Porites *community*

Dominated by corals of massive, rounded growth forms, principally of the genus *Porites*, which produce a most solid reef structure, this community is found lining the channels across the reefs from South East Island to Anse Etoile, in the reef passes of Anse aux Pins and Anse Royale, as knolls in the Cascade embayment and in the deeper water on the north-west and north of Cerf Island. It is in marked contrast to the more rapidly growing *Acropora* edges described above. Mixed *Porites–Acropora* communities are found on some parts of the reef on the western side of Cerf Passage and Port Victoria Harbour.

The *Porites* community flourishes in water which is generally calm with little or no wave action. Generally no algal ridge is present which is so characteristic of high wave action; the reef edge is defined by planed off coral colonies coated in *Sargassum* and *Turbinaria*. Circulation of water is limited and the enclosed pools on the reef-flat at Brilliant are very sheltered and still. Temperatures are generally a few degrees higher than the well-circulated waters of the *Acropora* edges, but are not sufficiently elevated to have any effect upon coral growth. Salinities in areas commonly occupied by this community are rather reduced; for much of the time water in reef channels has a salinity of between 30 and 33 ‰. However, as previously described, after heavy rain, water of much reduced salinity passes through the reef channels for short periods. With reduced circulation the amount of dissolved oxygen in the water is less and biogenous carbon dioxide will be less efficiently removed. This may be a limiting factor for some corals.

There is a high level of turbidity in these waters, which are normally very murky and full of suspended matter, much of which is presumably derived from the land. On some of the edges, such as close inshore at Cascade, underwater visibility is reduced to less than 1 m. Dead surfaces, branches of *Sargassum* and the spaces between coral colonies are coated with fine-grained muddy sediment which any movement in the water above stirs into suspended clouds. The turbidity seriously reduces the amount of light available and may be a limiting factor for some genera of corals. The deposition of this suspension is probably also a limiting factor.

With calm water and limited circulation, explanation of the source of food for these massive corals is difficult. Sufficient food cannot come in from the open sea, which is originally low in plankton, to reach most areas of the *Porites* community for it must first cross another reef edge and a reef flat. Either, most of the food is produced on the reef flat and reaches the community by tidal currents, or it is land derived.

The dominant species of this community is a massive rounded form of *Porites*, which occurs in colonies up to about 5 m high and 2 to 3 m in diameter. Several growth variations may be recognized but are probably not of taxonomic significance. The colonies can be completely smooth, or their sides can be deeply gullied or a hummocky appearance. When in deepish water the tops of the colonies are living and rounded, but in shallow water the upper surfaces are often flat. Sometimes a rim of living coral may be growing around the dead top; this dead surface is often colonized by smaller fast growing corals such as *Pocillopora damicornis* or *Acropora digitifera*, but is more usually colonized by the soft algae *Turbinaria*, *Sargassum* and '*Chaetomorpha*'.

The massive rounded 'brain coral' growth forms of *Leptoria phrygia* and *Platygyra rustica* form colonies, never much more than 2 m in diameter. Both have coalescent calices forming a meandrine pattern and are distinguished in that *Leptoria* has a lamellar columella, whereas that of *Platygra* is parietal. Also found are *Favia* sp. and *F. speciosa*, all large polyped forms; the polyps are partially expanded during the daytime and show great variation in colour, from brown and purple to emerald green. Generally colonies are rather low, and rounded, but sometimes banks are formed. *Goniastrea*, which is a semi-encrusting form on *Acropora* edges, is here massive, *G. pectinata* forming rounded colonies not usually more than 1 m in diameter. *G. retiformis* also occurs. *Galaxea clavus* is found in even the most turbid areas; it grows as a mass of cushion growths, each about 15 cm in diameter, spreading over several metres. The long exsert calices protrude up to 4 cm above the main skeleton, which is no doubt an adaptive feature to prevent inundation of the coral polyp by sediment. *Goniopora* is found at Cascade in bank-like growths about 4 m long and 1 m high. The bank is formed of closely packed club-shaped branches with only the outer 10 cm living. Polyps are long and expanded at low tide during the daytime. *Lobophyllia corymbosa* is characteristic of this community. It has large calices, and occurs in fasciculate hemispherical mounds.

In the very sheltered spaces between the massive coral colonies, small clones of five to six individuals of *Fungia fungites* are found. Individuals may be up to 25 cm in diameter, and frequently they are so congested that they lie in an oblique or overlapping position. The similar free-living but colonial coral *Herpolitha limax* has a very localized distribution on several knolls off Cascade.

In deeper positions, at 4 to 5 m, colonies of *Echinopora lamellosa* with large, thin, delicate, plate-like branches are found.

Pocillopora damicornis is quite common in this habitat but always in the shallower areas; it often attains a very delicately branched growth form. *P. eydouxi*, more restricted to this community, grows as long, flattened, club-shaped, vertical branches up to 30 to 40 cm long. *Cyphastrea*, *Montipora* and *Hydnophora exesa* in their encrusting and semi-encrusting habits are common but inconspicuous elements of the fauna.

Below about 5 m most of the corals have disappeared with the exception of *Porites* which extends down into the dark, deep water. Reef edges in the *Porites* community are steep, for the edge is usually formed by the superposition of one colony on another. There is very little debris falling; the breakdown of these massive corals when dead must be a slow and gradual process of attrition, compared with the frequent collapse and disintegration of the less rigid branching structures on *Acropora* edges.

Alcyonacea are virtually absent from this community, but the actinian *Stochiactis*, which can reach a diameter of more than 30 cm is very common.

Associated organisms

In the calm environment calcareous algae are largely absent and soft algae are more important than in windward communities. Dead surfaces are clothed in *Sargassum* and *Turbinaria*, often with a turf of *Chaetomorpha*.

Echinoderms

Diadema setosus is again very common in crevices and on the open dead coral surface where light intensity is low and the water is calm. *Phyllacanthus imperialis*, with its thick smooth, cylindrical spines, wedges itself with tenacity into crevices between the smooth surfaces of this habitat; the spines often have an extensive epifauna with the prosobranch *Amalthea conica* adapted to the shape of the spines. A small clone of *Heterocentrotus mammillatus*, a large, long, cylindrically spined form, was found on a piece of largely dead *Porites* platform. Individuals were firmly wedged deep under an overhang and could only be extracted with difficulty.

The ophiuroids *Ophiocoma erinaceus* and *O. brevipes* are common beneath dead lumps and *Holothuria atra* is occasionally found on the small sand patches between the coral colonies.

Mollusca

Vasum turbinellus is probably the most abundant prosobranch in this habitat on dead and living coral surfaces. *Trochus maculatus* occurs on dead coral surfaces usually with a coating of soft and calcareous algae. *Conus vexillum*, *C. lividus* and, surprisingly, *Cypraea tigris* are found. *Nassarius albescens* is common in the small patches of fine sand.

The large oyster *Pycnodonte hyotis*, with zig-zag valve margins, is found cemented to dead coral surfaces, usually on the seaward-facing situations of the edges or knolls. It can attain a size of about 30 cm in length. *Tridanca squamosa* is commonly firmly byssally attached to the dead oral surface and frequently occupies sheltered crevices between coral colonies. *Streptopinna saccata* was found growing between club-shaped branches of *Goniopora*, the valves distorted by its growth position.

Discussion on the distribution of the coral communities

Having described the physical conditions, constituents and distribution of the two reef edge communities, certain suggestions can be ventured as to the reasons for their existence.

On windward reefs massive *Porites* is virtually absent except on the deepest parts, below the level of prolific *Acropora* growth; here colonies of *Porites*, *Favia* and *Leptoria* may be seen. This suggests that there may be some competition factor involved between the branching and massive corals; as shown below, *Porites* is tolerant of a wide range of conditions and there seems no reason why it should not be present on windward edges. In terms of the area occupied by each colony, the *Acroporidae*, *Pocillopora*, *Millepora* and *Stylophora*, because of their branching growths, are the fastest growing. A summary of results in Vaughan & Wells (1943) shows that in terms of length addition *Acropora* is usually the fastest and *Porites*, with the other massive forms, usually the slowest. Tamura found that six species of *Acropora* had an average increase of 82 mm per year, whereas *Porites* had an average increase of 14·6 mm per year. However, in terms of actual weight increase the poritids are higher. Goreau (1961), working in the West Indies with much more refined carbon isotope methods, found that *Acropora* is the fastest grower followed by *Millepora*, with *Porites* slowest. Therefore, it would appear that by sheer rate of growth and the occupation of space that *Acropora* and other species of branching corals prevent the massive forms from colonizing the reef edge.

It has been shown by Marshall & Orr (1931) that large polyped corals can deal with sediment falling from above far more easily than small polyped species. Genera such as *Fungia*, *Symphyllia*, *Goniastrea* and *Galaxea* readily remove large amounts of mud and sand falling upon them. But Marshall & Orr also found that even though massive *Porites* has small polyps it could remove fine sediment and mud, although it was incapable of removing sand. Branching *Acropora*, in which ciliary action is largely ineffectual in sediment removal, must be confined to a relatively sediment free environment. The branching nature of the colonies present few areas on which coarse sediment can settle in any quantity.

Porites as a genus appears more able to tolerate adverse conditions than any other. The experiments of Mayor (1918) are of interest in this respect; he found that on heating sea-water *Seriatopora* and *Acropora* are killed below 37 °C, whereas *Goniastrea* and various forms of *Porites* died at above this figure. On placing various corals in sea-water diluted to 50 % with rain-water he found that *Acropora* and *Seriatopora* survive less than $11\frac{1}{2}$ h, and the only three species to survive 24 h of this treatment were poritids. In the Persian Gulf massive *Porites* has been found living in extraordinarily high salinities (Kinsman 1964).

It is seen that *Porites* is able to tolerate a wide range of conditions which are extreme or fatal to any other coral genera. Therefore we find massive *Porites* virtually alone at the landward heads of reef channels, where salinities are often much reduced for short periods and turbidity is very high. It is found as small ball-like colonies in the grass beds, often semi-emersed at low tide, where the temperatures of these shallow tidal pools often reach nearly 40 °C.

Acropora and the other branching forms appear to be excluded from the reef passes and calm areas because of the very conditions which *Porites* and some of the other forms are able to tolerate. *Porites* and other massive corals are probably excluded from windward edges by competition from the Acroporidae.

Fauna from deeper water outside the reefs

The fauna of the sea bottom outside the reefs was investigated by grab sampling of the sediment and by dredging. Detailed dredging was carried out in Cerf Passage and Port Victoria Harbour but only to a limited extent in North West Bay and off Anse aux Pins and Anse Royale. The fauna obtained probably represents only a small part of that present and the results obtained must be regarded as tentative.

Dredging close to the reefs off Anse Royale and Anse aux Pins produced algal nodules and cobbles encrusted with *Lithophyllum* and corals; common species are *Alveopora*, *Porites*, *Acropora complanata* and *Millepora*. The echinoid *Diadema setosus* was commonly dredged. The ophiuroid *Ophiothrix tigris* is associated with *Acropora* colonies, the arms articulating in a dorso-ventral as well as a lateral plane enabling the ophiuroid to move easily on the branching coral. The gastropods *Drupa echinulata* and *Apollon pusillus* are common. Glimpses of the talus slope indicate algally coated debris and sporadic growth with many *Diadema*.

Further from the reefs, the bottom is uniformly level at about 25 m and consists of medium-grade clean coral shell sand. The small ahermatypic corals *Heteropsammia* and *Heterocyathus* which live unattached on the surface of the sand are common. Each of these corals harbours in its base a commensal sipunculid worm *Aspidosiphon corallicola*. *Acropora complanata* appears to grow as flat branching sheets above the sandy bottom. The small irregular sand burrowing echinoid *Maretia planulata* is common. Dominant bivalves are *Parvicardium sueziense*, *Ervilia bisculpta* and *Corbula subquadrata*. Gastropods are not so common but typical species are *Fenella scabra*, *Leptothyra candida* and *Triphora monilifera*.

The fauna obtained around the eastern side of the St Anne Cerf Island group is similar to that obtained outside the other windward reefs described above. Dredging between St Anne and Seche Islands produced much *Acropora complanata* in flat sheets which are also common between Harrison's Rocks and Long Islands. The gastropod *Oliva sidelia* is common in the surrounding clean white sand. Off the fore reef at Faon Island the corals *Cyphastrea*, *Porites*, *Acropora* and algal cobbles were found.

Cerf Passage and Port Victoria Harbour

More detailed dredging and grab sampling was undertaken here than any other area. The greater part of Cerf Passage lies at less than 20 m depth with many shallower coral banks and knolls. The surrounding sediment is coarse white sand with local patches of coral and algal debris. Most of Port Victoria Harbour lies deeper than 20 m and this line approximately marks a change to fine grey silt grade sediment which is often flocculent and smells strongly of hydrogen sulphide; this type of sediment is also found in the reef channels of Cascade, Port Victoria and Port Connan and Anse Étoile.

Corals

Coral was commonly found at stations in the middle and southern end of Cerf Passage where there are many coral knolls and patches. The most frequently obtained forms were *Acropora complanata*, *Stylophora*, *Millepora platyphylla*, *Galaxea and* nodular *Porites*. The solitary corals *Heteropsammia* and *Heterocyathus* are common on sandy bottoms. Coral was not usually found by dredging in Port Victoria Harbour but on a shallower bank in the north-west area off Anse Étoile there is a fauna of *Acropora*, *Pachyseris*, *Leptoseris* and *Turbinaria*.

Mollusca

Bivalves constitute about 55 % of the molluscan species obtained from Cerf Passage, 75 % are suspension feeders, which are also dominant in terms of numbers. This possibly indicates that sediments in this area are not rich in detritus available for deposit feeders.

About 40 % of the gastropods are predators on bivalves, polychaetes and echinoids, about 20 % feed upon algae and the rest are scavengers and other diets. The bottom topography and substrate type is very variable from coral patches to thick sand and the fauna is correspondingly diverse.

Gastropods

The most abundant species is *Nassarius albescens* which occurred in most successful dredges, however it is not a good community indicator as it occurs in all sandy habitats. *Terebellum terebellum* was dredged from the fine sediment of Port Victoria Harbour together with *Strombus plicata*. *Phos roseatus* and *Phos cyanostomus* were common in the sands of Cerf Passage. *Trivia oryza* and *Erato sulcifera* were found living upon green sponge in Cerf Passage. Other gastropods were very sporadic in distribution but this may be a result of incomplete sampling.

Bivalves

Bivalves may be separated into infaunal and epifaunal species, the latter living in or on coral and coral debris. The arcid *Barbatia helblingi* occur byssally attached to branching coral colonies, with its valves frequently very distorted. *Botula cinnamomea* is a mechanical borer into dead coral and algal debris; its valve margins are often eroded. Another borer, *Gastrochaena cunieformis*, is occasionally found in coral. Decatopecten *plica* lives on sandy bottoms whereas *Chlamys senatoria* is invariably byssally attached to coral or similar substrate and is very common in some parts of Cerf Passage. *Plicatula chinensis* lives cemented to algal and coral debris. *Pteria inquinata* and *Pinctada margaritifera* both occur byssally attached to coral. The oyster *Ostrea folium* was only found attached to the spines of the echinoid *Prionocidaris verticillata*.

One of the most diagnostic of the sand burrowing infaunal species is *Laevicardium australe*, which is common at nearly every dredge station. Its siphons are tentaculate and only protrude slightly with a strong active foot; this species is capable of making leaping movements. Large dead valves of *Vasticardium elongatum* were found, but never the living animals. The venerid *Lioconcha picta* is locally common; it has short stubby tentacled siphons and conspicuous colour ornament. *Austrodosinia histrio* and *Dosinia* sp. are extremely common; both have relatively long siphons and are deep burrowers.

Deposit feeders are uncommon. Two deep burrowing forms, with long divided siphons, are *Psammocola castrensis* and *Gari weinkauffi*; both live in the finer deposits deep in Port Victoria Harbour.

Crustacea

Many crabs were found in association with the corals of Cerf Passage the most common being *Tetralia glaberrima*, *Trapezia*, *cymodoce*, *Chlorodiella niger*. The crangonid shrimp *Coralliocaris graminea* was also found.

On sandy bottoms the crabs *Parthenope hoplonotus*, *Calappa hepatica*, *Neptuneus sanguinolenta* and the stomatopod *Goniodactylus* occur and in the finer silts *Actumnus setifer* is common.

Echinoderms

In Cerf Passage where the bottom is coralline, the echinoid *Prionocidaris verticillata* is common, the spines encrusted with barnacles, *Ostrea* and algae. *Diadema setosus* occurs in similar habitats and the large, black-spined echinoid *Astropyga radiata* appears to live on the surface of sand bottoms. *Temnotrema siamiense* is found amongst algae.

Burrowing irregular echinoids *Maretia planulata, Pseudomaretia alta* are common on the coarser sandy bottoms, but on the finer sands and silts the wide flattened species *Laganum depressum* and the less depressed *Clypeaster reticulatus* are found.

Holothurians were infrequently dredged and only *Holothuria atra* and *Microthele nobilis* were found. Ophiuroids are only common on coral and hard bottoms. *Ophiothrix tigris*, a bright green species, lives on the branches of *Acropora*: *Ophiocoma pica* and *Ophiothrix trilineata* were found amongst the coral.

North West Bay

A small amount of dredging was carried out in North West Bay which revealed an interesting fauna.

Immediately seaward of the reef at Glacis on a shallow platform large quantities of the alcyonaceans *Sinularia, Sarcophyton* and *Lobophyton* were obtained. It appears that the dark patches seen on aerial photographs from here are soft coral growths. From the surrounding sands *Rhinoclavis fasciatum, Nassarius albescens* and the burrowing echinoid *Maretia planulata* were obtained.

In the middle of the Bay off Beau Vallon at a depth of 15 to 25 m and about 300 m from the shore, there are beds of the marine angiosperms *Cymodocea rotundata* and *Thalassia hemprichi* which support a rather different community than on the shallower reef flats.

Fifty-five species of molluscs were obtained of which 65 % were gastropods and of these 60 % of the species are predators, 20 % algal feeders and 10 % scavengers. Suspension feeders make up 75 % of the bivalve species. The most abundant mollusc is *Hemicardia hemicardium* of which several hundred were obtained; it is a shallow-burrowing suspension feeder. Other suspension feeders are the burrowing arcid *Scapharca clathrata, Vasticardium elongatum, Lioconcha picta* and *Dosinia* sp. Deposit feeders are *Jactellina clathrata* and *Arcopagia robusta*, neither of which is common.

The gastropod fauna shows great variety; the only species common in both this habitat and the reef flat grass beds is the herbivor *Strombus gibberulus*. *Nassarius arcularis* is extremely abundant. *Archietectonica perspectiva* probably feeds upon zoanthids and *Xenophora solarioides* is a deposit feeder. Among the predators mitrids *Vexillum intermedium* and *Vexillum mucronatum* are common; they are probably specialized vermivors. Several species of *Terebra* are present.

On the grass patches the burrowing crab *Calappa hepatica* and the carnivorous swimming crabs *Thalamita sima, Neptunus gladiator* and *N. sanguinolenta* are abundant. The burrowing irregular echinoids *Clypeaster reticulatus, Maretia planulata* and *Melatia spatagus* were found.

Summary and conclusions

Reefs developed around oceanic islands of high relief such as Mahé, Saipan (Cloud 1959) and in the East Indies (Umbgrove 1947), show more variation in physico-chemical conditions than reefs developed around oceanic, generally flat lying coralline, islands, such as the Marshall Islands (Emery *et al.* 1954) and islands in the Amirante group. The heavy rainfall and rapid run off around Mahé produce reduced salinity communities on the reef flat and on reef edges. Rates of sedimentation due to terrestrial erosion are higher than in areas where sedimentation is almost wholly biogenic. The granite headlands and boulder areas, together with beach rock, provide more niches than are usually available for intertidal organisms on coralline islands.

In this study of the fauna of fringing reefs around Mahé distinct assemblages of animals and plants were recognized. These assemblages occupy distinctive positions on the reefs

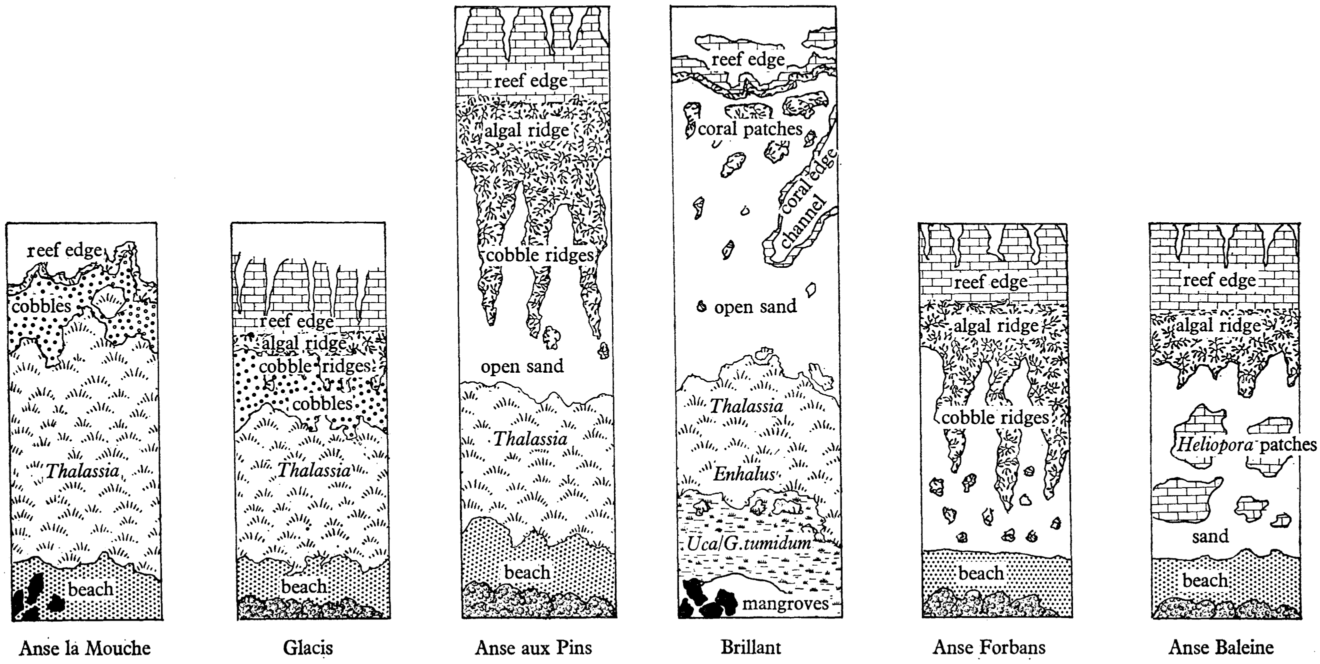

FIGURE 17. Comparative reef flat zonations around Mahé (semi-diagrammatic, not to scale).

and show a zonation parallel to the shore line established in response to a variety of environmental factors, principally wave action, substrate, depth of water, food supply and salinity variations. Because of the sediment accreting and reef-building faculties of some of the communities, e.g. the *Thalassia* beds and reef edge communities, the zones are both biological and physiographic. Plants generally show sharper zonation; they have, in the communities examined, narrower tolerance ranges than animals. Animal species tend to have less sharply defined boundaries. A normal zonation pattern cannot be defined, as each bay and reef is exposed to different sets of physical conditions which all produce locally different patterns. However, recognizable recurring patterns can be distinguished for windward and leeward reefs. On some reefs a maximum number of zones is developed, as at Anse aux Pins for windward reefs and at Brillant for sheltered reefs.

The position of the coral reef in the rocky shore zonation scheme as suggested by Stephenson (1958) and Doty (1957) is confirmed by the present work. The zones of the reef are related to the scheme contained in the most recent work on the ecology of rocky shores (Lewis 1964).

Reef environments and their corresponding communities recognized around Mahé are listed below. The information obtained for the faunas seaward of the reefs, does not at present warrant a division into communities.

1. *Supralittoral vegetation* consisting of salt spray resistant plants, such as *Ipomoea*, *Scaevola*, *Cocos* and *Calophyllum*. Inhabited by land crabs *Birgus* and *Coenobita*.
2. *Mangrove swamps and fringes*. Most abundant mangroves are *Rhizophora* and *Avicennia*. Crabs such as *Uca*, *Scylla*, *Sesarma*, and gastropods *Terebralia* and *Littorina* inhabit the swamps.
3. *Littoral rocky shore*. In the littoral fringe *Littorina* and blue green algae are common. In the Eulittoral zone barnacles, species of *Nerita* and the limpets *Cellana* and *Scutellastra* are abundant.
4. *Sandy beach*. Supports a fauna of burrowing crabs *Ocypode*, *Hippa* and the burrowing bivalves *Donax* and *Atactodea*.
5. *Ex-mangrove fringes* (Uca annulipes–Gafrarium tumidum *community*). The most common macroinvertebrate is the crab *Uca annulipes*. The bivalves *Gafrarium tumidum* and the gastropod *Cerithium morum* are abundant.
6. *Thalassia beds*. Sand covered with a thick growth of *Thalassia* and *Cymodocea*. Burrowing bivalves *Codakia*, *Tellinella* and *Quidnipagus* common. *Holothuria atra* abundant.
7. *Sands and cobble ridges*. Characteristic molluscs of the sandy areas include several species of *Terebra* and *Cerithium*, and the bivalves *Fragum fragum*, *Quadrans gargadia* and *Tellinella crucigera*. *Cypraea helvola* is common on the cobble ridges.
8. *The algal ridge*, formed by the prolific growth of calcareous red algae *Lithophyllum* and *Porolithon*. Abundant gastropods. *Diadema setosus* and crabs common.
9. *Reef edges and reef fronts*
   (*a*) *ACROPORA community*, dominated by corals with branching growth forms, *Acropora*, *Stylophora*, *Pocillopora* and *Millepora*.
   (*b*) *PORITES community*. Mainly corals with massive rounded growth forms such such as *Porites*, *Favia* and *Platygyra*.

Similar types of assemblages and zones, though not necessarily occurring together, have been recognized on reefs over the Indo-Pacific region (well summarized by Wells 1957) and in the West Indies (Storr 1964).

The fauna from the mangrove swamps at Low Isles described by Stephenson *et al.* (1931) shows great resemblance to that occurring around Mahé. Many species such as *Terebralia palustris*, *Metopograpsus messor* and *Scylla serrata* are common to both areas. The Australian list is longer and shows more variety than that for Mahé, but it seems that a more varied habitat was sampled. The presence of the bivalves *Quidnipagus palatam* and *Gafrarium pectinatum* was recorded in mangroves; both species occur around Mahé in a reduced salinity community on the sites of old mangrove swamps.

Thalassia beds show a sporadic occurrence on reefs in the Indo-Pacific area. For example they are well developed on the Kenya–Tanzania coast (personal observation) at Low Isles on the Great Barrier Reef (Stephenson *et al.* 1931), the Palao Isles (Abe 1937) and

Saipan (Cloud 1959). But they are absent at Gan (Stoddart 1966), Hawaii (Kohn 1959), Bikini (Emery *et al.* 1954), Fanning Island (Wainwright, personal communication) and Raroia (Newell 1956). *Thalassia* beds are well developed in the Bahamas area; around Abaco Island, *Codakia* is the bivalve in the community as it is around Mahé (Storr 1964). But in the other parts of the Bahamas Bank *Glycimeris* and *Tellina radiata* are the most common bivalves, although the faunal lists do include five species of lucinids (Newell *et al.* 1959).

Cobble ridges developed normal to the reef edge as seen on windward reefs around Mahé are a phenomenon not often seen on Indo-Pacific reefs, though they appear to exist on some islands on the Great Barrier Reef (aerial photographs in Gillett & McNeil (1959)). The algal ridge is a well known structure of Indo-Pacific reefs (Wells 1957; Johnson 1963). The two distinctive corals, reef edge and front communities, the *Acropora* and the *Porites* communities do not seem to have an exact counterparts on other Indo-Pacific reefs. Windward reefs in the Maldives appear to be dominated by *Acropora* (Stoddart 1966) as around Mahé, but there does not appear to be a corresponding sheltered *Porites* community. Lizard Island, an island of high relief off Queensland, has a reef edge consisting predominantly of massive *Porites* colonies (Stephenson *et al.* 1931). The distribution of coral communities on various structural regions of the large Bikini Atoll has been fully discussed by Wells (1957).

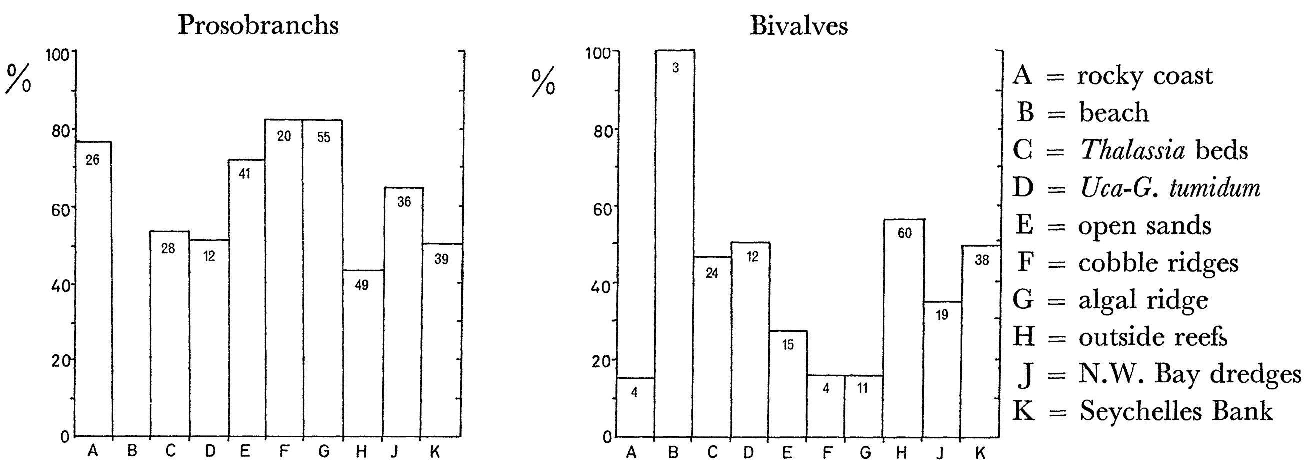

FIGURE 18. Gastropod–bivalve percentages of molluscan fauna in various environments. (Samples collected from the Seychelles Bank between 20 and 40 fathoms added for comparison.) Actual numbers indicated.

The analysis of feeding types amongst molluscan species in the various communities is summarized in figures 18 to 20. It supports the obvious conclusion that bivalves are subordinate, or absent, where the substrate is hard, but that when they do occur, they are all suspension feeders, either byssally attached, or cemented to the substrate. In sandy substrates up to 55 % of species may be bivalves; of these, suspension feeders make up about 75 %. The great percentage of prosobranch species on hard intertidal surfaces are algal grazers, but on the other hard substrates, such as the algal ridge, feeding types are more diverse. Gastropods living on the open surfaces of hard substrates are usually trochiform,

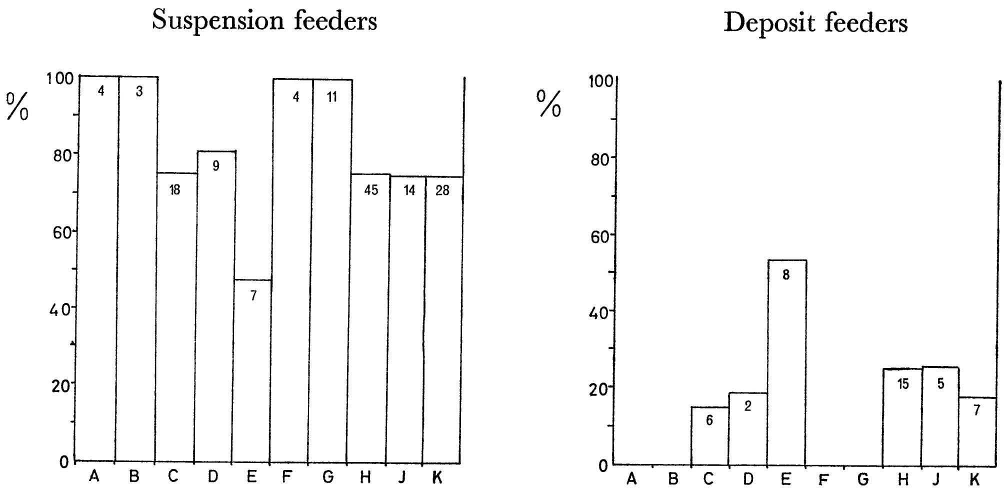

FIGURE 19. Mode of feeding of bivalve fauna in various environments. Notation as in figure 18.

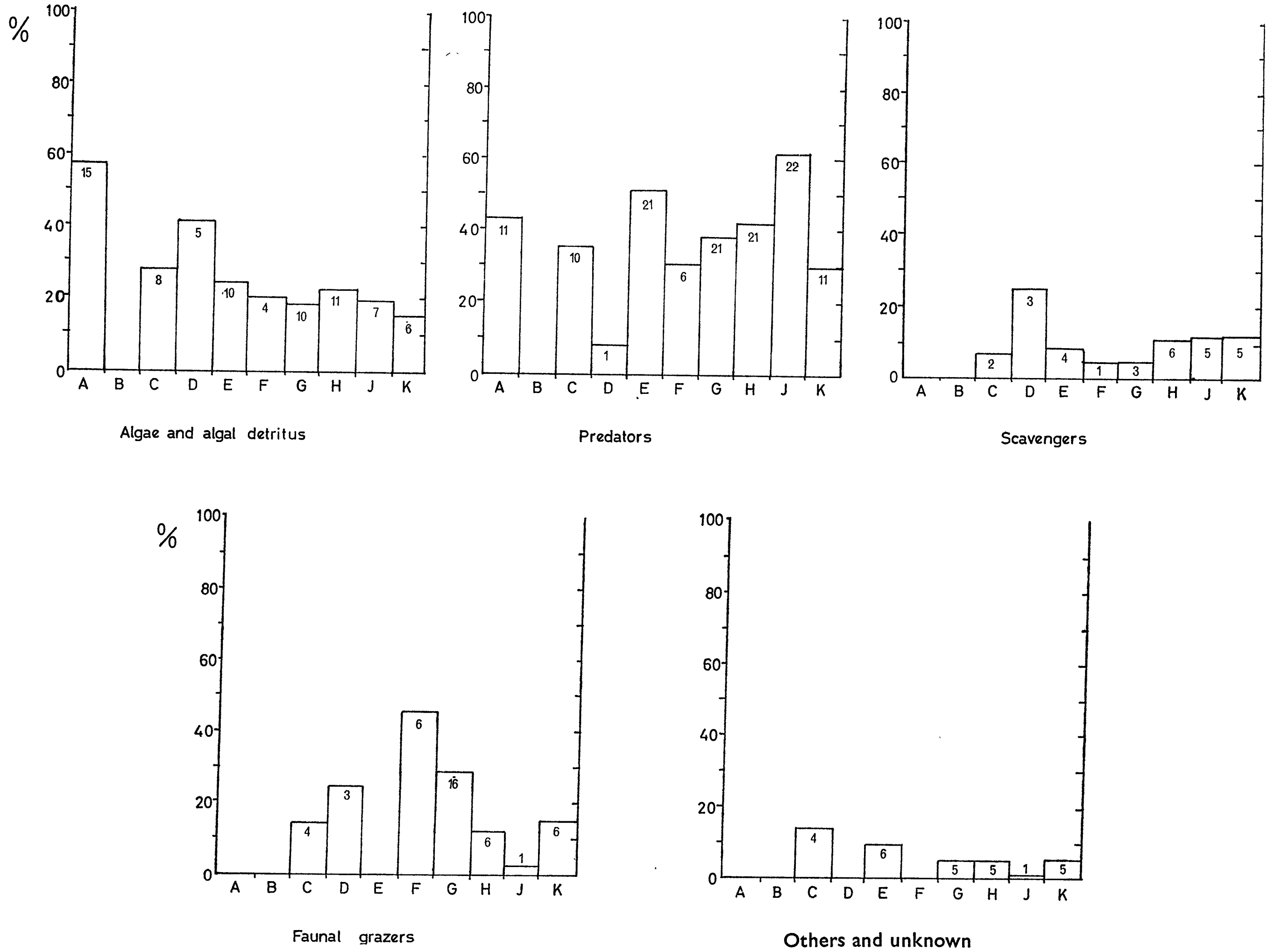

FIGURE 20. Diets of prosobranch gastropods in various environments. Actual numbers indicated. Notation as in figure 18.

turbiniform and patelliform, usually thick shelled and strongly adherent. On sandy substrates they tend to be turretted, fusiform, often polished and very mobile. However, the cryptofauna, living in crevices and beneath cast-up blocks, may not show these adaptive modifications.

Gerlach (1961) has found that an area of living coral supports a smaller population of microfauna than an equivalent area of red algae. In the present study it has been found that macrofaunal molluscs and crustaceans have low population densities on areas of living coral when compared with other areas of the reef flat such as the algal ridge and the *Thalassia* beds, which are dominantly plant communities. However, areas of dead coral, such as flat tops of *Acropora* patches and knolls, support a larger population. Gerlach (1961) attributes the lack of microfauna on *Acropora* colonies to the production by this coral of large amounts of mucus when irritated by a foreign body. The paucity of fauna, other than corals, on *Porites* community edges around Mahé may also be partly explained by the fact that the large rounded coral surfaces offer new microniches for occupation by smaller invertebrates.

Statements made about the reefs around Mahé by Gardiner (1907) deserve correction (on p. 161): '...the reefs around Mahé etc. have no real homologues in the Indian Ocean. Caution will hence have to be exercised in making any deductions from the presence or absence from them of any species or genera of animals or plants as compared to other reefs.' The reefs around Mahé can only be considered typical in that reef fronts are limited in depth by the Seychelles Bank Platform at approximately 25 to 30 m immediately around Mahé. There is no evidence from the extensive collections made that the fauna examined is in any way restricted when compared with other areas. Gardiner also states (p. 456): 'immediately around the granitic islands are here and there fringing reefs especially in bays...Nullipores practically do not enter into their composition and such coral masses as grow are of small size.' The present work has shown that calcareous red algae (nullipores) are important around Mahé and play a major part in reef construction and sediment formation. Although the coral growth is not so prolific as in some Indo-Pacific areas, colonies in the *Porites* community can be up to 5 m in height and 3 to 4 m in diameter which can hardly be considered small.

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Appendix

Distribution table of some invertebrates

Key to symbols

Environments:

I = Mangroves and supralittoral
II = Sandy beach
III = Rocky shore
IV = Ex-mangrove fringes, *Uca/Gafrarium tumidum* community
V = Grass beds
VI = Sands and cobble ridges
VII = Algal ridge
VIII = Reef edges and reef fronts

Qualitative abundance: R = rare X = present C = common A = abundant.

List of species	Environments								
	I	II	III	IV	V	VI	VII	VIII	IX
Coelenterata									
Hydrozoa									
Millepora dichotoma Forskål	.	.	.	.	.	.	.	C	.
M. platyphylla Ehrenberg	.	.	.	.	.	.	X	C	.
Millepora sp.	.	.	.	.	.	X	.	.	.
Distichopora violacea (Pallas)	.	.	.	.	.	.	X	X	.
Anthozoa: Stolonifera									
Tubipora musica Linnaeus	.	.	.	.	.	.	.	X	.
Anthozoa: Alcyonacea									
Sinularia sp.	.	.	.	.	.	.	.	X	C
Sarcophytan sp.	.	.	.	.	.	X	.	X	.
Lobophytom sp.	.	.	.	.	.	.	.	C	.
Xenia umbellata Milne Edwards & Haime	.	.	.	.	.	.	C	X	.
Anthozoa: Trachysammiacea									
Heliopora caerulea (Pallas)	.	.	.	.	X	X	.	X	.
Anthozoa: Scleractinia									
Stylocoeniella armata Ehrenberg	.	.	.	.	.	X	X	X	.
Psammocora contigua (Esper)	.	.	.	.	C	.	.	.	.
Stylophora mordax Dana	.	.	.	.	.	.	.	C	X
Seriatopora caliendrum Ehrenberg	.	.	.	.	.	.	.	X	X
Pocillopora danae Verrill	.	.	.	.	.	.	A	A	.
P. damicornis (Pallas)	.	.	.	X	C	C	.	X	.
P. eydouxi (Milne, Edwards & Haime)	.	.	.	.	.	.	.	C	.
P. meandrina Dana	.	.	.	.	.	.	C	.	.
P. verrucosa (Ellis & Solander)	.	.	.	.	.	.	.	X	.
Acropora complanata (Brook)	.	.	.	.	.	.	.	.	X
A. digitifera (Dana)	.	.	.	.	.	X	A	A	.
A. diversa (Brook)	.	.	.	.	X	C	.	C	.
A. humilis (Dana)	.	.	.	.	.	.	X	X	.
A. irregularis (Brook)	.	.	.	.	.	.	.	X	X
A. palifera (Lamarck)	.	.	.	.	.	.	.	X	.
A. patuta (Brook)	.	.	.	.	.	X	.	X	.
A. pharaonis (Milne Edwards & Haime)	.	.	.	.	.	X	.	A	.
Montipora venosa (Ehrenberg)	.	.	.	.	.	X	.	X	.
M. verrucosa (Lamarck)	.	.	.	.	.	X	.	X	.
Pavona clavus Dana	.	.	.	.	.	.	.	X	.
P. frondifera Lamarck	.	.	.	.	A	.	.	.	.
P. maldivensis (Gardiner)	.	.	.	.	.	.	.	X	.
P. varians Verrill	.	.	.	.	.	X	.	X	.
Agaricia ponderosa Gardiner	.	.	.	.	.	.	.	R	.
Leptoseris papyracea (Dana)	.	.	.	.	.	.	.	.	X
Pachyseris speciosa (Dana)	.	.	.	.	.	.	.	.	X
Fungia fungites (Linnaeus)	.	.	.	.	.	C	.	A	.

List of species	Environments I	II	III	IV	V	VI	VII	VIII	IX
Anthozoa: Scleractinia (*cont.*)									
Herpolitha limax (Esper)	.	.	.	.	.	.	.	X	.
Porites lutea Milne Edwards & Haime	.	.	.	X	C	C	X	.	.
Porites nigrescens Dana	.	.	.	.	X	C	.	X	.
Porites sp. (Massive)	.	.	.	.	.	.	.	A	.
Synarea sp.	.	.	.	.	.	X	.	.	.
Goniopora sp.	.	.	.	.	.	X	.	.	.
Favia favus (Foskål)	.	.	.	.	.	.	.	X	.
F. halicora (Ehrenberg)?	.	.	.	.	.	X	.	.	.
F. speciosa (Dana)	.	.	.	.	.	.	.	C	.
Favites abdita (Ellis & Solander)	.	.	.	.	.	.	.	X	.
Goniastrea pectinata (Ehrenberg)	.	.	.	.	.	C	C	C	.
G. retiformis (Lamarck)	.	.	.	.	.	.	.	C	.
Platygyra rustica (Dana)	.	.	.	.	.	X	.	C	.
Leptoria phrygia (Ellis & Solander)	.	.	.	.	.	.	.	X	.
Hydnophora exesa (Pallas)	.	.	.	.	.	.	.	X	.
H. microconos (Lamarck)	.	.	.	.	.	.	X	.	.
Cyphastrea chalcidicum Klunzinger	.	.	.	.	.	.	.	X	.
C. microphthalma (Lamarck)	.	.	.	.	.	C	X	.	.
Leptastrea purpurea Dana	.	.	.	.	.	.	X	X	.
Echinopora lamellosa (Esper)	.	.	.	.	.	X	.	X	.
Galaxea clavus (Linnaeus)	.	.	.	.	.	X	.	C	X
G. fasicularis (Dana)	.	.	.	.	.	.	.	X	.
Acanthastrea echinata (Dana)	.	.	.	.	.	.	X	.	.
Lobophyllia corymbosa (Forskål)	.	.	.	.	.	X	.	C	.
Symphyllia sinuosa (Quoy & Gaimard)	.	.	.	.	.	.	.	X	..
Heterocyathus aequicostatus (Milne Edwards & Haime)	.	.	.	.	.	.	.	.	X
Heteropsammia michelini (Milne Edwards & Haime)	.	.	.	.	.	.	.	.	C
Turbinaria peltata (Esper)	.	.	.	.	.	R	.	.	X
ARTHROPODA									
Crustacea: Cirripedia									
Tetrachthalamus oblitteratus Newman	.	.	A	.	.	.	.	.	.
Balanus tintinnabulum var. *occator* Darwin	.	.	C	.	.	.	.	.	.
Tetraclita squamosa (Bruguière)	.	.	C	.	.	X	.	.	.
Pyrgoma sp.	.	.	.	.	.	C	.	C	.
Lithothyra sp.	.	.	.	.	.	.	.	C	.
Crustacea: Malacostraca: Decapoda									
Achaeus sp.	.	.	.	.	.	.	.	.	.
Manaethius monoceros (Latreille)	.	.	.	.	C	C	X	.	X
Micippia philyra (Herbst)	.	.	.	.	.	C	.	.	X
Lambrus validens de Haan	.	.	.	.	X	.	.	.	.
Parthenope hoplonotus Adams & White	.	.	.	.	.	.	.	.	X
Pinnothores sp.	.	.	.	.	.	.	.	X	.
Ocypode ceratopthalma (Pallas)	.	A	.	X	.	.	.	.	.
O. cordimanus Desmarest	.	C	.	.	.	.	.	.	.
Uca annulipes (Milne Edwards)	A	.	.	A	.	.	.	.	.
Macrophthalma parvimanus (Lacaille)	.	.	.	A	.	.	.	.	.
Cardisoma carnifex (Herbst)	C	.	.	.	.	.	.	.	.
Grapsus strigosus (Herbst)	.	.	C	.	.	.	.	.	.
Metopograpsus messor (Forskål)	C	.	X	C	.	.	.	.	.
Sesarma longipes Krauss	C	.	.	.	.	.	.	.	.
Neptunus gladiator (Fabricus)	.	.	.	.	.	.	.	.	X
Neplunus sanguiolenta (Herbst)	.	.	.	.	.	.	.	.	X
Thalamita admete (Herbst)	.	.	.	.	X	C	C	.	.
T. crenata (Latreille)	.	.	.	A	.	.	.	.	.
T. danae Stimpson	.	.	.	.	.	.	X	.	.

List of species	Environments I	II	III	IV	V	VI	VII	VIII	IX
Crustacea: Malacostraca: Decapoda (*cont.*)									
T. prymna (Herbst)	.	.	.	.	.	.	A	.	.
T. sima (Milne Edwards)	.	.	.	.	.	.	.	.	C
Carpilius convexus (Forskål)	.	.	.	.	.	.	X	X	X
Atergatis roseus (Rupell)	.	.	.	.	R	.	X	.	.
Chlorodiella niger (Forskål)	.	.	.	.	A	.	.	.	X
Phymodius monticulosus (Dana)	.	.	.	.	A	.	X	.	.
P. sculptus (Milne Edwards)	.	.	.	.	.	.	X	X	.
Chlorodopsis aereolata (Milne Edwards)	.	.	.	.	.	.	A	.	.
Cymo andreossyi (Andouin)	.	.	.	.	.	.	.	X	.
Xantho impressus (Lamarck)	.	.	.	.	.	.	X	.	.
Leptodius hydrophilus (Herbst)	.	.	.	.	C	C	C	.	.
L. sanguineus (Milne Edwards)	.	.	.	.	C	.	.	.	.
Actaea hirsutissima (Rupell)	.	.	.	.	.	X	C	.	.
A. parvula (Krauss)	.	.	.	.	.	.	.	.	X
A. tomentosa (Milne Edwards)	.	.	.	.	.	A	A	C	.
Lachnopodus rodgersi (Stimpson)	.	.	.	.	.	.	C	.	.
Liomera cinctimanus (White)	.	.	.	.	.	.	X	.	.
L. monticulosus (Milne Edwards)	.	.	.	.	.	X	.	.	.
Xanthias lamarcki (Milne Edwards)	.	.	.	.	.	.	.	.	X
Etisius electra (Herbst)	.	.	.	X	.	C	A	.	.
Libystes nitidus (Milne Edwards)	.	.	.	.	.	.	.	.	R
Epixanthus frontalis (Milne Edwards)	.	.	X	X	.	.	.	.	.
Pilumnus hirsutus Stimpson	.	.	.	.	.	X	X	.	.
Pilumnus vespertilio Fabricus	.	.	.	.	C	.	.	.	.
Actumnus setifer (de Haan)	.	.	.	.	.	.	.	X	C
Nectopanope sp.	.	.	.	.	R	.	.	.	.
Trapezia cymodoce (Herbst)	.	.	.	.	.	X	.	A	C
T. guttata Rupell	.	.	.	.	.	.	.	X	.
T. rufopunctata Herbst	.	.	.	.	.	.	.	R	.
Tetralia glaberrima (Herbst)	.	.	.	.	.	.	.	C	X
Percnon planissimum (Herbst)	.	.	.	.	.	.	C	.	.
Dromia dormia Linnaeus	.	.	.	.	.	.	X	.	.
Calappa hepatica (Linnaeus)	.	.	.	X	C	X	.	.	X
Matuta banksii (Leach)	.	X	.	.	.	.	.	.	.
Ebalia sp.	.	.	.	.	.	.	.	.	.
Leucosia marmorea Bell	.	.	.	.	.	.	.	.	X
Pagurus 1	.	.	A	.	.	.	.	.	.
Pagurus 2	.	.	.	.	.	.	A	.	.
Birgus latro	R	.	.	.	.	.	.	.	.
Coenobita rugosus Milne Edwards	X	C	.	.	.	.	.	.	.
Petrolisthes lamarkii (Leach)	.	.	.	.	.	C	A	.	.
Palinurus sp.	.	.	.	.	.	.	X	X	.
Alpheus rapax Fabreille	.	.	.	C	C	.	.	.	.
A. ventrosus Milne Edwards	.	.	.	.	.	.	.	X	.
Coralliocaris graminea (Dana)	.	.	.	.	.	.	.	C	X
Concodytes meleagrinae Peters	.	.	.	.	.	.	.	X	.
Hippa adactyla Fabreille	.	X	.	.	.	.	.	.	.
Haplocarinus marsupialis Stimpson	.	.	.	.	.	.	.	A	.
Cryptochirus coralliodytes Heller	.	.	.	.	.	.	.	A	.
Malacostraca: Stomatopoda									
Pseudosquilla ciliata (Fabricus)	.	.	.	C	C	.	.	.	.
Goniodactylus falcatus (Forskål)	.	.	.	.	.	.	.	.	X
G. chiragra (Fabricus)	.	.	.	.	.	.	X	.	.
MOLLUSCA									
Gastropoda: Prosobranchia									
Scissurella sp.	.	.	.	.	.	R	.	.	R
Emarginula peasei Theile	.	.	.	.	.	R	.	.	R
Scutus elegans (Gray)	.	.	.	.	.	R	.	.	.
Diodora singaporensis (Reeve)	.	.	.	.	.	X	X	X	X

List of species	I	II	III	IV	V	VI	VII	VIII	IX
	Environments								
Gastropoda: Prosobranchia (*cont.*)									
Scutellastra pica (Reeve)	.	.	A	.	.	.	.	.	.
Cellana cernica (H. Adams)	.	.	A	.	.	.	.	.	.
Euchelus gemmatus (Gould)	.	.	.	.	.	X	.	.	X
Monodonta australis Lamarck	.	.	C	.	.	.	.	.	.
M. labio Linnaeus	.	.	C	.	.	.	.	.	.
Trochus flammulatus Lamarck	.	.	.	.	.	.	A	C	.
T. maculatus Linnaeus	.	.	.	.	.	.	C	C	.
Clanculus flosculus Fischer	.	.	.	.	.	X	.	.	.
Tectus mauritianus (Gould)	.	.	.	.	.	.	C	.	.
Minolia singaporensis Pilsbry	.	.	.	.	X	.	.	.	.
Gena varia (A. Adams)	.	.	.	.	.	X	.	.	.
Broderipia rosea (Broderip)	.	.	.	.	R	.	.	.	.
Stomatia ivisata (Dufo)	.	.	.	.	X	X	.	.	.
Turbo argyrostomus Linnaeus	.	.	.	.	.	.	C	C	.
T. setosus Gmelin	.	.	X	.	.	.	C	C	.
Leptothyra candida Pease	.	.	.	.	C	C	.	.	.
Phasianella aethiopica Philtipi	.	.	.	.	X	.	.	.	.
Nerita albicilla Linnaeus	X	.	A	C	C	.	.	.	.
N. debilis Dufo	.	.	X	.	.	.	.	.	.
N. textilis Dillwyn	.	.	A	.	.	.	.	.	.
N. plicata Linnaeus	.	.	A	.	.	.	.	.	.
N. polita Linnaeus	.	.	A	.	.	.	.	.	.
N. undata Linnaeus	.	.	X	.	.	.	.	.	.
Smaragdia rangiana (Recluz)	.	.	.	A	A	.	.	.	.
Phenecolepas asperulata	.	.	.	.	X	.	.	.	.
Littorina scabra Linnaeus	A	.	A	.	.	.	.	.	.
L. undulata Gray	A	.	A	.	.	.	.	.	.
Peasiella sp.	.	.	C	.	.	.	.	.	.
Rissoina ambigua Gould	.	.	.	.	X	C	A	X	.
R. cerithiformis (Dunker)	.	.	.	.	.	X	.	.	X
R. media Schwartz	.	.	.	.	X	X	.	.	.
R. obeliscus Recluz	.	.	.	.	.	X	.	.	.
R. plicata A. Adams	.	.	.	.	.	X	A	X	.
Turritella fascialis Menke	.	.	.	.	.	.	.	.	X
Heliacus variegatus (Gmelin)	.	.	.	.	.	X	X	.	.
Architectonica perspectiva (Linnaeus)	.	.	.	.	.	.	.	.	X
Vermetus sp.	.	.	X	.	.	.	.	.	.
Planaxis acutus Krauss	.	.	C	.	.	.	.	.	.
P. sulcatus (Born)	.	.	X	.	.	.	.	.	.
Modulus tectum (Gmelin)	.	.	.	.	.	R	.	.	.
Terebralia palustris (Linnaeus)	C	.	.	X	.	.	.	.	.
Fenella pupoides A. Adams	.	.	.	.	.	.	.	.	A
F. scabra A. Adams	.	.	.	X	X	X	.	.	A
Scaliola arenosa A. Adams	.	.	.	X	X	.	.	.	.
Diala sp.	.	.	.	.	.	.	.	.	R
Obtortio pyrahacme Melvill & Standen	.	.	.	X	.	X	.	.	.
Cerithium articulatum Adams & Reeve	.	.	.	.	X	C	.	.	X
C. (*Rhinoclavis*) *asperum* (Linnaeus)	.	.	.	.	C	C	.	.	X
C. columna Sowerby	.	.	.	.	X	X	.	.	.
C. echinatum	.	.	.	.	.	A	.	.	.
C. (*Rhinoclavis*) *fasciatum* Bruguière	.	.	.	.	.	.	.	.	X
C. morum Lamarck	A	.	A	A	X	.	.	.	.
C. nodulosum Bruguière	.	.	.	.	.	X	.	.	.
C. piperitum Sowerby	.	.	.	.	.	X	.	.	.
C. rostratum Sowerby	.	.	.	X	A	X	.	.	.
Triphora aurea (Hervier)	.	.	.	.	.	.	R	.	X
T. coetiviensis (Melvill)	.	.	.	.	.	.	X	.	.
T. corrugata (Hinds)	.	.	.	.	.	.	X	.	.
T. incisa (Pease)	.	.	.	.	.	.	X	.	.
T. monilifera (Hinds)	.	.	.	.	.	X	C	X	.
T. rubra (Hinds)	.	.	.	.	X	X	C	.	.

List of species	Environments								
	I	II	III	IV	V	VI	VII	VIII	IX
Gastropoda: Prosobranchia (*cont.*)									
Eulima labiosa Sowerby	.	.	.	.	X	.	X	.	.
Melanella robillardiana (Pilsbry)	.	.	.	.	.	.	X	.	.
Oscilla tornata Melvill	.	.	.	X	.	.	.	.	R
Odostomia zaleuca Melvill	.	.	.	X	.	R	.	.	.
Syrnola aperanta Melvill	.	.	.	X	X	.	.	.	R
Turbonilla basilica Melvill	.	.	.	.	.	R	.	.	.
Otopleura mitralis A. Adams	.	.	.	.	.	R	.	.	.
Pyramidella maculosa Lamarck	.	.	.	.	.	A	.	.	X
P. terebellum (Maller)	.	.	.	.	.	C	.	.	.
Fossarus lamellosus Montrouzier	.	.	C	.	.	.	X	.	.
Vanikoro cancellata Lamarck	.	.	.	.	.	X	.	.	.
Amathea conica (Schumacher)	.	.	.	.	X	X	X	.	.
Amalthea lissa (Smith)	.	.	.	.	.	.	.	.	X
Cheilea equestris (Linnaeus)	.	.	R	.	.	.	X	.	.
Thyca crystallina Gould	.	.	.	.	X	.	.	.	.
Xenophora solariodes (Reeve)	.	.	.	.	.	.	.	.	X
Terebellum terebellum (Linnaeus)	.	.	.	.	.	.	.	.	X
Strombus gibberulus (Linnaeus)	.	.	.	.	A	X	.	.	X
S. luhuanus Linnaeus	.	.	.	.	X	X	.	.	.
S. mutabilis Swainson	.	.	.	.	X	.	.	.	.
S. plicata Lamarck	.	.	.	.	.	.	.	.	X
Lambis crocata Link	.	.	.	.	.	R	.	.	.
Polynices mammilla (Linnaeus)	.	.	.	.	.	C	.	.	X
Natica marochiensis (Gmelin)	.	.	.	C	X	.	.	.	.
N. onca (Röding)	.	.	.	.	X	X	.	.	.
N. simiae (Deshayes)	.	.	.	.	.	.	.	.	X
Erato sulcifera Sowerby	.	.	.	.	.	.	.	.	X
Trivia oryza Lamarck	.	.	.	.	.	.	C	.	X
C. annulus Linnaeus	.	.	.	C	A	X	X	.	.
C. carneola (Linnaeus)	.	.	.	.	.	.	.	.	.
C. caputserpentis Linnaeus	.	.	.	.	.	.	C	X	.
C. fimbriata Gmelin	.	.	.	.	.	.	C	X	.
C. helvola Linnaeus	.	.	.	.	R	C	X	.	.
C. histrio Gemlin	.	.	.	.	.	.	A	X	.
C. isabella Linnaeus	.	.	.	.	.	.	X	.	.
C. lynx Linnaeus	.	.	.	.	.	.	X	.	.
C. moneta Linnaeus	.	.	.	X	C	X	C	.	.
C. scurra Gmelin	.	.	.	.	.	.	X	X	.
C. teres Gmelin	.	.	.	.	X	.	X	.	.
C. tigris Linnaeus	.	.	.	.	C	.	.	.	.
C. vitellus Linnaeus	.	.	.	.	.	X	X	.	.
Apollon bituberculare (Lamarck)	.	.	.	.	.	.	.	.	R
A. pusillus (Broderip)	.	.	.	.	.	.	.	X	.
Cymatium tuberosus (Lamarck)	.	.	.	.	.	.	.	.	X
C. pileare (Linnaeus)	.	.	.	.	X	.	C	.	X
Bursa bufonia (Gmelin)	.	.	.	.	.	X	.	.	.
B. granularis (Roding)	.	.	.	.	.	.	A	.	.
B. rubeta (Linnaeus)	.	.	.	.	.	.	.	X	.
Murex adustus Lamarck	.	.	.	.	.	.	.	.	X
Chicoreus incarnatus (Roding)	.	.	.	.	.	X	.	.	.
Maculotriton digitalis A. Adams	.	.	.	.	.	.	A	.	.
Morula anaxeres (Duclos)	.	.	C	.	.	.	.	.	.
M. granulata (Duclos)	.	.	A	.	.	.	X	.	.
M. uva (Rodina)	.	.	C	.	.	.	X	.	.
Drupa clathrata Lamarck	.	.	X	.	.	.	.	.	.
D. cornus (Roding)	.	.	.	.	.	X	.	.	X
D. margariticola (Broderip)	.	.	.	X	C	C	.	.	.
D. morum Roding	.	.	C	.	.	.	C	.	.
D. ochrostoma (Blainville)	.	.	.	.	C	X	X	X	.
D. ricinus (Linnaeus)	.	.	C	.	.	X	A	.	.
D. spathulifera (Blainville)	.	.	.	.	.	.	R	.	.

List of species	Environments I	II	III	IV	V	VI	VII	VIII	IX
Gastropoda: Prosobranchia (*cont.*)									
Nassa sertum (Bruguière)	.	.	X	.	.	.	X	.	.
Thais aculeatum Deshayes	.	.	X	.	.	.	X	.	.
T. armigera (Lamarck)	.	.	C	.	.	.	X	.	.
T. echinulata (Lamarck)	.	.	.	.	.	.	.	X	.
Purpura rudolphi (Lamarck)	.	.	C	.	.	.	.	.	.
Coralliophilia violacea (Kiener)	.	.	.	.	.	X	.	X	.
Quoyala monodonta (Quoy & Gaimard)	.	.	.	.	.	X	.	X	.
Pyrene azora (Duclos)	.	.	.	C	A	X	C	.	.
P. cincinnata (Martens)	.	.	.	.	.	R	.	.	R
P. flava (Bruguière)	.	.	.	.	.	.	.	.	R
P. troglydytes (Souvier)	.	.	.	.	.	C	.	.	C
Columbella turturina Lamarck	.	.	.	.	.	C	X	.	.
Phos cyanostoma (A. Adams)	.	.	.	.	.	.	.	.	X
P. roseatus Hinds	.	.	.	.	.	.	.	.	X
Engina lineata (Reeve)	.	.	.	.	.	.	X	.	.
Nassarius albescens (Dunker)	.	.	.	A	A	C	.	X	C
N. arcularis (Linnaeus)	.	.	.	C	C	.	.	.	C
N. coronatus (Bruguière)	.	.	.	.	.	.	.	.	X
N. elegans (Kiener)	.	.	.	.	.	.	.	.	X
Cantharus undosus (Linnaeus)	.	.	.	.	.	.	.	C	.
Pleuroploca filamentosa (Lamarck)	.	.	.	.	.	.	X	X	.
P. trapezium (Linnaeus)	.	.	.	.	X	C	X	.	.
Latirus craticulatus (Lamarck)	.	.	.	.	.	.	R	.	.
L. polygonus (Gmelin)	.	.	.	.	.	X	.	.	.
Peristernia nassatula (Lamarck)	.	.	.	.	X	X	A	.	.
Leucozonia smaragdulus (Linnaeus)	.	.	.	.	.	.	X	X	.
Vasum turbinellus (Linnaeus)	.	.	.	.	.	X	C	C	.
Ancilla ampla (Gmelin)	.	.	.	.	.	.	.	.	X
Olivia episcopalis Lamarck	.	.	.	.	.	X	.	.	.
Oliva erythrostoma Menschen	.	.	.	.	.	C	.	.	X
O. sidelia Duclos	.	.	.	.	.	.	.	.	C
Vexillum deshayesi (Reeve)	.	.	.	R	.	.	.	.	X
V. exasperatum (Gmelin)	.	.	.	.	.	.	.	.	X
V. intermedium (Kiener)	.	.	.	.	.	.	.	.	X
V. sanguisugum (Linnaeus)	.	.	.	.	.	X	.	.	X
Mitra cucumerina Lamarck	.	.	X	.	.	.	.	.	.
Cancilla clathrus (Gmelin)	.	.	.	.	.	.	.	.	X
Strigatella paupericula (Linnaeus)	.	.	X	.	.	.	.	.	.
Lophiotoma acuta (Perry)	.	.	.	.	.	.	.	.	X
Xenuroturris cingulifera (Lamarck)	.	.	.	.	.	.	.	.	X
Cythara euselma Melvill & Standen	.	.	.	.	.	.	.	.	X
Clathurella euzonata (Hervier)	.	.	.	.	.	.	.	.	X
Conus arenatus Linnaeus	.	.	.	.	.	C	.	.	.
C. betulinus Linnaeus	.	.	.	.	R	.	.	.	.
C. catus Hwass	.	.	.	.	.	.	X	.	.
C. chaldeus (Röding)	.	.	X	.	.	.	X	.	.
C. coronatus Gmelin	.	.	.	.	.	C	X	.	.
C. ebraeus Linnaeus	.	.	C	.	.	.	A	.	.
C. flavidus Lamarck	.	.	.	.	X	X	.	.	.
C. imperialis Linnaeus	.	.	.	.	.	R	.	.	.
C. litteratus Linnaeus	.	.	.	.	C	X	.	.	.
C. lividus Hwass	.	.	.	.	X	X	A	X	.
C. miles Linnaeus	.	.	.	.	.	.	X	.	.
C. nussatella Linnaeus	.	.	.	.	.	R	.	.	.
C. textile Linnaeus	.	.	.	.	.	.	C	X	.
C. rattus Hwass	.	.	.	.	.	.	C	.	.
C. tendeneus Hwass	.	.	.	.	.	.	R	R	.
C. tessulatus Born	.	.	.	.	C	A	.	X	.
C. vexillum Born	.	.	.	.	.	.	X	.	.
C. virgo Linnaeus	.	.	.	.	.	X	X	.	.
Terebra affinis Gray	.	.	.	.	.	A	.	.	X

List of species	Environments I	II	III	IV	V	VI	VII	VIII	IX
Gastropoda: Prosobranchia (*cont.*)									
T. babylonia Lamarck	.	.	.	.	.	X	.	.	X
T. cerithina Lamarck	.	.	.	.	.	R	.	.	.
T. crenulata (Linnaeus)	.	.	.	.	.	X	.	.	.
T. dimidiata (Linnaeus)	.	.	.	.	.	X	.	.	X
T. laevigata Gray	.	.	.	.	.	R	.	.	X
T. muscaria Lamarck	.	.	.	.	.	R	.	.	.
T. pertusa Born	.	.	.	.	.	.	.	.	C
T. subulata (Linnaeus)	.	.	.	.	X	X	.	.	.
Gastropoda: Opisthobranchia									
Bulla ampulla (Linnaeus)	.	.	.	.	C	C	.	.	.
Atys cylindricus (Helbling)	.	.	.	.	.	X	.	.	.
Pupa sulcata (Gmelin)	.	.	.	.	.	X	.	.	.
Umbraculum umbraculum (Humphrey)	.	R	.	.	R	.	.	.	.
Hydatina physis (Linnaeus)	.	.	.	.	.	X	.	.	.
Dolabella auricularia (Lightfoot)	.	.	.	.	C	.	.	.	.
Julia borbonica (Deshayes)	.	.	.	.	.	R	.	.	.
BIVALVIA									
Nucula sp.	.	.	.	.	.	R	.	.	R
Arca avellana Lamarck	.	.	.	X	.	.	X	X	.
A. navicularis Bruguière	.	.	.	.	.	.	.	.	C
A. symmetrica Reeve	.	.	.	.	.	.	.	.	R
A. plicata Dillwyn	.	.	.	.	C	C	C	C	.
Anadara antiguata Linnaeus	.	.	.	X	C	.	.	.	.
A. clathrata (Reeve)	.	.	.	.	.	.	.	.	A
A. uropigmelana (Bory)	.	.	.	R	.	.	.	.	.
Barbatia fusca Bruguière	.	.	.	.	.	.	.	C	C
B. helblingi Bruguière	.	.	.	.	.	.	X	C	.
B. tenella (Reeve)	.	.	.	.	.	.	.	.	X
Cucullaea granulosa Jonas	.	.	.	.	.	.	.	.	R
Glycimeris hoylei Melvill & Standen	.	.	.	.	.	.	.	.	R
G. tenuicostatus Reeve	.	.	.	.	.	.	.	.	R
Brachiodontes variabilis Krauss	.	.	.	A	.	.	.	.	.
Musculus sp.	.	.	.	.	.	.	.	.	C
Modiolus auriculatus (Krauss)	.	.	X	.	X	X	C	.	.
Septifer bilocularis (Linnaeus)	.	.	X	.	.	.	.	.	.
Botula cinnamomea (Lamarck)	.	.	.	.	.	.	.	X	A
Lithophaga teres Phillipi	.	.	.	.	.	.	.	X	.
Leiosolenus obesa Phillipi	.	.	.	.	.	.	X	X	.
Isognomon dentifer Krauss	.	.	A	.	.	.	.	.	.
Vulsella spongiarum Lamarck	.	.	.	.	.	.	.	.	R
Electroma alacorvi (Dillwyn)	.	.	.	.	.	X	.	X	.
Pinctada margaritifera (Linnaeus)	.	.	.	.	.	X	Z	C	X
Pinna muricata Linnaeus	.	.	.	.	C	.	.	.	.
Streptopinna saccata (Linnaeus)	.	.	.	.	.	.	.	R	.
Chlamys cuneolus (Reeve)	.	.	.	.	.	.	R	.	.
C. dringii (Reeve)	.	.	.	.	.	.	.	X	.
C. histrionica (Gmelin)	.	.	.	.	.	.	R	.	.
C. irregularis (Sowerby)	.	.	.	.	.	.	.	.	C
C. lemniscatus (Reeve)	.	.	.	.	.	X	.	X	.
C. senatorius (Gmelin)	.	.	.	.	.	.	.	X	A
Lyropecten noduliferus (Sowerby)	.	.	.	.	.	.	.	.	R
Decatopecten plica (Linnaeus)	.	.	.	.	.	.	.	.	R
Gloripallium pallium (Linnaeus)	.	.	.	.	.	.	.	X	.
Plicatula chinensis Morch	.	.	.	.	.	.	.	X	X
Spondylus hystrix Roding	.	.	.	.	.	.	.	X	.
Lima fragilis Gmelin	.	.	.	.	.	X	.	.	.
Ctenoides annulata Lamarck	.	.	.	.	.	.	.	.	X
Pycnodonte hyotis (Linnaeus)	.	.	.	.	.	.	.	C	.
Crassostrea cucullata (Born)	X	.	A	X	X	.	.	.	.

List of species	Environments I	II	III	IV	V	VI	VII	VIII	IX
BIVALVIA (*cont.*)									
Ostrea cristagalli Linnaeus	.	.	.	.	X	.	.	.	.
O. folium Linnaeus	.	.	.	.	.	.	.	.	X
O. numisma Lamarck	.	.	.	.	X	C	C	C	.
Cardita variegata Bruguière	.	.	.	.	.	X	C	X	X
Carditella sp.	.	.	.	.	.	X	.	.	X
Trapezium oblongum (Linnaeus)	.	.	.	.	.	.	.	X	.
Coralliophaga decussata (Reeve)	.	.	.	.	.	.	.	.	X
Diplodonta lateralis Smith	.	.	.	.	.	.	.	.	R
Divaricella ornata Reeve	.	.	.	.	.	.	.	.	R
Anodontia edentula Linnaeus	.	.	.	X	C	.	.	.	.
Ctena divergens (Philippi)	X	.	.	X	A	.	.	.	X
Codakia interrupta (Lamarck)	.	.	.	.	.	.	.	.	R
C. punctata (Linnaeus)	.	.	.	.	A	C	.	.	X
C. tigerina (Linnaeus)	.	.	.	.	A	C	.	.	X
Erycina sp.	.	.	.	X	.	.	.	.	X
Kellia revimentalis Melvill	.	.	.	.	.	.	.	.	R
Galleoma argentea (Deshayes)	.	.	.	.	.	.	.	.	R
Scintilla ambigua (Deshayes)	.	.	.	.	.	.	X	.	.
Chama aspersa Reeve	.	.	.	.	.	.	X	.	.
Laevicardium australe (Sowerby)	.	.	.	.	.	.	.	.	X
L. biradiatum (Bruguière)	.	.	.	.	.	.	.	.	C
Fragum fragum (Linnaeus)	.	.	.	.	.	A	.	.	.
Hemicardia hemicardium (Linnaeus)	.	.	.	.	.	.	.	.	C
Trachycardium elongatum (Bruguière)	.	.	.	.	.	.	.	.	R
T. leucostomum (Born)	.	.	.	.	X	.	.	.	.
Parvicardium sueziense (Issel)	.	.	.	X	A	A	.	.	A
Tridacna maxima (Roding)	.	.	.	.	.	.	.	X	.
T. squamosa Lamarck	.	.	.	.	.	X	X	X	.
Lioconcha ornata (Dillwyn)	.	.	.	.	.	.	.	.	X
Lioconcha sp.	.	.	.	.	.	.	.	.	.
Gafrarium dispar (Dillwyn)	.	.	.	.	X	X	.	.	X
Gafrarium pectinatum (Linnaeus)	.	.	.	C	.	.	.	.	.
G. tumidum (Roding)	X	.	.	A	.	.	.	.	.
Pitar affinis (Gmelin)	.	.	.	.	.	.	.	.	X
P. obliquata (Hanley)	.	.	.	.	X	X	.	.	X
Amiantis grata (Deshayes)	.	.	.	.	.	.	.	.	X
Austrodosinia histrio (Gmelin)	.	.	.	.	.	.	.	.	C
Antigona lamellaris (Schumacher)	.	.	.	.	.	.	.	.	X
Periglypta puerpera (Linnaeus)	.	.	.	.	.	.	.	.	X
Tapes litteratus Linnaeus	.	.	.	.	X	.	.	.	R
Timoclea marica (Linnaeus)	.	.	.	.	.	C	.	.	X
Notirus macrophyllus (Deshayes)	.	.	.	X	.	X	.	X	.
Atactodea glabrata Gmelin	.	A	.	.	X	.	.	.	.
Mactra achatina Dillwyn	.	.	.	.	.	.	.	.	X
M. lilacea Lamarck	.	.	.	.	.	.	.	.	R
Ervilia bisculpta (Gould)	.	.	.	.	A	.	.	.	A
Donax faba (Gmelin)	.	A	.	.	.	.	.	.	.
D. cuneatus Linnaeus	.	A	.	.	.	.	.	.	.
Asaphis deflorata Linnaeus	.	.	.	.	X	.	.	.	.
Psammotea radiata (Deshayes)	.	.	.	X	.	.	.	.	.
Gari weinkauffi (Crosse)	.	.	.	.	.	.	.	.	R
Psammocola castrensis (Spengler)	.	.	.	.	.	.	.	.	X
Grammotomya pulcherrima (Deshayes)	.	.	.	.	.	.	.	.	R
Iacra seychellarum A. Adams	.	.	.	.	.	.	.	.	X
Leptomya rostrata Hanley	.	.	.	.	X	.	.	.	X
Pinguitellina robusta (Hanley)	.	.	.	.	C	C	.	.	C
Scutarcopagia linguafelis (Linnaeus)	.	.	.	.	.	.	.	.	R
S. scobinata Linnaeus	.	.	.	.	.	X	.	.	.
Jactellina clathrata (Deshayes)	.	.	.	.	.	C	.	.	.
Scissulina dispar (Conrad)	.	.	.	.	C	C	.	.	.
Clathrotellina carnicolor (Hanley)	.	.	.	.	.	.	.	.	X

List of species	Environments							
	I	II	III	V	VI	VI	VII	VIII	IX
BIVALVIA (*cont.*)									
Pharaonella rostrata (Linnaeus)	.	.	.	.	.	X	.	.	.
Cadella roblini (Sowerby)	. .	.	.	.	C	C	.	.	X
C. semen (Hanley)	.	.	.	.	C	C	.	.	C
Quadrans gargadia (Linnaeus)	.	.	.	.	.	C	.	.	X
Q. spinosa (Hanley)	.	.	.	.	.	.	.	.	X
Quidnipagus palatam Iredale	X	.	.	A	A	.	.	.	.
Tellina fabrefacta Pilsbry	.	.	.	.	.	.	.	.	X
Tellinella crucigera (Lamarck)	.	.	.	.	.	A	.	.	X
T. staurella (Lamarck)	.	.	.	.	C	C	.	.	X
T. virgata (Linnaeus)	.	.	.	.	.	.	.	.	.
Corbula subquadrata Melvill	.	.	.	.	.	.	.	.	C
Gastrochaena cunieformis (Spengler)	.		.	.	.	.	.	X	X
MOLLUSCA: AMPHINEURA									
Acanthopleura brevispinosa (Sowerby)	.	.	C	.	.	.	.	.	.
BRACHIPODA									
Lingula sp.	.	.	.	.	.	.	.	.	R
ECHINODERMATA									
CRINOIDEA									
Comanthus parvicirra (Müller)	.	.	.	.	.	.	C	X	.
Ophiuroidea									
Astroboa clavata (Lyman)	.	.	.	.	.	.	.	R	.
Ophiocoma brevipes Peters	.	.	C	.	A	C	X	.	.
O. erinaceus Müller & Troschel	.	.	.	.	.	X	A	A	.
O. insularia Lyman	.	.	.	.	.	.	.	C	X
O. scolopendrina (Lamarck)	.	.	.	.	X	.	.	.	.
O. valenciae Müller & Troschel	.	.	.	.	C	C	.	.	
Ophiothela tigris Lyman	.	.	.	.	.	.	.	C	C
Ophiothrix trilineata Lutken	.	.	.	.	.	.	.	C	C
Ophioplocus imbricata Müller & Troschel	.	.	.	.	X	.	C	.	.
Asteroidea									
Culcita schmideliana Retz	.	.	.	.	R	.	.	.	.
Protoreaster linckii (Blainville)	.	.	.	.	X	.	.	.	.
Nardoa variolata (Lamarck)	.	.	.	.	.	.	.	X	.
Nardoa sp.	.	.	.	.	.	X	.	.	.
Linckia multifora (Lamarck)	.	.	.	.	A	X	X	.	.
Ophidaster hemprichi Müller & Troschel	.	.	.	.	.	.	.	X	.
Asterina burtoni Gray	.	.	.	.	.	.	X	.	.
Mithrodia clavigera (Lamarck)	.	.	.	.	.	.	.	R	.
Echinoidea									
Prionocidaris baculosa (Lamarck)	.	.	.	.	.	.	.	R	.
P. verticillata (Lamarck)	.	.	.	.	.	.	.	A	C
Phyllacanthus imperialis (Lamarck)	.	.	.	.	.	.	.	A	.
Diadema setosum (Leske)	.	.	.	.	R	C	C	C	X
Astropyga radiata (Leske)	.	.	.	.	.	.	.	.	X
Stomopneustes variolaris (Lamarck)	.	.	.	.	.	X	.	.	.
Temnotrema siamense Mortensen	.	.	.	.	.	.	.	.	R
Toxoneustes gratilla (Linnaeus)	.	.	.	.	C	C	.	.	R
Tripneustes pileolus (Lamarck)	.	.	.	.	C	C	.	.	.
Echinometra matthai (Blainville)	.	.	.	.	C	C	C	X	.
Heterocentrotus mammillatus Linnaeus	.	.	.	.	.	.	.	X	.
Echinoneus cyclostomus Leske	.	.	.	.	.	.	X	.	.
Clypeaster reticulatus (Linnaeus)	.	.	.	.	.	.	.	.	C
Laganum depressum Lesson	.	.	.	.	.	.	.	.	X
Maretia planulata (Lamarck)	.	.	.	.	.	.	.	.	X
Pseudomaretia alta (Agassiz)	.	.	.	.	.	X	.	.	X
Melatia spatagus (Linnaeus)	.	.	.	.	.	X	.	.	X

List of species	Environments I	II	III	IV	V	VI	VII	VIII	IX
Holothuroidea									
Synapta maculata (Chamisso & Ensenhardt)	.	.	.	.	X	X	.	.	.
Polyplectona sp.	.	.	.	.	.	.	.	X	.
Stichopus chloronotus Brandt	.	.	.	.	C	A	.	.	.
Actinopyga mauritiana (Quoy & Gaimard)	.	.	.	.	.	.	.	X	.
Actinopyga sp.	.	.	.	.	C	X	.	.	.
Microthele nobilis (Selenka)	.	.	.	.	.	.	.	.	R
Holothuria atra (Jager)	.	.	.	.	A	C	.	X	X
H. arenicola Semper	.	.	.	.	X	C	C	.	.
H. cinerascans (Brandt)	.	.	.	.	.	.	X	.	.
H. monocaria Lesson	.	.	.	.	.	X	C	.	.
H. scabra Jager	.	.	.	.	.	.	.	.	X
Afrocucumis africana (Semper)	.	.	.	.	.	.	A	.	.

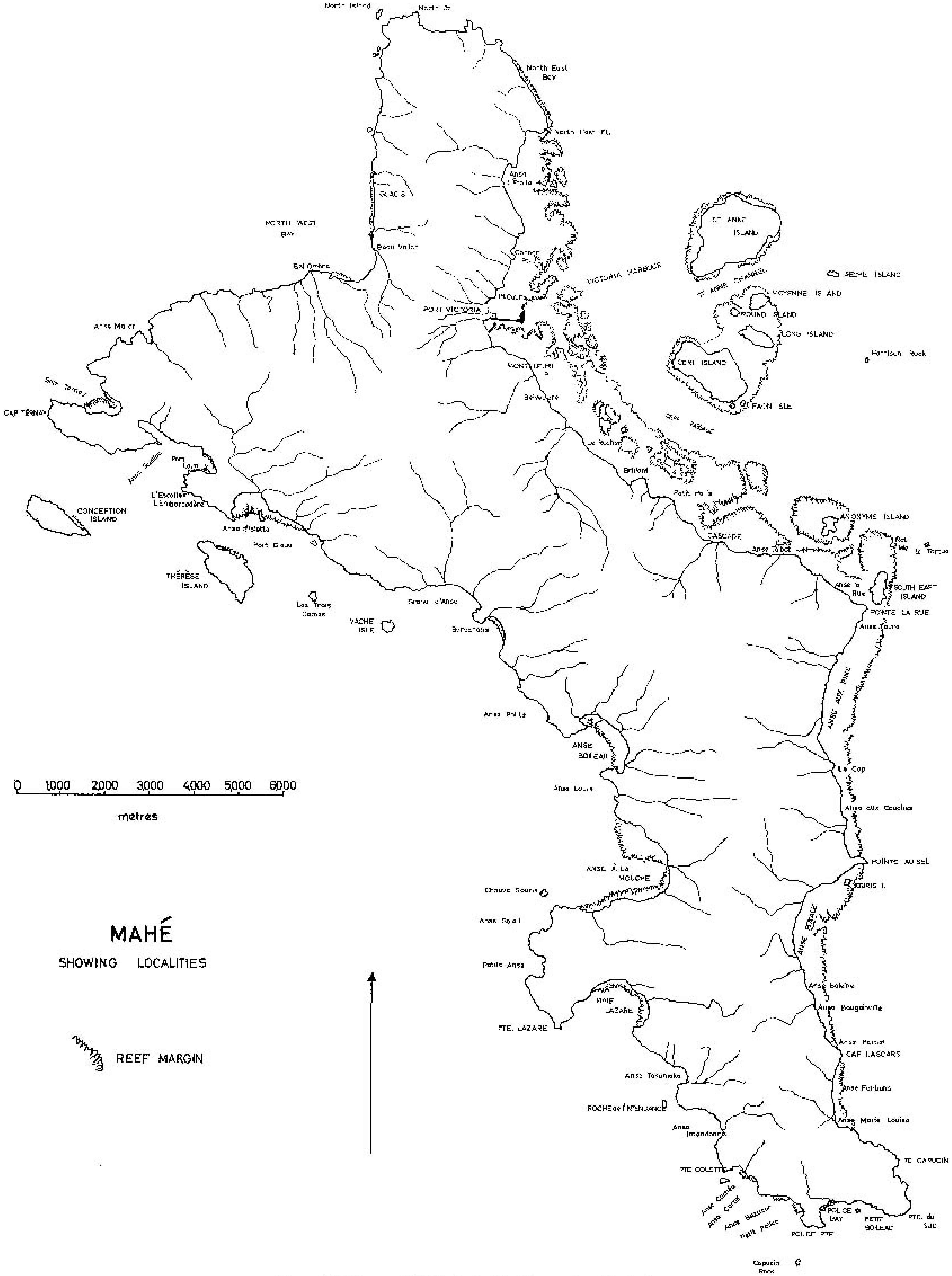

Figure 2. Sketch map of Mahé showing localities mentioned in the text.

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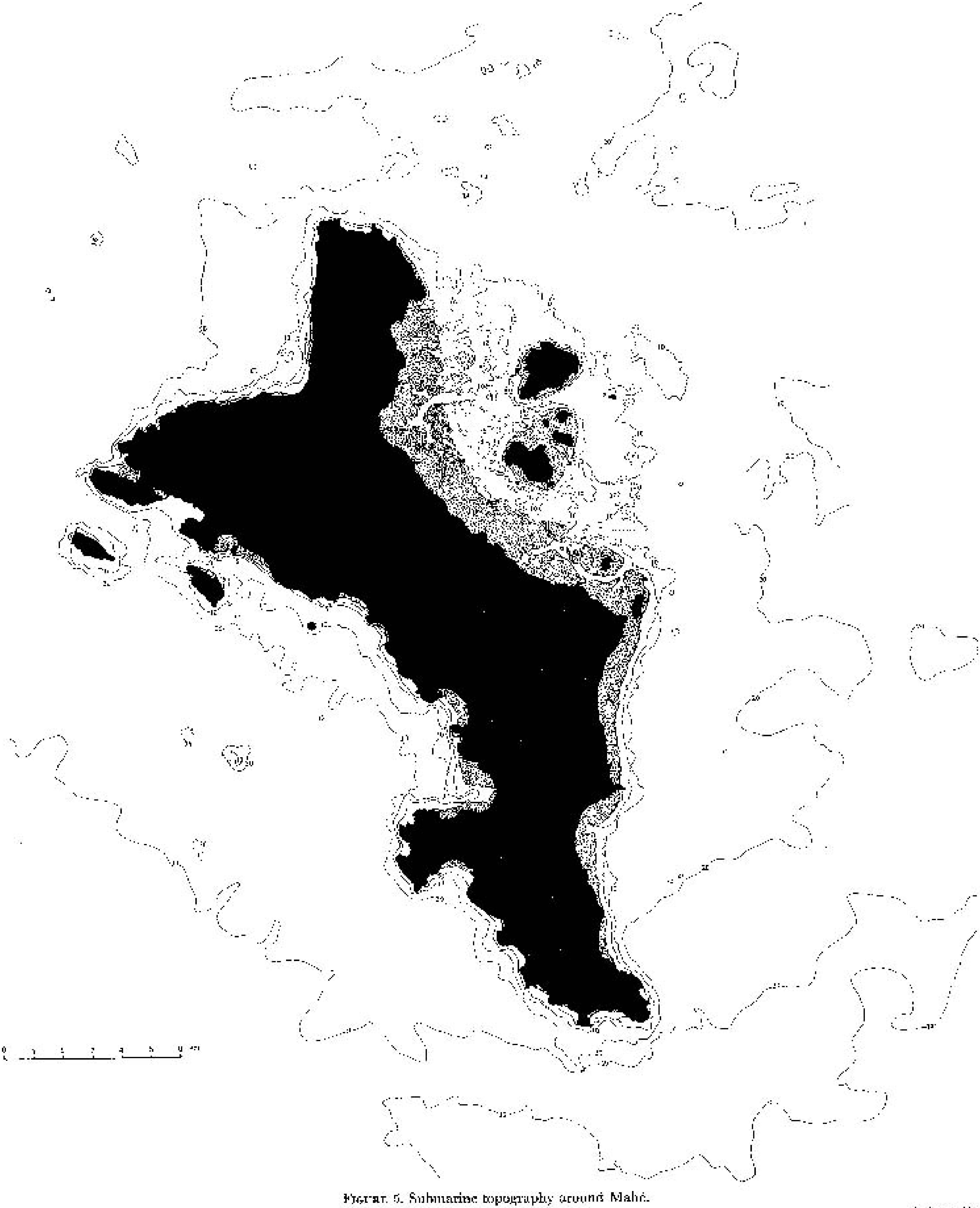

Figure 5. Submarine topography around Mahé.

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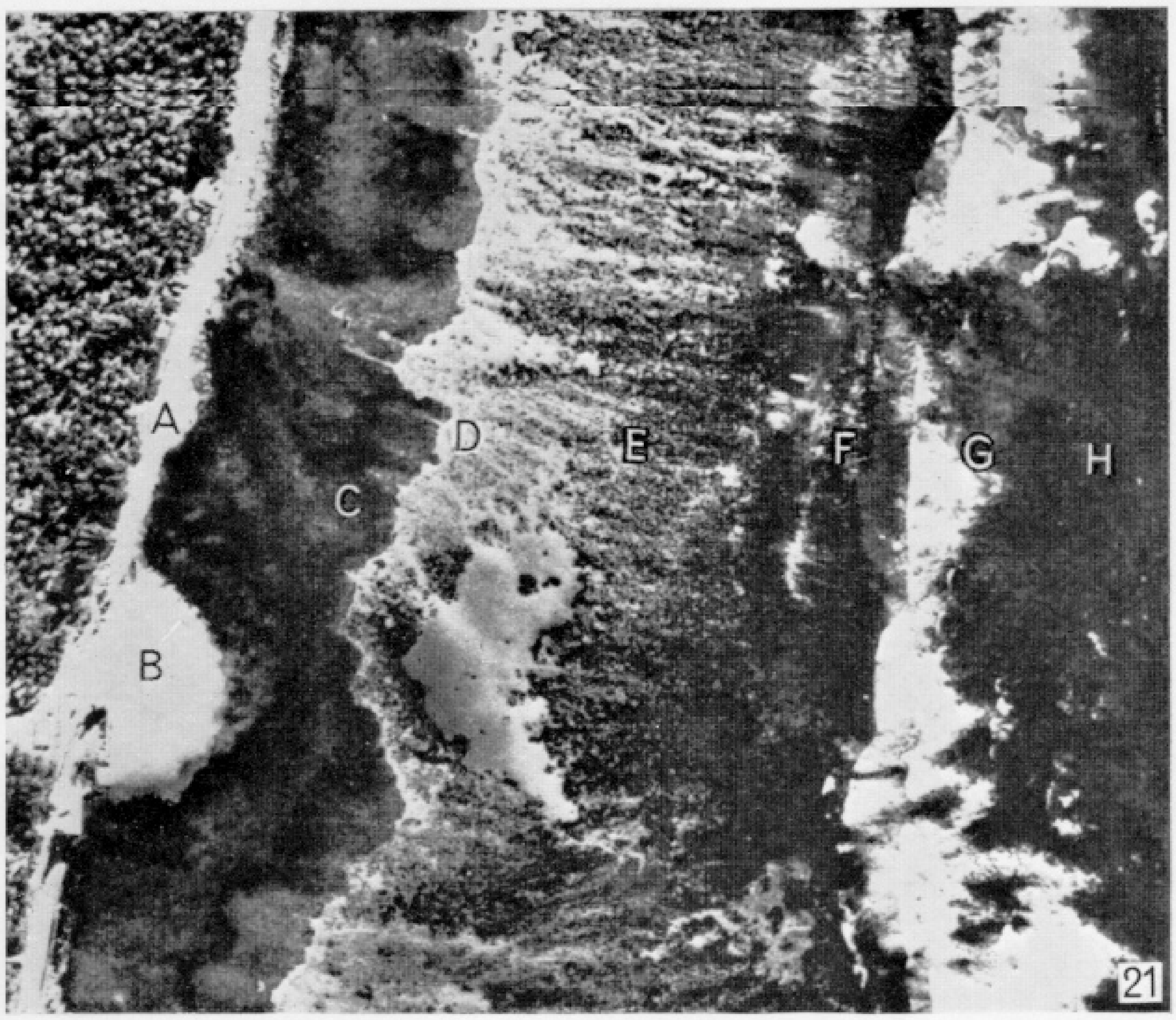
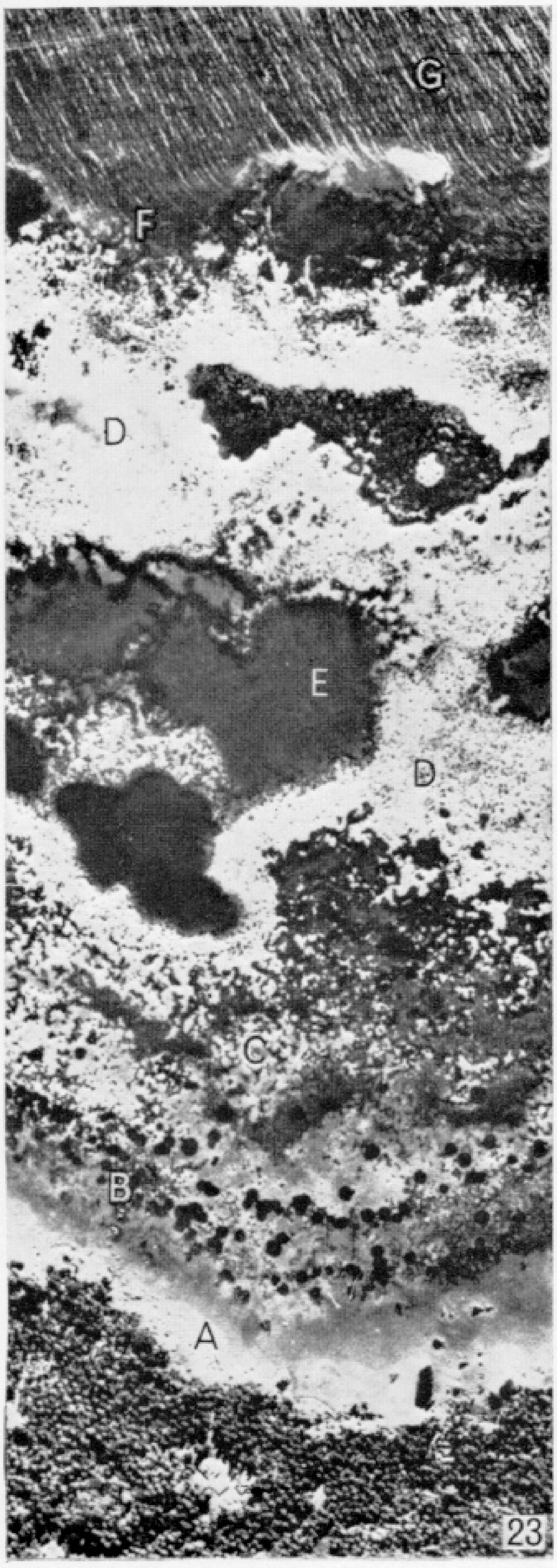




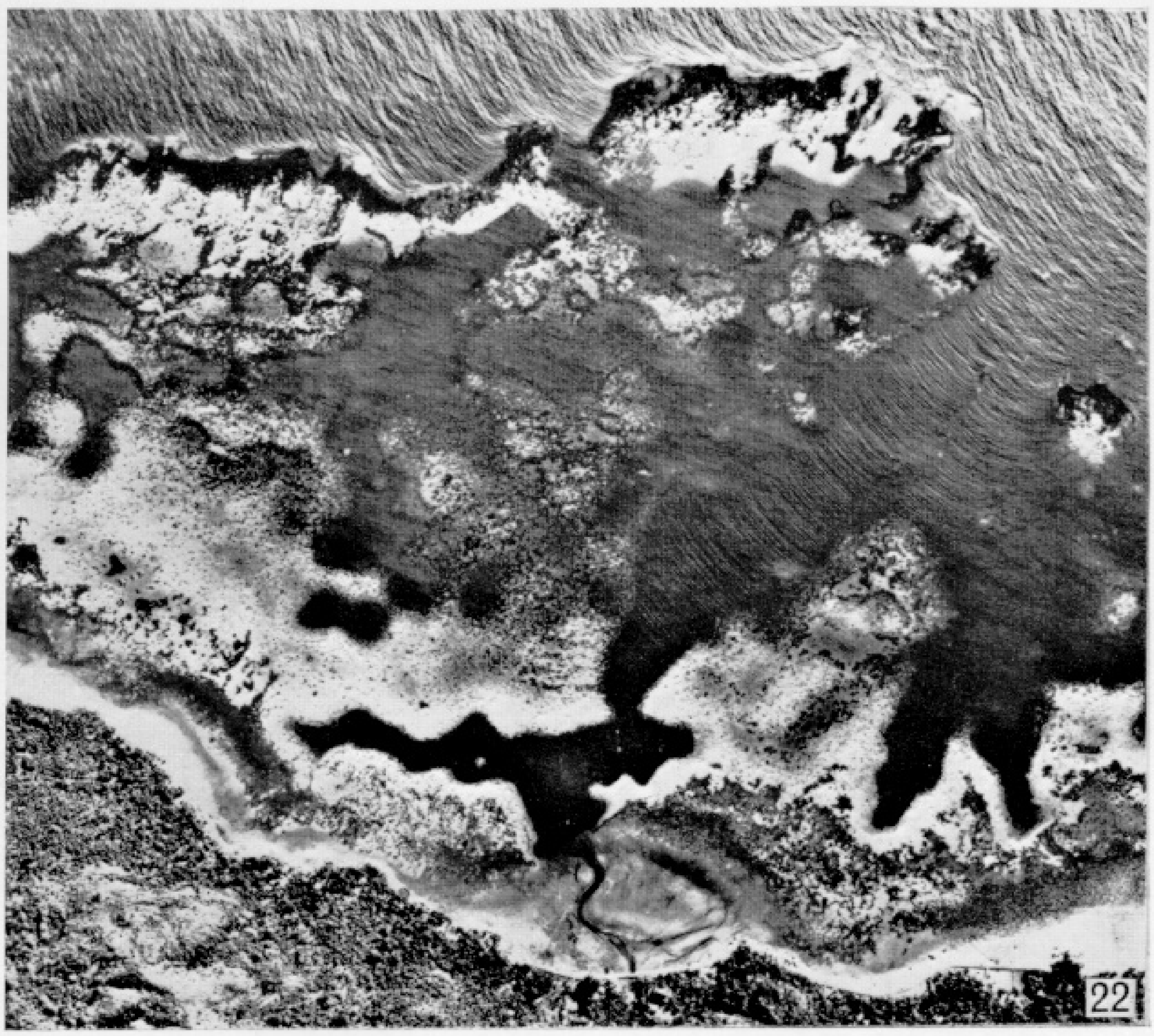


FIGURE 21. Aerial view of the reef flat at Anse aux Pins Village with reef zones indicated. *A* = Beach; *B* = delta spread from incoming stream; *C* = *Thalassia* beds with well marked seaward edges; *D* = fairly open sand; *E* = cobble ridges normal to the reef edge with interdigitating sands; *F* = algal ridge; *G* = Reef edge with strong surf; *H* = Reef front.

FIGURE 22. Aerial view of the reef flat at Cascade showing the large embayment, channels and pools associated with an incoming freshwater stream.

FIGURE 23. Enlarged aerial view of the sheltered reef flat near Brillant showing zonation. *A* = *Uca*/*Gafrarium tumidum* community, ex-mangrove fringes; *B* = belt of the marine angiosperm *Enhalus acoroides* (black patches) in surrounding Thalassia; *C* = *Thalassia* beds; *D* = open sands with occasional coral colonies and *Sargassum* covered masses; *E* = deeper enclosed pools lined with *Porites*; *F* = poorly developed algal ridge and reef edge with little surf; *G* = Cerf Passage.

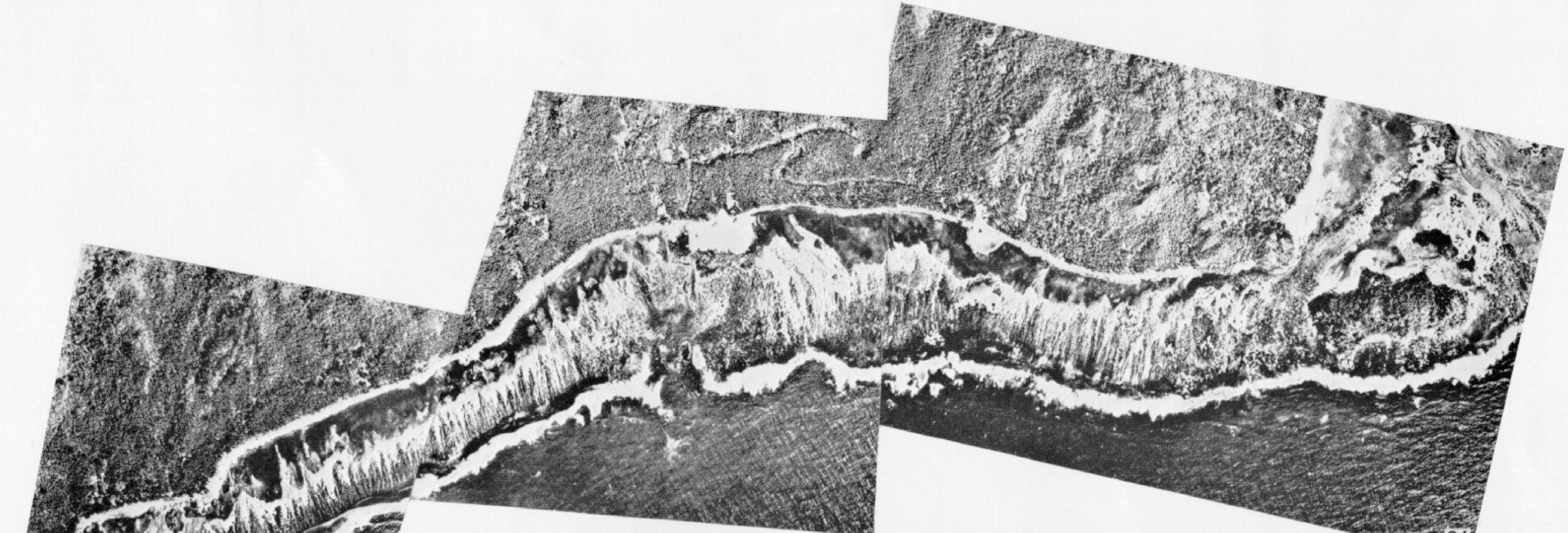
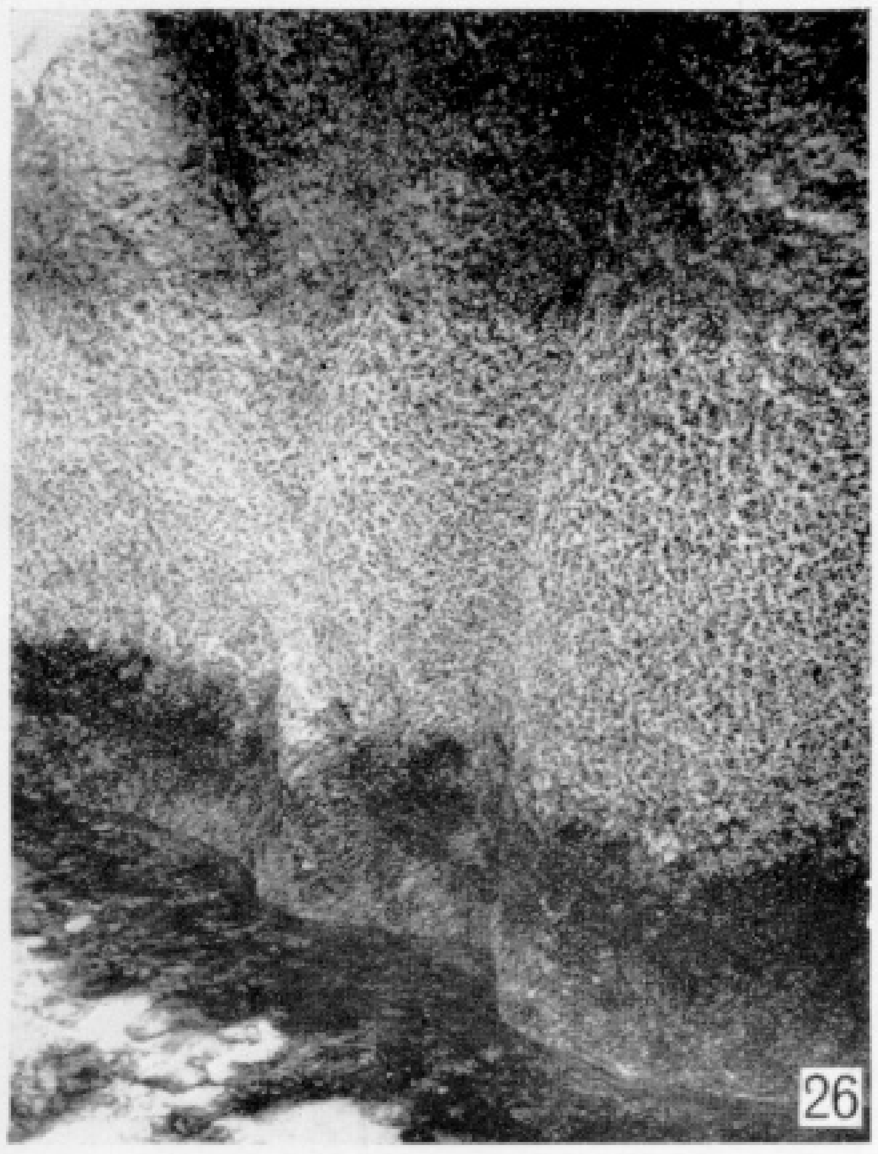
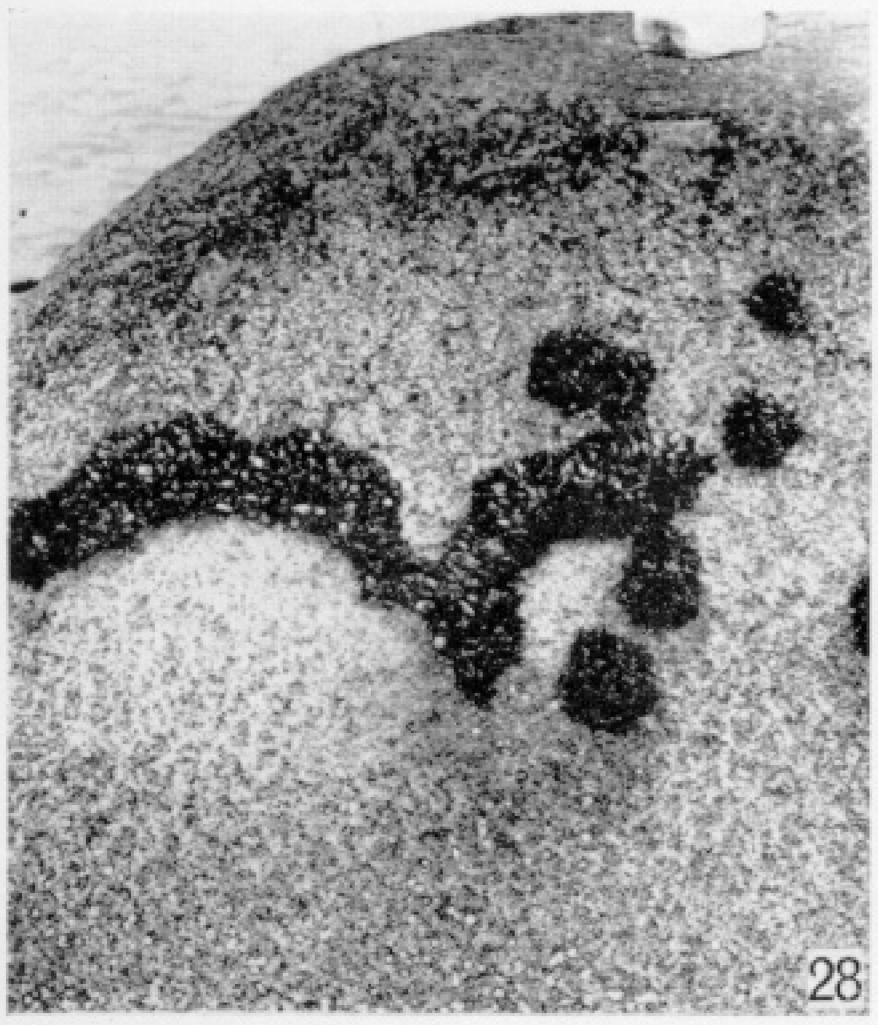
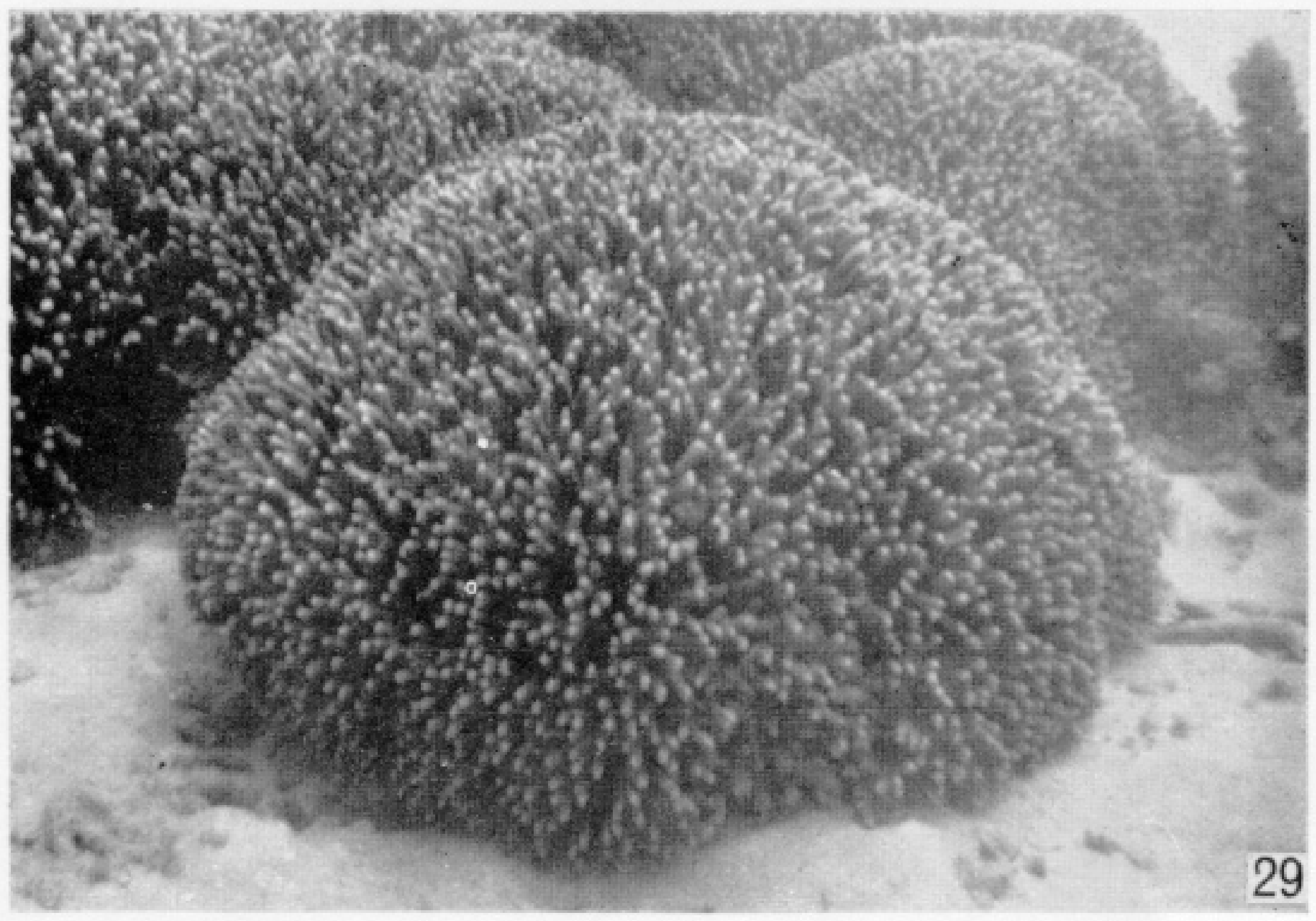


FIGURE 24. Aerial view of the entire windward fringing reef at Anse aux Pins, showing the attenuation of zones at each end, the cobble ridges alined normal to the reef edge and the relation of the reef pass to incoming streams. Length of reef = 5·6 km.

FIGURE 25. Aerial view of Anse Royale reef. Note the large deep pass opposite a stream mouth, the *Thalassia* beds restricted to small patches, the incipient spur and groove formation off the reef front and the arcuate arrangement of the cobble ridges around the reef pass.







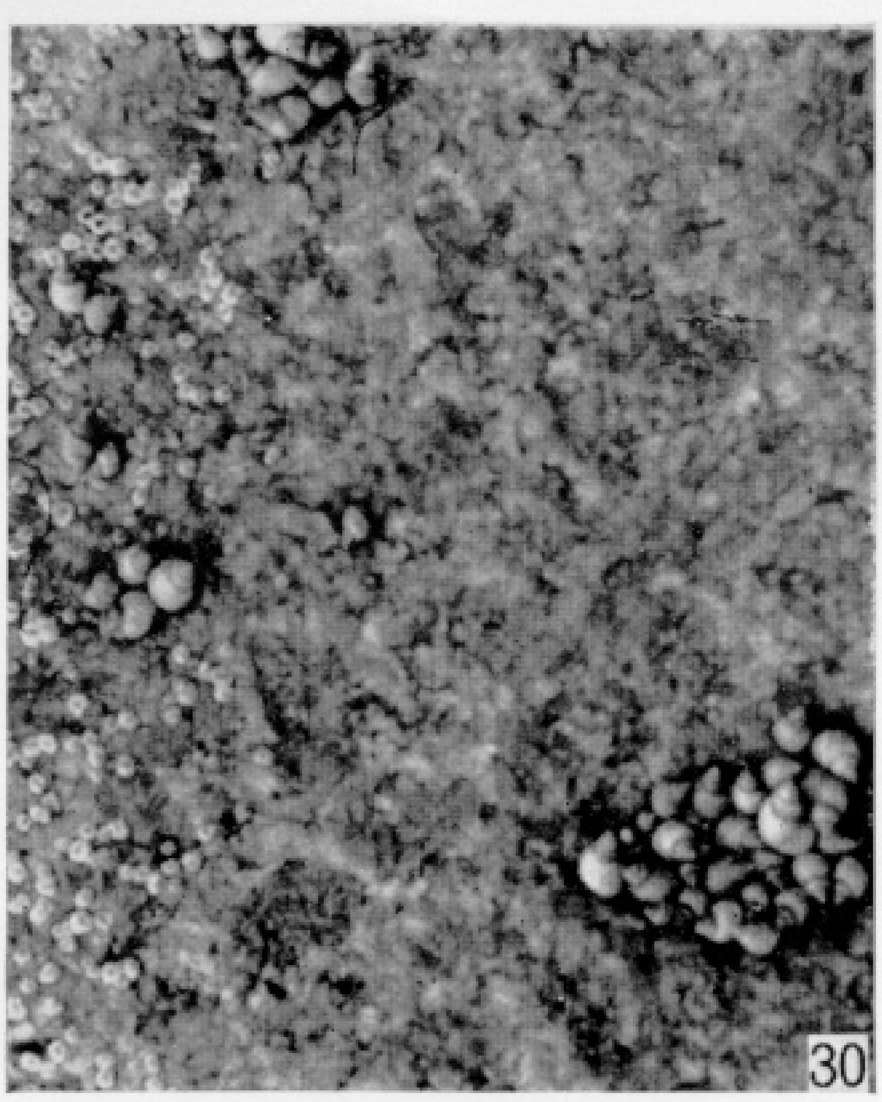


FIGURE 26. Barnacle zone (*Tetrachthalamus oblitteratus*) on granite shore at Pointe au Sel with green algae and *Sargassum* below.

FIGURE 27. Underwater view of beds of the marine angiosperm *Syringodium isoetifolium* with mounds of burrowing crustacea. Anse la Rue. Water depth 3 m.

FIGURE 28. Band of the bivalve *Isognomon dentifer* in byssally attached groups in the upper part of the eulittoral zone at Glacis.

FIGURE 29. Hemispherical colonies of *Porites nigrescens* (1 m high) on reef flat at Anse aux Pins. Water depth 2 m.

FIGURE 30. Clusters of *Littorina undulata* on granite surface at Pointe la Rue.

FIGURE 31. Underwater view of *Acropora pharaonis* on reef flat at Anse aux Pins on sandy bottom. Water depth 2 m.

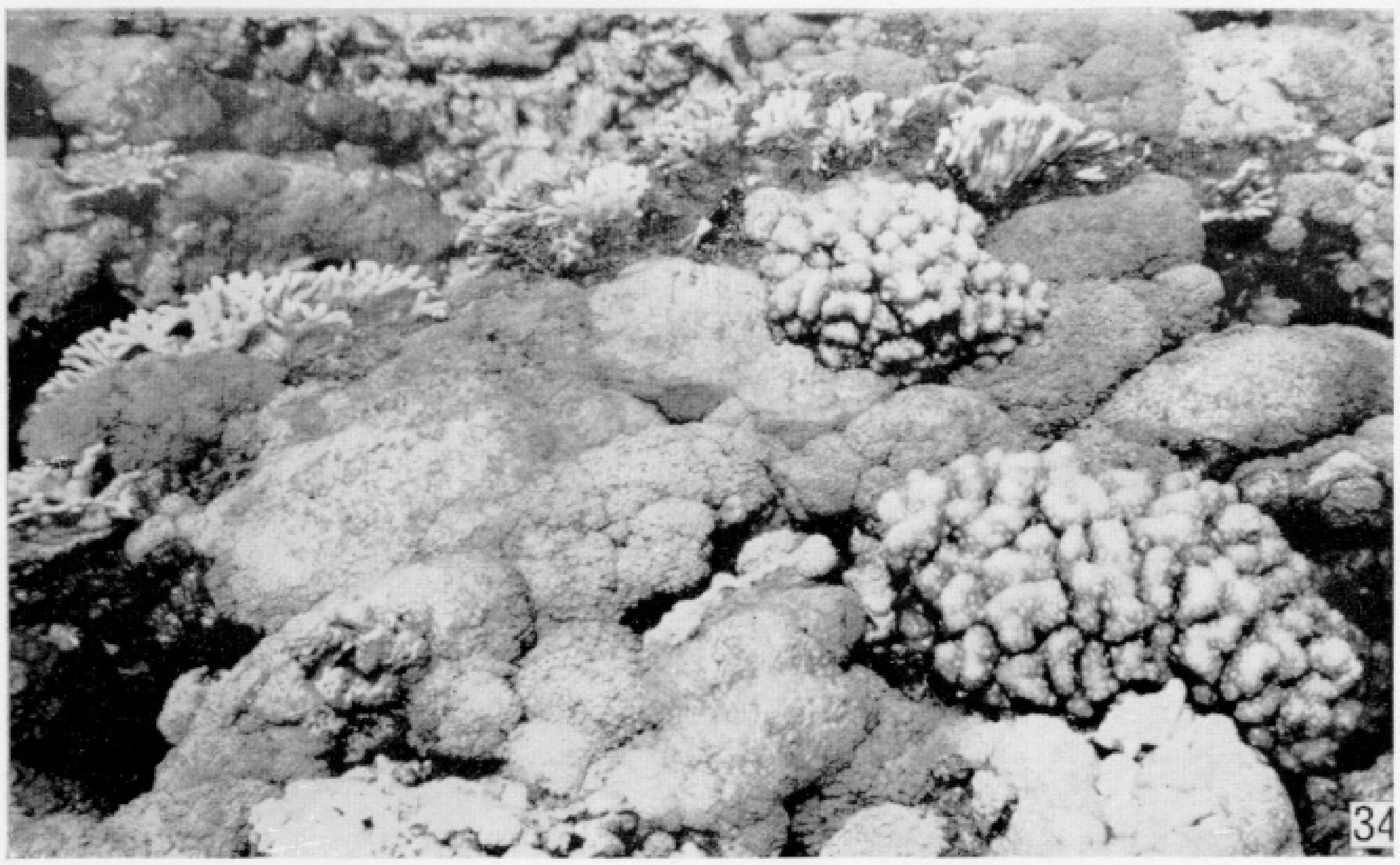
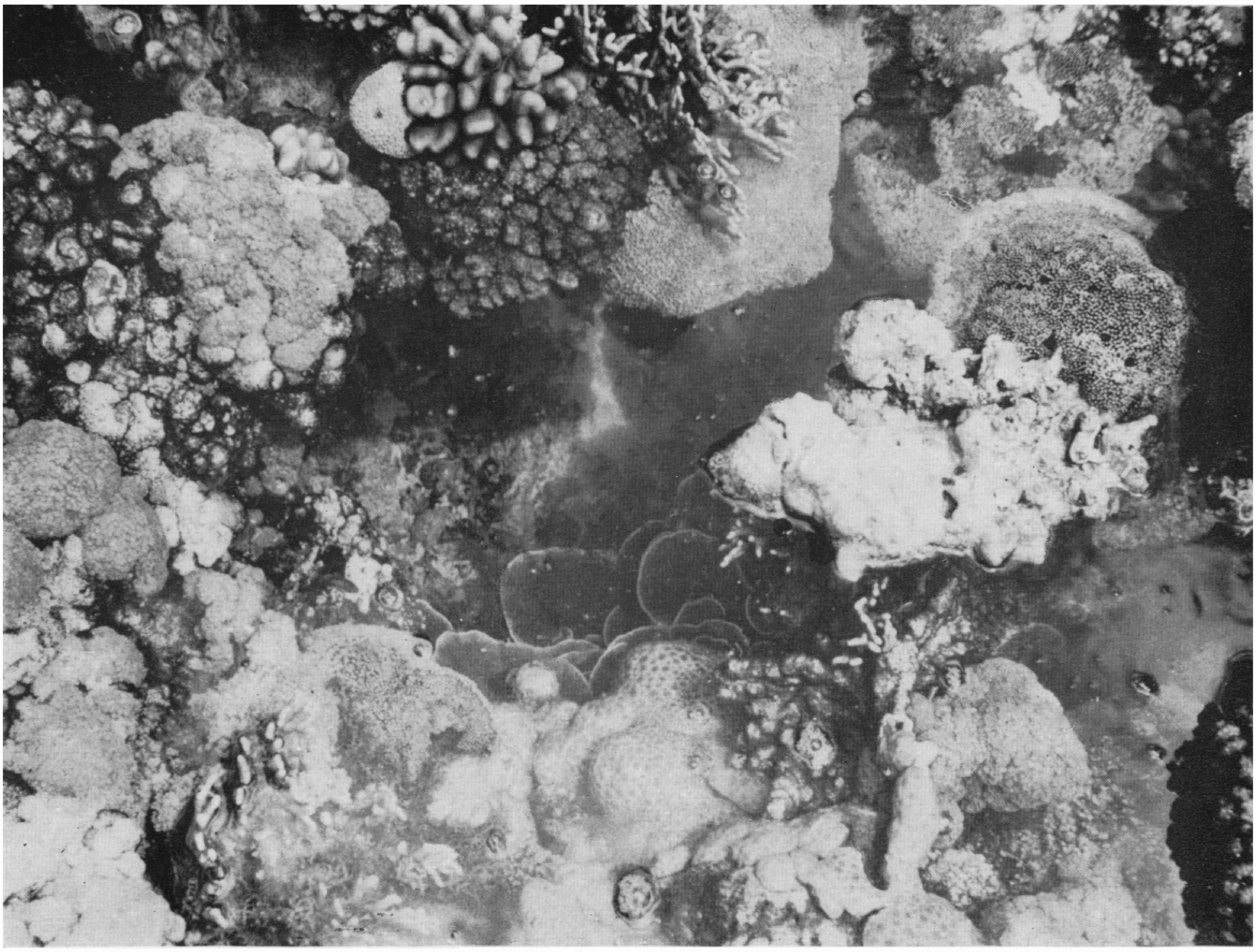


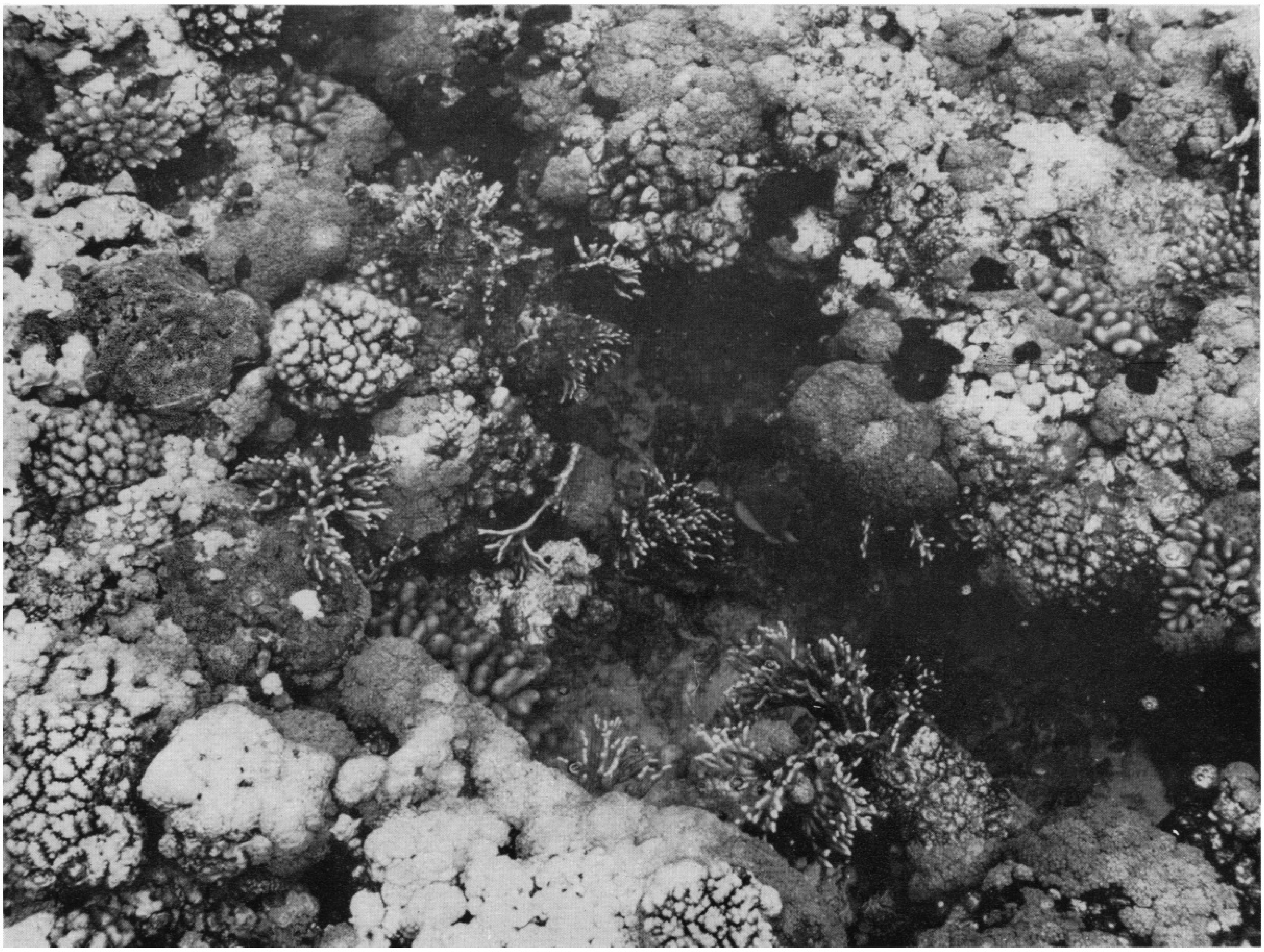
FIGURE 32. Supralittoral vegetation on an exposed shore at Anse Bazacar showing the outpost creeper *Ipomoea pescaprae* backed by *Scaevola* shrubs and *Cocos*.

FIGURE 33. Reef edge at lowest spring tides on a calm day off the northern end of Anse aux Pins reef.

FIGURE 34. Reef edge at Anse Faure emersed at low spring tides showing masses of *Xenia*, *Pocillopora danae* and *Millepora platyphylla*.



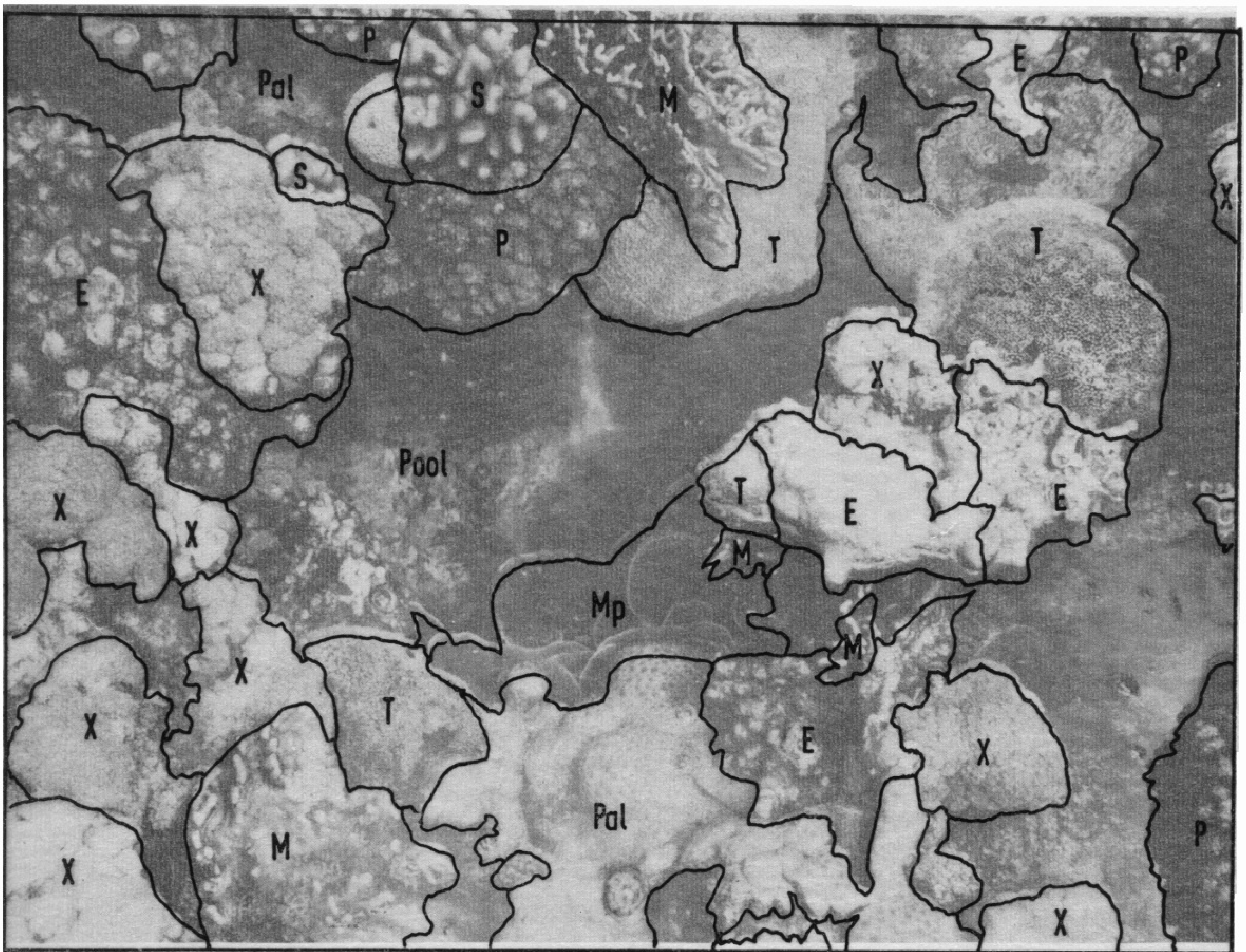
35



36

FIGURE 35. Coral fauna surrounding an enclosed pool on reef edge at northern end of Anse aux Pins reef.

FIGURE 36. Coral fauna surrounding a deeper pool on reef edge at northern end of Anse aux Pins. Key: *A* = *Acropora digitifera*; *E* = encrusting zoanthid; *M* = *Millepora platyphylla*; *Mp.* = plates of *Montipora*; *Pa* = *Palythoa*; *Pal* = *Palythoa*; *P* = *Pocillopora danae*; *S* = *Stylophora*; *T* = *Tubipora musica*; *X* = *Xenia*.



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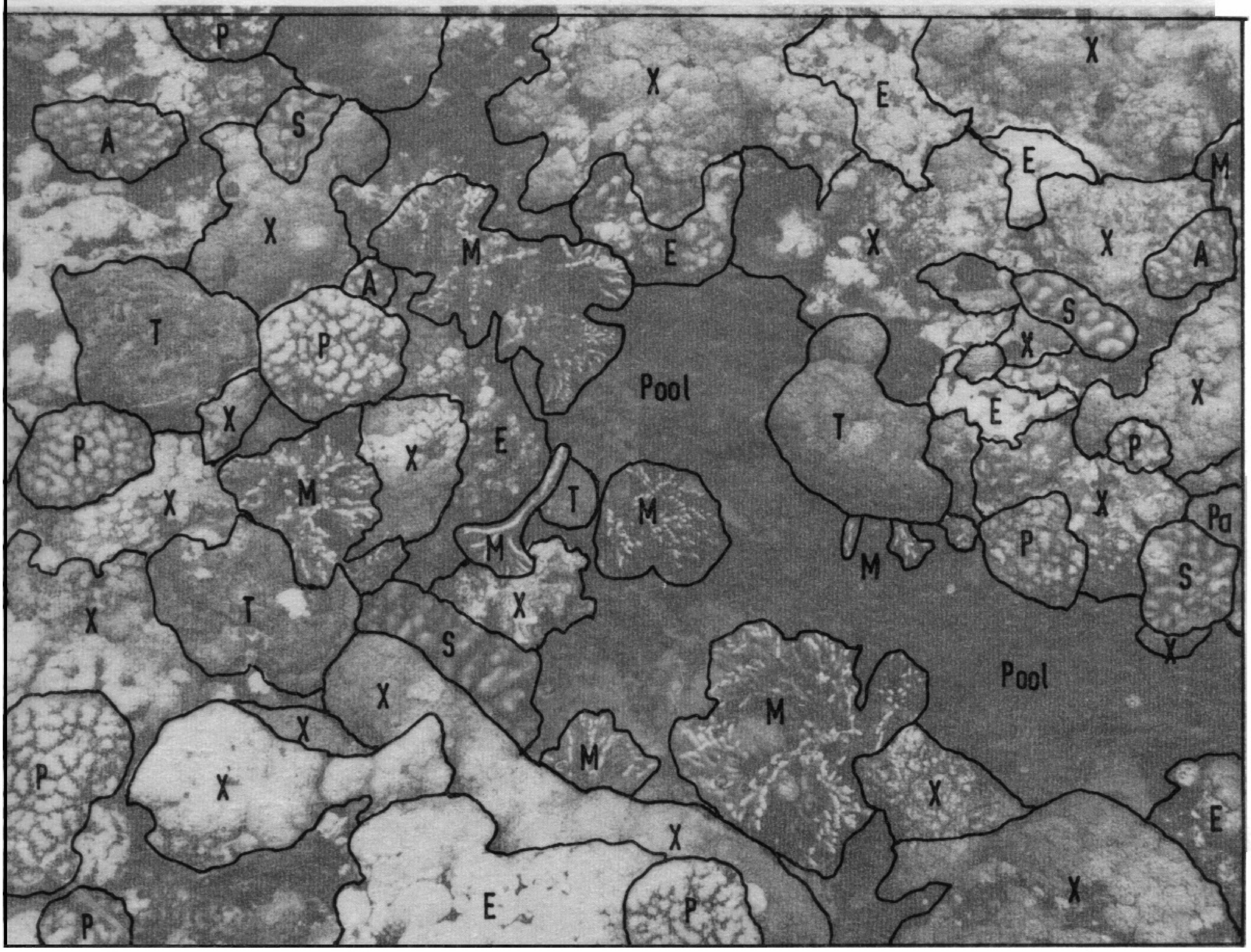

36

FIGURE 35. Coral fauna surrounding an enclosed pool on reef edge at northern end of Anse aux Pins reef.

FIGURE 36. Coral fauna surrounding a deeper pool on reef edge at northern end of Anse aux Pins. Key: *A* = *Acropora digitifera*; *E* = encrusting zoanthid; *M* = *Millepora platyphylla*; *Mp.* = plates of *Montipora*; *Pa* = *Palythoa*; *Pal* = *Palythoa*; *P* = *Pocillopora danae*; *S* = *Stylophora*; *T* = *Tubipora musica*; *X* = *Xenia*.