CALCAREOUS ENCRUSTING ORGANISMS OF THE RECENT AND
PLEISTOCENE REEFS OF BARBADOS, WEST INDIES.

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The anatomy, morphology and distribution of calcareous encrusting organisms (crustose coralline algae, bryozoans, foraminiferans, serpulid worms and corals) from the Recent reefs of Barbados has been related to both physical environmental and biotic factors within the marine environment in order to produce a model of encruster ecology. This model has been used in the interpretation of the conditions of growth of uplifted Pleistocene reefs on the island.

Patterns of encruster distribution are based on measurements of encruster size and/or density of colonisation of both natural (reef) and artificial (glass, brick, wood, perspex and concrete) substrates. For each encruster group, distribution can be related to the influence of specific environmental factors on the settlement and growth of developing individuals. The specific way in which this mechanism operates has been investigated for each encruster group. The differing ability of the various encrusters to withstand and to utilise variations in the physical and biotic environments results in a zonation of species on the Recent reefs. This zonation is summarised in the form of a model of encruster distribution which lists the dominant encrusters found within each habitat (as defined by depth, degree of illumination and hydrodynamic exposure) on the reef.

The distribution model is used in the investigation of the palaeoecology of Pleistocene reefs of Barbados where encrusters have documented not only the environmental conditions prevailing at the time of growth of the reef framework, but, by continued growth, have recorded the entire preservational history of the various framework components after their death and prior to burial by sediment. By using encrusters, a detailed picture of Pleistocene reef ecology has been constructed.

Finally, the various methods of crust growth are outlined, along with a discussion of the role of encrusters in the construction of the reef and a description of the way in which other processes interact with and affect crust growth and the products which result.
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The Bellairs Research Institute of McGill University is situated at the lower centre of the picture.
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<th>No.</th>
<th>Taxon</th>
</tr>
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<tbody>
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<td>foraminiferans</td>
</tr>
<tr>
<td>3</td>
<td>serpulids</td>
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<table>
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<tr>
<th>No.</th>
<th>Taxon</th>
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<tbody>
<tr>
<td>3</td>
<td>Neoroniolithon</td>
</tr>
<tr>
<td>4</td>
<td>Tenarea</td>
</tr>
<tr>
<td>5</td>
<td><em>L’esophyllum</em></td>
</tr>
<tr>
<td>6</td>
<td><em>Lichenopora sp.</em></td>
</tr>
<tr>
<td>7</td>
<td><em>Parellisina latirostris</em></td>
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<tr>
<td>8</td>
<td><em>Cribrina radiata</em></td>
</tr>
<tr>
<td>9</td>
<td><em>Trypastera venusta</em></td>
</tr>
<tr>
<td>10</td>
<td><em>Stylopoma informata</em></td>
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<td>11</td>
<td><em>Escharina red anseris</em></td>
</tr>
<tr>
<td>12</td>
<td><em>Paramithina ophidiana</em></td>
</tr>
<tr>
<td>13</td>
<td><em>Crepidacantha longicosa</em></td>
</tr>
<tr>
<td>14</td>
<td><em>Nymnchozoon rastarum</em></td>
</tr>
<tr>
<td>15</td>
<td><em>Cleidochaeta vestita</em></td>
</tr>
<tr>
<td>16</td>
<td><em>Bryozoan AN.</em></td>
</tr>
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1.1. General Introduction and Objectives

The study of the environments of growth and formation of ancient reef complexes has, until recently, been hampered by a lack of understanding of the ecology of the various organic components. Reconstructions based largely on indirect evidence such as reef structure and associated sediments often prove inaccurate from the point of view of reef palaeoecology (Ladd 1957). In the study of reef assemblages composed of extinct organisms, this may be the only method of approach. With more recent assemblages, however, the existence of living analogues allows morphological and ecological comparisons to be made, which, assuming the principle of uniformitarianism, allow greater accuracy in palaeo environmental reconstructions.

With the advent of S.C.U.B.A.* diving, in-situ observations of the growth and distribution of primary framebuilding components (such as corals and coralline algae) has been possible. However, although direct comparisons of living organisms can now be made with their fossil analogues, underwater observations have indicated that most reef framebuilders are distributed over too great an environmental range to be of benefit as specific environmental indicators in palaeoecological reconstructions. In addition, the long-held assumption that reef organisms were entirely of tropical, shallow-water occurrence has recently been disproved, with the discovery of corals (Teichert 1958) and coralline algae (Johnson 1961, Adey 1973) growing in arctic waters, the corals often growing at depths of 100m, well below the photic zone.

* Self-contained underwater breathing apparatus
Ideally, therefore, any attempt at palaeoenvironmental reconstruction should be based, not on the general requirements of one particular group of organisms (for examples, corals, sponges, coralline algae) but on the specific ecological requirements and distribution of one or more individual species. This should be based on information gained from in-situ observations of the living organisms, both underwater and in the laboratory, which is reinforced by knowledge of the effect on distribution of skeletal morphology and internal anatomy.

Even at a specific level, however, the ecology and distribution of individuals is often too diverse to be of use in detailed environmental reconstructions of fossil assemblages.

Reef-dwelling calcareous encrusting organisms,* however, provide an alternative means of environmental analysis, satisfying most of the requirements of a palaeoenvironmental indicator:

1. unlike the reef coral population, the encrusting biota is usually highly diverse at both phyletic and specific levels, covering an extensive range of environmental parameters.
2. environmental requirements of individual species are usually well defined and since all encrusters are of a relatively small size (compared to corals), accurate delimitations of their ecology and

* Calcareous encrusting organisms: defined as any organism, whether colonial or an individual, having a continuous (i.e. non-spicular) calcareous skeleton which is permanently attached by a carbonate or an organic cement to the primary framework of a reef. Encrusters so defined, can range from laminar to mound-like in form.
therefore their surrounding micro-environment in fossil occurrences is possible.

(3) the calcareous skeletons of most encrusters are preserved with little or no structural alteration upon diagenesis and burial, thereby allowing easy recognition in the fossil record.

In addition to indicating the (palaeo) environment, the growth and accumulation of encrusters on the reef both before and after the death of the primary coral framework can document the entire history of the reef, both up to and after burial by sediment.

The present study is concerned with the reef-dwelling calcareous encrusters of one particular area. The island of Barbados is, in part, composed of uplifted Pleistocene reef limestone and is fringed along its sheltered west coast by coral reefs of both shallow and deep water (50m) occurrence. The variety of exposed and concealed habitats in both the Pleistocene and Recent reefs provide a number of different environments for the study of encrusters. Except in some of the older reef tracts, most of the encrustations found on Pleistocene reef corals are in an excellent state of preservation.

The first part of their study (chapters 1 and 2) is concerned with the growth and distribution of the various encrusting organisms on the living reefs and on experimental substrates in the Bellairs region of the mid-west coast. It is concluded with a summary model of encruster distribution which is used in chapter 3 to interpret the environmental conditions and history of growth of selected Pleistocene reef tracts on the island. The work is concluded with a study of the methods of encrustation, the role of encrusters on the reefs and the way in which crusts are affected both during and after their growth by the various processes operating on the reefs.
Morphological and anatomical descriptions of all Barbados encrusters are given in Appendices 1-3.

1.2. Geology of Barbados

1.21. Regional setting and Tertiary to Sub-Recent Geology

Lying 140 Km (90 miles) east of the Lesser Antilles on top of a North-South trending submarine ridge (the Barbados Ridge - Ewing et al 1957, Bunce et al 1970), Barbados is the most easterly and the only non-volcanic island in the Lesser Antilles chain. The island itself consists of a core of complex and highly folded Tertiary sediments which are only exposed, as a result of erosion, in the East Coast, Scotland District (Jukes-Brown and Harrison 1891, Trechmann 1937, Senn 1940) (Fig. 1). Prolific coral growth during climatically warm periods, combined with periodic tectonic uplift during the Pleistocene (Russell 1966, Mesolella 1967, Mesolella et al 1969, 1970) has resulted in a terraced veneer of coral rock which covers some 70% of the underlying Tertiary basement (Figs. 40, 41).

1.22. Recent reefs on the West Coast

Despite its exposed location within the tropics (this chapter, section 1.3), active reef growth on Barbados is confined to the leeward, west, coast of the island (Lewis 1960b), where small (100m wide by 200m long), shallow-water fringing reefs grow seaward from coastal promontaries (Frontispiece and Fig. 2). In addition, submerged bank or barrier reefs, occurring at a depth of 10-15m, 1-2 Km off the west coast, also support coral growth,
Fig. 1
Location and Regional setting of Barbados

CARIBBEAN SEA
LESser ANTIlLES
BARBADOS

VENEZUELA
GUYANA
SURINAM

N. Equatorial Current
S. Atlantic Drift

C.00
5°00
10°00
15°00 N

0 100 200 300 400 500 km
Fig 2 General Bathymetry of the Bellairs Region showing Fringing Reefs and Transect lines with. insert. Location of Study Area.
usually to a depth of 40-50m (Macintyre 1967) (Fig. 4). Unlike the actively growing fringing reefs, however, these submerged banks owe their morphology primarily to Pleistocene geomorphological processes and now occur at a depth at which accretionary reef growth is extremely slow (Macintyre 1967, Ott 1975).

1.221. Fringing reefs of the mid-West coast, Bellairs, region (Fig. 2)

The majority of the west coast fringing reefs grow from the intertidal zone, adjacent to the shore, out to a depth of 5-10m. Beyond this depth, coral growth is abundant, but generally does not form a distinct topographic feature (Figs. 3, 4).

In addition to the general descriptions of zonation of west coast reefs, made by Lewis (1960b), specific investigations of the faunal composition and zonation of a small area of the west coast (the Bellairs region) have recently been undertaken by Stearn, Scoffin and Martindale (in press).

In general, the fringing reefs off Bellairs consist of a shallow (0-3m deep) inshore zone of coalesced coral knobs and spurs (Zones a to c of Figs. 3 and 4) which support a prolific growth of crustose coralline algae, with lesser amounts of the corals Porites porites, P. astreoides, Favia fragum, Agaricia agaricites and species of Millepora (Plate 1).

Seaward of the knob zone in depths of 3 to 10m, fringing reefs develop a pronounced east-west trending spur and groove configuration. Spurs commonly support prolific growths of Porites porites along their tops (Plate 2a), while the sides
Detailed Bathymetry of the Bellairs Shelf. Ecological Zones shown on overlay are as follows:

a) Dead coral and sand 'swash' zone
b) Encrusting red algal zone
c) Mixed coral, coalesced spurs zone
d) Mixed coral, spur and groove zone
e) Forites porites bank zone
f) Clean sand zone
g) Diploria coral, rubble and sand zone
h) Madracis mirabilis bank zone
i) Acropora cervicornis zone
j) 'Pillar' coral zone
k) 'brain' coral, bank zone
l) Platy coral, 'drop-off' zone.

For detailed descriptions of individual zones, see Chapters 1 and 2 and Stearn, Scoffin and Martindale (1976).
Fig 4 Bathymetric Profiles of the Bellairs Shelf & offshore bank at Nurses Jetty (for ecological zones a–l see fig 3).
INSHORE, RED ALGAL AND COALESCED SPUR ZONE OF THE FRINGING REEFS OFF BELLAIRS. DEPTH: 0-1m

a) Highly irregular topography of the red algal zone, consisting of Acropora palmata plates which are now heavily encrusted by crustose coralline algae (c) and corals (Porites porites - P, and Favia fragum ). Abundant cavities in this zone support a rich growth of crustose corallines (Mesophyllum), bryozoans (Reptadeonella sp, Schizoporella sp and Trematoecia sp) and foraminiferans (Homotrema rubrum) of intermediate photophilic/sciaphilic affinities. Scale as for Plate 1b below.

b) Prolific coral growth in coalesced spur zone. Substrates of dead A.palmata plates and massive coral heads are colonised by crustose coralline algae (Lithophyllum - L and Porolithon - P) and by corals (Millepora complanata, M.squarrosa, Porites astreoides and P. porites). Divisions on scale bar = 5cm

c) Close-up view of an almost dead head of Siderastrea sp, heavily grazed by the spiny sea-urchin Diadema antillarum and encrusted by the corals Millepora squarrosa (H) and Agaricia acaricites. Horizontal scale approximately 40cm.
a) View along a spur top illustrating the prolific growth of the finger coral *Porites porites*. Water depth 1-2m

Scale divisions: 5cm

b) Growth of corals and crustose coralline algae on spur sides.

Dominant corals are *Amaricia azaricites*, *Porites astreoides*, *P. porites* and *Millepora squarrosa*. Crustose coralline algae present are *Porolithon* sp (P) and the knobby form of *Lithophyllum* sp (L).

Scale divisions: 5cm

c) Channel or groove between spurs. Spur sides are lined either by a mixed coral assemblage (see b above) or by platy growth forms of *Montastrea annularis* (left-hand side of channel) or by massive heads of *Siderastrea* sp (right-hand side of channel).

The channel floor is composed of rippled sand and dead coral rubble. Water depth approx. 4m

Horizontal scale in foreground 3m
support a more varied fauna of the corals *P. porites*, *P. astreoides*, *F. fragrum*, *A. agaricites*, *Madracis sp.*, *Millepora sp.*, *Siderastrea sp.*, *Montastrea annularis*, *M. cavernosa*, with lesser amounts of *Diploria strigosa* and *Eusmilia fastigiata* (Plates 2b and 2c).

Intervening grooves are floored by rippled carbonate sand and coral rubble (Plate 2c) (zone d of Figs. 3 and 4).

Beyond the irregular topography of the fringing reefs, the sea bed assumes a much lower relief, varying gradually in depth from 8m seaward to 15m. Ecological zones in this area occur as bands roughly parallel to the shore (Fig. 3).

The zone immediately adjacent to the fringing reefs is composed of isolated coral heads, rubble and sand (zone g in Figs. 3 and 4).

Seaward of this are zones of *Madracis mirabilis*, *Acropora cervicornis* and carbonate sand (zones h, i and f respectively in Figs. 3 and 4). On the inward-sloping edges of depressions within this fore-reef shelf area, irregular, pillar-like growths of corals occur in depths of 15-30m.

On the seaward-slope of the fore-reef shelf, coral growth is similar in form and composition to that on the offshore bank, consisting of massive and platy growth forms of corals such as *Diploria sp.*, *Montastrea sp.*, *Agaricia sp.*, *Colpophyllia sp.* and *Manicina sp.* (zones k and l of Figs. 3 and 4) (see section 1.222 following).

1.222. Offshore Bank (barrier) reef, Nurses Jetty area (Fig. 2)

The offshore bank (or first ridge – Macintyre 1967) occurs as a submarine
ridge which parallels the west coast of Barbados, approximately 1.5 Km west of the present coastline. On its seaward side at Nurses Jetty at a depth of 50m, the bank rises at an angle of 15-30° from a gently sloping sand bottom (Fig. 4). Initially, the outer slope consists of sand with patchy coral and sponge growth, but at increasingly shallower depths, coral growth becomes more prolific. The gradient of the slope gradually decreases, until at its shallowest depth of 10m at the reef crest, the slope is less than 5° (Fig. 4). The crest of the offshore bank is variable in width, being approximately 35m wide across the line of transect at Nurses Jetty (Figs. 3 and 4). Corals on the reef crest and upper region of the seaward slope consist of massive, domed heads of Colpophyllia sp., Montastrea sp., Siderastrea sp., Diploria sp. and Meandrina sp. (Plate 3) (see Ott 1975 for comprehensive species list). Also abundant are large vase-shaped and tubular sponges (Verongia sp., Xestospongia sp.) as well as fan-like and bushy gorgonians (e.g. Gorgonia flabellum, Pseudopterogorgia sp. - Kinzie 1973).

The inner, landward slope at Nurses Jetty has an initial slight gradient near the reef crest and is populated by large, platy growth forms of Colpophyllia sp. Diploria sp. and Montastrea sp. (Plate 4a). Subsequently at depths of 20-25m, the gradient of the slope increases to 45°. From here to its base at 30m, the inner slope consists of large, vertical pillar-like outgrowths which support small platy corals on their tops and heavy encrustations on their sides (Plate 4b, c). At a depth of 30m, coral growth is replaced by a landward-sloping sand-mud floor of low gradient (Fig. 4) which extends from the outer bank
PLATE 3
CORALS AND ENCRUSTERS ON TOP OF THE OFFSHORE BANK REEF AT NURSES JETTY.
DEPTH: 10-15m

a) General assemblage of massive, platy and branched corals on the reef top. Massive heads include Siderastrea sp and Montastrea cavernosa. Platy growth forms are represented by Montastrea annularis and Meandrina sp. Branched coral in foreground is Eusmilia fastigiata. Encrustations are confined to dead coral heads and to the sides and undersides of living corals.

Scale divisions: 5cm

b) Dead head of Diploria sp encrusted by crustose coralline algae (Neogoniolithon sp), corals (Porites astreoides, Meandrina sp and Eusmilia fastigiata) and by sponges.

Scale divisions: 5cm

c) Massive coral heads encrusted by crustose coralline algae and sponges.

Living tissue of Diploria sp (left) is restricted to upward-facing surface. Sides are encrusted by sponges and crustose coralline algae. The dead coral head (centre) is encrusted by crustose corallines (Porolithon and Neogoniolithon) and by the corals Porites astreoides and Agaricia agaricites.

The head of Siderastrea sp (extreme right) is gradually being corroded by boring algae and/or grazing and is being overgrown by the foraminiferan Gypsina plana. Scale divs: 5cm
CORAL GROWTH ON THE INNER, LANDWARD SLOPE OF THE OFFSHORE BANK REEF, NURSES JETTY. DEPTH: 20-35m

a) Platy growth forms of *Montastrea annularis* near the reef crest. Depth approx. 20m. Scale divisions: 5cm

b) Pillar-like growth forms at 30-35m. Small platy growth forms of *Montastrea annularis, Acaricia* sp, *Meandrina* sp and *Lycophyllia* sp are attached to the upper surface of the pillar. Shaded and dim sides support growth of the encrusting, deep-water form of *Hadracis* sp, various encrusting sponges, crustose coralline algae (*Hesophyllum, Archaeolithothamnium* and *Lithothamnium*), encrusting foraminiferans and serpulid worms.

Scale divisions: 5cm

c) Highly irregular substrate at base of inner slope at 35m. Coral growth is similar to that on pillar growth forms. Additional species illustrated include *Buscula fastigiata, Porites* sp and the solitary coral *Scolymia* sp.

Scale divisions: 5cm
to the base of the seaward slope of the fringing-reef shelf (Macintyre 1967).

1.223. General Distribution of Encrusters

In general, growth of encrusting organisms is most prolific on hard substrates in areas of reduced coral growth. In the shallow inshore zone of coalesced spurs and knobs, crustose coralline algae achieve their greatest abundance, covering some 70% of the reef surface. In other zones on the fringing reef and on the fore-reef shelf area, however, colonization by encrusters is restricted to the dead sides and undersides of coral heads and sticks. (Plate 2b).

Similarly, on the upper slopes and reef crest of the offshore bank, encrustation is restricted to the dead sides and undersides of dome-shaped, massive coral heads. (Plate 3c). With increasing depth on the inner and outer slopes, however, both the abundance of coral and the area of each individual covered by living tissue decreases. As a result, the percentage cover by encrusters gradually increases to a maximum at 40-50m - deeper than this, the solid reef substrate is replaced by sand and mud.

Encrusters of exposed, lighted situations are predominantly crustose coralline algae with lesser amounts of foraminiferans. Encrusters of deeper and more shaded environments, however, are represented by bryozoans, foraminiferans, serpulid worms and solitary corals, with only minor amounts of crustose coralline algae. (Chapter 2).
1.3. Hydrography of the Inshore waters off the West Coast of Barbados

1.3.1. Introduction

As the most easterly of the Lesser Antilles chain of islands, Barbados lies in the path of both the North-East trade winds and two major, North-Westerly flowing ocean currents, the North Equatorial Current and the South Atlantic Drift. (Parr 1937, Sverdrup et Al 1942) (Fig. 1).

While the majority of Caribbean Islands support prolific reef growth along their exposed, windward coasts (for examples, see Newell and Rigby 1957, Goreau 1959, Ginsburg and Schroeder 1973), heavy run-off from the exposed east coast of Barbados restricts active reef growth to the island's south and sheltered west coasts (Lewis 1960b). Although hydrographic conditions (for example, wave action and turbulence) on the west coast are never as extreme as those on the east and south coasts, there appears to be adequate water circulation to promote reef growth.

The hydrography of the inshore waters off the west coast is outlined below. The specific effect of each of these factors on the growth and distribution of the various encrusters is described in Chapter 2.

1.3.2. Tidal Effects

The tides around Barbados are of the mixed, semi-diurnal type (Lewis 1960a) with a maximum spring tide range of 1.3m. Except for the alternating North - and South - flowing tidal currents experienced on the outer bank, 1.5 Km W. of Holetown, the influence of tides on the movement of water inshore appears to be minimal.
1.33. Temperature

Neither of the oceanic currents entering the Caribbean Sea from the east (Fig. 1) show a significant seasonal variation in temperature (Lewis et al. 1962). The mean oceanic sea surface temperature off Barbados varies from 25.5°C in February to 27.7°C during August-October (Lewis 1960a) (Fig. 5). Coastal surface waters, however, exhibit a greater range in temperature from 25.2°C in February to 28.4°C during August. Superimposed on these seasonal fluctuations is a diurnal variation of some 1-2°C (Lewis 1960a) (Fig. 5).

Although there are no consistent variations of temperature with depth in the shallow, photic (0-100m) zone off the west coast of Barbados (Lewis et al. 1962, Beers et al. 1968), Ott (1975) found that short-lived temperature and density inversions were quite common, indicating that the shallow part of the water column is in the process of continual mixing (see Sections 1.34 and 1.36 below).

1.34. Salinity

The surface and subsurface salinities off the west coast of Barbados show a minor seasonal variation from 33.0‰ (parts per thousand) during the summer months to 36.0‰ during the winter (Lewis 1960a) (Fig. 6). Low summer salinities are probably the result of a fresh water influx, introduced from the North East coast of South America at a time of high rainfall by the South Atlantic Drift (Whiteleather and Brown 1945) (Fig. 1). In addition, tropical storms on the island itself probably cause temporary reductions in salinity as a result of heavy run off from the west coast (June-August data, Fig. 6). However, investigations by Ott (1975) have shown that turbulence associated with the west coast reefs eventually destroys any salinity gradient (Oct-April data, Fig. 6).
Fig 5  Mean monthly sea surface temperatures, West Coast of Barbados. (After Lewis 1960, fig 3)

Fig 6  Monthly salinities at various depths off Holetown, West Coast of Barbados, 1972 (data courtesy of H. Powles)
such that the inshore waters remain essentially isohaline to the limits of coral growth at 50m.

1.35. Turbidity and Sedimentation

Underwater visibilities in excess of 30m suggest that turbidity off the west coast of Barbados is low. Ott (1975) recorded sedimentation rates, 5 cm above the reef surface at a depth of 13m, at 50-100 gm of sediment/metre$^2$/day. However, during times of storms and heavy run-off from land, sedimentation rates may be increased by a factor of 10 (Ott 1975). Although the penetration of light is significantly reduced during this period, the increase in turbidity is temporary and neither coral nor encruster growth appear to be adversely affected.

1.36. Wave action and Turbulence

Whereas wave height on the east and south coasts usually exceeds 3m, waves on the sheltered west coast of Barbados are normally less than 1m in amplitude. The fringing reefs and offshore bank along the west coast impose a barrier to waves refracted around the island, as well as to occasional long-period swells generated in the Caribbean Sea to the west (F. Sander 1974 - personal communication). Although the west coast reefs are rarely subject to the conditions of extreme hydrodynamic exposure associated with exposed reef tracts in other areas of the Caribbean (for example Jamaica - Goreau 1959, Netherlands Antilles - Scatterday 1974), wave activity inshore is sufficient to induce turbulence which destroys temperature and salinity stratifications, at least to the base of reef growth. (Lewis et Al 1962, Beers et Al 1968, Ott 1975).

Locally, considerable variations in the degree of hydrodynamic exposure
(= turbulence) exist within the shallow areas of reef growth.

Within any moving body of water, however, friction along the substrate/fluid boundary gradually reduces water movement, resulting in a vertical gradient of decreasing current velocity immediately above the substrate (Shapiro 1961, Allen 1970) (Fig. 7). The thickness of this gradient or boundary layer is related to the current velocity (which is equivalent to the degree of hydrodynamic exposure) and to the surface characteristics of the substrate (Fig. 7). Although their effect on overall movement of water across the reef is minimal, boundary layers significantly affect currents in the immediate vicinity (i.e. within 1.0 cm) of attached reef organisms. The feeding and growth restrictions which are imposed by a boundary layer are thought to be responsible for the observed zonation of many encruster species on the reef's off Bellairs (Chapter 2).

1.37. Light

While the amount of light reaching the surface of the sea is related to the angle of the sun's rays and to the amount of cloud cover, the proportions of this incident light which actually penetrates the surface of the sea is governed by the angle of incidence of the rays, as well as by the surface characteristics of the water (that is, whether calm or rough) (Holmes 1957).

Both the intensity and spectral quality of this transmitted light vary with depth as a result of scattering and absorption by water molecules and by dissolved and suspended material (Jerlov 1951, 1965; Holmes 1957) (Fig. 8). On the basis of light measurements made in the present study (Section 1.41 below), the inshore waters off Bellairs are seen to correspond to the tropical turbulent (that is, coastal) waters defined by Jerlov (1951).
External flow of uniform velocity

Boundary layer with velocity gradient

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Fig 67  Boundary layer development on planar and irregular substrates

(Adapted from Allen 1970, fig 17)

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West Coast Barbados

Tropical Turbulent waters

Tropical Oceanic waters

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Fig 8  Percentage of surface irradiation at different depths off the West coast of Barbados. Other waters types, included for comparison, are from Jerlov 1965
Whereas maximum transmittance (= least absorption) of clear, tropical oceanic water is at the blue end of the visible spectrum, suspended sediment and dissolved organic material in tropical coastal waters absorb a greater proportion of the short-wave (blue) radiation, such that maximum transmittance occurs at slightly longer wavelengths, in the green (475 μ) band of the visible spectrum (Fig. 9 and 10). In both turbulent coastal and clear oceanic waters, however, long wavelength (red and orange) radiations are completely absorbed within 5m of the surface (Jerlov 1951) (Fig. 9 and 10). Consequently, shallow water fringing reefs, such as those off the west coast of Barbados, are irradiated by incident light of both high intensity and full spectral composition. With increase in depth, however, the intensity of this light decreases exponentially along its line of travel, until at 50m (the maximum depth recorded in the present study), the incident light is only 7% of its sub-surface value (Fig. 8). At the same time, increase in depth produces a change in spectral composition, such that incident light becomes increasingly monochromatic (green) with depth (Fig. 9) (Jerlov 1951).

Whereas the light at shallow depth is variable in direction, (depending on the position of the sun), increased refraction of the light with depth progressively reduces the angle of incidence of the transmitted light to 0° (that is, vertical).

In addition to this direct downward illumination, water molecules and, in turbulent waters, suspended sediment and organics, reflect and scatter some 10% of all incident radiation (Holmes 1957). As a result, caves and overhangs are weakly illuminated from the sides and below. In shallow, turbulent water, this reflected light is of full spectral composition, whereas at depth, indirect illumination is of the same, short-wavelength composition as the direct, incident illumination (Holmes 1957).
Fig 9  Spectral energy of the downward illumination at various depths (E. Caribbean). (after Jerlov 1951)

Fig 10  Percentage of surface irradiation at different depths for every 25 μm (E. Caribbean). (Jerlov 1951)
The effect of this variation in the quality and quantity of both direct and indirect illumination on the distribution of encrusting organisms is outlined in Chapter 2 below.

1.4. Methods of Study

1.4.1. Field Methods

1.4.1. Recent Reefs

Composition of reef framework

In order to assess the faunal and floral composition of the Recent reefs off the West Coast of Barbados, underwater transects were established across the fringing reefs at Bellairs and across the offshore bank reef at Nurses Jetty, approximately 1 Km west of Holetown (Fig. 2). Transect studies included basic descriptions of reef morphology and overall composition (in terms of living and dead organisms and sand coverage), as well as specific investigations of the type and distribution of encrusting organisms. At 1 metre intervals along each transect, representative hand specimen-sized samples of reef material with attached biota were collected from all possible locations (such as reef top, reef side and base, the underside of overhangs and the interior of reef cavities). The location and environmental setting of each sample was noted at the time of collection. Parameters recorded included depth, degree of hydrodynamic exposure, value of incident light and the orientation of the specimen. In addition, underwater colour photographs, taken at regular intervals along the line of transect, provided a permanent record of the actual distribution and field relationships of corals and encrusters.
Spatial and temporal distribution of encrusting organisms - evidence from Natural and Artificial substrates

In addition to the distributional studies of encrusters on the reefs themselves, experimental blocks consisting of both natural (coral) and artificial (glass, perspex, brick, wood and concrete) substrates were placed in various locations on the reef and left for different periods of time in order to monitor the growth, distribution and succession of encrusting organisms (Chapter 2, Section 2.3).

Assessment of Hydrographic factors

Descriptions of the hydrography of the inshore waters off the west coast of Barbados are based on published data and personal observation. Although equipment for measuring the various micro-environmental conditions (for example current flow, temperature etc.) in the immediate vicinity of reef organisms was unavailable, the influence of sub-marine illumination (one of the more variable hydrographic factors off Barbados) on the distribution of encrusting organisms was investigated with the aid of a selenium cell light meter. Both direct incident and reflected illumination were measured in this way. The size of the instrument however (10cm x 6cm x 6cm) prevented the measurement of light in cavities of less than 20 cm diameter. Fig. 8 represents light values recorded at 12 noon on 5 successive clear days during July, 1973 with the sun directly overhead, when the surface of the sea was calm and the underwater visibility in excess of 50m.
Specific analyses related to encruster distribution

a) Pigment composition of Crustose coralline algae

In order to explain the observed zonation of crustose coralline algae in response to incident light (Chapter 2, Section 2.21), photosynthetic pigments were extracted from representative samples of living crustose corallines collected from a variety of environments off the west coast of Barbados. These were then analysed using a spectrophotometer (Appendix 5 and Chapter 2, Section 2.213).

b) Symbiotic organisms associated with Foraminiferans

Analysis of Foraminiferan distribution on the west coast reef indicate that certain species are light-loving or photophilic in nature. In order to explain this anomalous distribution of normally sciaphilic (that is shade-loving) animals, decalcified specimens of photophilic species were squashed and the remains examined under the microscope for evidence of possible symbiotic algae (Chapter 2, Section 2.23).

1.412. Pleistocene reefs

Specimens of well-preserved organic encrustations were encountered in 15 of the 50 localities examined in the uplifted Pleistocene reef tracts on

* Squashing: a technique which involves squashing the specimen between two glass microscope slides in order to break down cells and thus liberate their contents.
Barbados. At each locality, data relevant to both the specimen (that is: orientation, substrate characteristics, growth form and thickness) and its immediate environment (that is: composition and structure of the reef frame, its thickness and elevation and state of preservation) were recorded. (See Appendix 6 for Pleistocene sample locality descriptions).

1.4.2. Laboratory Methods

1.4.2.1. Distribution and ecology of Recent Encrusters

All specimens of Recent material were soaked in freshwater for 2 days after collection and then oven dried in the shade at 60°C for a further 2 days. Samples treated in this manner retain the original colour contrasts of the various encrusters, thus simplifying the task of recognition and identification at a later date.

Binocular microscope, scanning electron microscope and thin section examinations were all used in the determination of encruster taxonomy.

In order to determine the abundance, distribution, ecology and habitat success of each encruster species, the maximum dimensions of each individual were recorded*, along with its location on the

* Since most encrusters grow linearly or radially, the success of an encruster in a particular habitat is assumed to be related to the length of the individual or to the surface area of substrate covered. Because of the irregular shape of most encrusters, determinations of surface area were based on maximum and minimum dimensions of the crust, rather than on a mean radial value (see introduction to Chapter 2).
reef, its relationships with neighbouring organisms and the character of the immediate physical environment (for example, the value of incident light or the degree of hydrodynamic exposure). This data was then summarised for each encruster species in both graphical and tabular form. Along with the information obtained from experimental substrates, all data on the distribution and ecology of Recent encrusting organisms was correlated and summarised in the form of a model of encruster distribution (Chapter 2, Section 2.44).

1.422. **Internal structure of Recent and Pleistocene crusts**

Thin section, acetate peel and scanning electron microscope techniques were used in the examination of the internal structure and cementation of crusts. The etching medium E.D.T.A.* was found to be most successful in resolving fine cellular detail of crustose coralline algae in acetate peels.

*Ethylendiaminetetra acetic acid, Disodium salt*
CHAPTER 2

DISTRIBUTION AND ECOLOGY OF CALCAREOUS ENCRUSTING ORGANISMS ON RECENT REEFS
2.1 Introduction

2.1.1 Ecological Principles

The ecology and distribution of an organism is determined by a number of factors, both environmental and biological in nature. For any sessile encrusting organism, initial patterns of distribution are the result of an interplay of environmental and behavioural factors which acted during the free-living larval or spore stage, as well as during the settlement and growth of the developing individual or colony. The initial choice of substrate is probably determined by behavioural responses of the larva/spore to prevailing environmental factors, such as light, water currents and temperature (Pomerat and Reiner 1942, Crisp and Ryland 1960, Ryland 1960) (Fig. 11). The subsequent form and distribution of the adult individual or colony, however, is brought about by the action of a number of interrelated environmental and biological factors which continue to act throughout the life of the individual (Fig. 11).

While all factors have some effect on the individual organism, certain of these, termed limiting factors, exert a greater influence on the ecology and distribution of the organism than do others. Two basic concepts explain the mechanism of limiting factors: Leibig's 'Law of the Minimum' (defined in Odum 1959) states that an organism is no stronger than the weakest link(s) in its ecological chain of requirements. Each weak link can be considered as a limiting factor in the distribution of the organism. Shelfords Law (defined in Odum 1959) adds that not only too little, but also too much of a requirement may be a limiting factor. The range in between the maximum and minimum ecological requirements represents
Fig 11  The Interaction of Various Environmental & Biotic Factors on the Growth & Distribution of Encrusters.
the limit of tolerance for a particular individual. Consequently, the distribution of an organism is governed by its limits of tolerance to a particular element, as well as to the quantity and variability of the element itself. However, since the range of tolerance to most factors is quite broad, the distribution of an organism can usually be interpreted in terms of those few factors to which the range of tolerance is quite narrow (that is, limiting factors). In addition, variability within a factor itself (such as the amount of food or light available) to which there is only a narrow range of tolerance will also limit distribution.

By applying the above concepts to the encrusting fauna and flora of the Bellairs reefs, it is possible to eliminate a number of elements as potential limiting factors. In terms of the physical environment, these are temperature, salinity, dissolved $O_2$, $CO_2$ and nutrient content of the water. A number of authors (for example Lewis 1960a, Lewis et Al 1962, Ott 1975) have shown that the inshore waters off Bellairs are well mixed and are essentially isothermal and isohaline throughout the year within the area encompassed by the present study (see Chapter 1, Section 1.3). Whereas this uniformity in the physical environment will exclude those organisms (such as arctic species) whose range of tolerance lies outside its limits, its invariant nature will mean that within the tropical coral reef environment, the range of tolerance of any tropical species of normal salinity and nutrient requirements will not be exceeded.

Other factors within the physical environment, such as light and hydrodynamic exposure, however, are continually variable, either vertically or laterally, within the inshore, reef area. Since the majority of species have fairly well defined ranges of
tolerance to these factors, they are more instrumental in effecting zonation, than are other, more constant, factors.

In addition to physical environmental factors, biotic factors such as availability of food (itself related to variable environmental factors such as water movement and light), inter- and intra-specific competition and the mode of growth of the individual can also be considered as potential limiting factors in the growth and distribution of a sedentary organism.

The manner in which each group of encrusting organisms is affected by this variability in the physical and biotic environment is discussed in the relevant sections below. Difficulty in simulating the marine micro-environment in the laboratory prevented experimental study of the physiological and behavioural responses of encrusters. Conclusions regarding their ecology are therefore based on the observed distribution of species in the natural environment and on analysis of external morphology in relation to this distribution.

2.12. Quantitative Methods of Analysis of Encruster Distribution

2.121. Crustose Coralline Algae, Bryozoans and Foraminiferans (Gypsina plana)

The most extensive colonisers of any substrate are the crustose coralline algae, the bryozoans and the foraminiferan Gypsina plana. Because of the vegetative (crustose coralline algae) or colonial mode of growth of each group, lateral expansion of the colony in all cases exceeds vertical (accretionary) growth. Therefore, it was decided that colony area would be more representative of the success and distribution of an encruster species within a particular environment.
than would, for example, volume or thickness.

As outlined in Chapter 1, Section 1.421, the majority of encrusters are irregular in shape. As a result, areal calculations were based on mean linear dimensions (that is, length and breadth), rather than on mean radial dimensions (which assumes the colony to be circular in form). Because of the difficulty of recognition and identification of most encrusters underwater, and because of the inordinate length of time which would be involved in an underwater transect study of areal coverage, approximately 400 samples of reef substrate, 200-300 sq cm in area, were taken from different environments at regular intervals (every 3m) along each transect line. For each individual of a particular species, colony area was plotted against depth (as a relative measure of hydrodynamic exposure) and against the value of incident light at that depth. In this way, both the relative abundance (in terms of number of individuals) and the variation in colony areas at different depth and light intervals can be monitored. The distribution of the more readily identifiable encrusters (most crustose coralline algae and some bryozoans) was subsequently confirmed by random observations underwater along the areas of the transect studies.

Although the average areas of colonies within a particular depth and light interval have often been plotted in order to simplify the data, the encrusting community is continually undergoing a process of growth and development. Consequently, average colony areas are not entirely representative of the success of a particular group within a community, since they include developing, as well as mature individuals. However, since mean values invariably reflect the general trend of the distribution of a species, their inclusion in
the appropriate figures is considered to be justified.

2.122. Foraminiferans (excluding G. plana) and Serpulid Worms

Whereas the vegetative crustose coralline algae and the colonial bryozoans are capable of extensive areal coverage, individual animals such as the unicellular foraminiferans (excluding G. plana) and serpulid worms are only capable of limited growth, probably determined by the availability of food and mobility of dissolved gasses (such as O\textsubscript{2} and CO\textsubscript{2}) within the tissues. Consequently, size of individual (foraminiferan) or length of tube (serpulid) are considered to be unsuitable as indicators of the success of an organism within an environment. In both groups, however, density of colonisation (expressed as number of individuals/decimetre\textsuperscript{2}) was found to vary considerably between different environments. The success of any particular species is assumed to be related to its density of colonisation of a substrate.

Average values for the density of colonisation, which were found to be representative of the general trend of distribution within a particular environment were used in descriptions of foraminiferan and serpulid worm distribution.

For each group of encrusters, the distribution of the various species in relation to depth and light has been summarised in graphical form (for example, Fig. 20). Included within each summary is a list of substrates colonised by each individual. In addition, brief descriptions are given of common habitats and, where appropriate, mention is made of particular skeletal features which are thought to affect the distribution of that species.
In Section 2.2 following, each group of calcareous encrusting organisms is described in terms of its distribution on the Recent reefs and the various ecological factors which may influence this distribution. Morphological and anatomical descriptions of each member of the various groups of encrusters are presented in Appendices 1-3. A generalised model of encruster distribution is presented as a summary to Chapter 2, along with a discussion of competition and dominance both within and between the various groups of encrusters.
SECTION 2.2

INDIVIDUAL ENCRUSTER GROUPS
2.21 Crustose Coralline Algae

2.211 Introduction and Previous Research

The crustose coralline algae are composed of 3 sub-families (Melobesioideae, Lithophyloideae, Mastophoroideae) of the phylum Rhodophyta (the Red Algae). Their ability to secrete calcium carbonate (as High Mg calcite) both within and between cell walls (Chave 1954, Moberley 1970), along with their rapid growth as extensive encrusting sheets, not only results in their success as principal frame binder of modern tropical reefs but also enables them to compete favourably with scleractinian corals as principal frame builder of the reef (Gardiner 1931, Tracey et Al 1948, Ladd and Tracey 1949, Ladd 1961).

Although the crustose coralline algae were the subject of a number of earlier works (Kjellman 1883, Rothpletz 1891, Foslie 1894, Howe 1912, Lemoine 1913), the difficulties encountered in the study of their taxonomy (and thus indirectly a knowledge of their distribution) have only recently been resolved by Johnson (1957, 1961) and Adey (1973). Previous studies of tropical coral reefs have tended to combine all crustose corallines into groups variously termed Nullipores (Kuenen 1950), Lithothamnion (Howe 1912, Tracey et Al 1948), Lithothamniod algae (Goreau 1963) and Melobesioid algae (Lee 1967) – ambiguous terms which have led to considerable misunderstanding. Johnson (1961) clarified the 'Lithothamnion ambiguity', by stating that Lithothamnium (correct spelling) was, in fact, seldom present on tropical reefs, adding that the Lithothamnion (sic) ridges of Pacific reefs were usually constructed of species of Porolithon.

Adey (1973) has refined earlier identification keys of Kylin (1956) and Johnson (1961), so that rapid and accurate generic
identifications of the crustose coralline algae are now, in theory, possible using fractured surfaces and microtome sections of living material. In the present study, however, microtome sectioning of live, decalcified algae proved unsatisfactory. Instead identifications were made with the aid of ultra-thin (10-15μ) rock sections of dried, preserved material. By comparing identified thin sections with the surface morphology of the parent plant, it has been possible to produce a key for Barbados crustose corallines based on both internal anatomy and on external morphological features, such as colour and surface characteristics (see Appendix 1).

Ten genera of crustose coralline algae were found on the reefs at Bellairs. Of these, only Neogoniolithon and Lithophyllum are known to be represented by more than one phenotype* or species. Taxonomic difficulties prevented identification to a specific level - it is probable that, at this level, a more clearly defined zonation of the crustose corallines will exist.

The distribution of each crustose coralline genus is outlined in the following sections. Brief illustrated descriptions of the internal and external features of each genus, are given in Appendix 1 and as captions to appendix plates 1 to 10.

* Phenotype - organisms which are the same genetically (that is, they are the same species), but which appear different because of environmentally induced morphological variations.
2.212 Distribution of Individual Genera

Genus Porolithon (Foslie)

Porolithon occupies an extremely restricted range of habitats. Both crustal areas and number of recorded occurrences decreases rapidly away from shallow, well-lit environments (Figs. 12a and b). In these environments, Porolithon and Lithophyllum together cover approximately 70-80% of the exposed reef surface. Porolithon occurs as extensive, thick (often 1-2cm) sheets with gently contoured surfaces which, in shallow well-lit environments frequently overgrow (but are only rarely overgrown by) other crustose corallines, such as Lithophyllum and Neogoniolithon, as well as corals such as Favia fragum and Agaricia sp. and the sheet-like foraminiferan Gypsina plana (Plate 1).

The dominance of Porolithon in shallow, exposed environments may be equivalent to the situation on algal ridges of Pacific and Atlantic windward reefs, where Porolithon forms extensive pavements at the reef front in shallow, exposed environments (Tracey et al. 1948, Ladd et al. 1950, Johnson 1961, Glynn 1971, Adey 1973).

Below 2-3m depth, Porolithon is restricted in its distribution to well-lit and lighted (see Fig. 8 for actual light values of the various zones) upward-facing surfaces and is rapidly overgrown by other crustose corallines (e.g. Menophyllum, Neogoniolithon), if growth spreads to less-well illuminated areas (Fig. 20).

Genus Lithophyllum (Philliri)

Although it is distributed throughout the 0-30m depth range in both lighted and well-lighted situations, maximum abundance of Lithophyllum (in terms of both number of crusts and their surface area) occurs in well-lit, shallow (0-8m) water environments, where it is often
Fig 12  Distribution of POROLITHON in terms of depth and light

Fig 13  Distribution of LITHOPHYLLUM in terms of depth and light
Fig 14  Distribution of NEOGONIOLITHON in terms of depth and light

Fig 15  Distribution of TENAREA in terms of depth and light
co-dominant with Porolithon (Fig. 13).

The 'Knobby' crusts of Lithophyllum which develop in exposed locations (that is, areas subject to high levels of illumination and extremes of hydrodynamic exposure) are usually only overgrown at their edges by Porolithon and Neogoniolithon and by the corals Agaricia sp. and Millepora sp. In addition, the sides and undersides of individual 'knobs' are often overgrown by the bryozoans Trematoecia turrita and T. magnifera (Plate 5b).

The planar, sheet-like crusts of Lithophyllum which are produced in less-favourable areas (calmer and/or less-well lit situations) are commonly overgrown by encrusters which are more successful in these environments (for example Neogoniolithon, Mesophyllum, Gypsina plana) (Fig. 20).

The extent of knob development on crusts of Lithophyllum appears to be related to the degree of turbulence and the amount of light to which the crust is subject. Comparison of phenotypes from various situations indicates that those crusts which have developed in well-lit, hydrodynamically exposed environments show a growth of knobs which are often interlocked and distally flattened (Plate 5c), whereas crusts from progressively calmer, less-well lit situations show a gradual reduction in the size and number of knobs (Plate 5a, b). These observations suggest that high growth rates in favourable areas results in vertical accretion by way of knob development, rather than by simple laminar thickening (as in Porolithon).

Genus Neogoniolithon (Setchell and Mason)

Maximum abundance of Neogoniolithon occurs in depths of 17-30 metres, in lighted and just-lighted areas (Fig. 14). Although both Tenarea and Neopolyporolithon occur within the same habitats (see Fig. 20), its
a) Smooth glossy crust of *Lithophyllum* sp overgrowing *Neogoniolithon* sp on dead coral substrate. Offshore bank, Nurses Jetty. 20m depth from Just Lighted locality.

Small scale divisions: 1mm

b) Smooth crust of *Lithophyllum* (right) developing into knobby crust. 5m depth from Lighted zone of fringing reef off Bellairs. Both knobs and smooth crusts are colonised by the bryozoans *Trematoecia magnifera* (Tm) and *T. turrita* (Tt).

Small scale divisions: 1mm

c) Extreme development of knobs on a crust of *Lithophyllum* sp from a Well Lighted habitat at a depth of 1.5m on the fringing reefs off Bellairs.

Small scale divisions: 1mm
abundance (in terms of number of individuals and their crustal area) suggests that *Neogoniolithon* is the dominant alga within this habitat.

Both the substrates occupied by *Neogoniolithon* and the colonisers of its surface are related to the environment of growth. In well-lit areas, these include *Porolithon* and *Lithophyllum*, whereas in just lighted and shaded areas, *Hydrolithon* and *Mesophyllum* and the foraminiferan *Gypsina plana* are more common as substrates and colonisers.

**Genus Tenarea (Bory)**

Maximum abundance of *Tenarea* occurs at depths of 10-25m in lighted situations (Fig. 15). Locally, at depths of 15-20m, *Tenarea* may be the dominant crustose coralline alga and will often overgrow the more abundant *Neogoniolithon*. Substrates and colonisers of *Tenarea* include *Neogoniolithon*, *Hydrolithon*, *Mesophyllum* and the foraminiferan *Gypsina plana*.

**Genus Hydrolithon (Foslie)**

*Hydrolithon* occurs at most depths in just-lighted and shaded environments (Fig. 16). Crustal area increases at depths greater than 33m in just lighted environments where *Hydrolithon* may locally be the dominant crustose coralline. Within these habitats, substrates are restricted to crustose corallines such as *Mesophyllum* and to dead skeletal surfaces. At the same time it may be overgrown by *Neogoniolithon*, *Tenarea*, *Neopolyporolithon* and *Mesophyllum* if growth occurs beyond its optimum habitat (Fig. 20).

**Genus Neopolyporolithon (Adey and Johansen)**

The thin, loose crusts of *Neopolyporolithon* (Appendix Plate 6) are restricted to just-lighted environments at depths of 7-40m. Greatest abundance
Fig 16  Distribution of HYDROLITHON in terms of depth and light

Fig 17  Distribution of NEOPOLYPOROLITHON in terms of depth & light
occurs at depths of 25-30m where locally it may be the dominant crustose coralline. Potential substrates, as well as competitors within this environment include Mesophyllum, Hydrolithon and Neogoniolithon (Fig. 20), as well as the foram Gypsina plana.

Genus Mesophyllum (Lemoine)

Although Mesophyllum occurs throughout the range of depths sampled, maximum abundance occurs in shaded environments at depth, where Mesophyllum is the dominant crustose coralline. Throughout its entire depth range, crustal area appears to be inversely proportional to the value of incident light (Figs. 18 and 20). Substrates within these shaded environments include dead skeletal surfaces and other crustose coralline algae. Mesophyllum is rarely overgrown by more photophilic crustose corallines, except when growth occurs in more lighted habitats. However, overgrowth by other sciaphilic encrusters (e.g. foraminiferans, bryozoans, serpulid worms) in shaded and dim habitats is quite common.

Within just-lighted environments, crusts of Mesophyllum are frequently raised at their centres to form irregularly-shaped 'Knobs' (Plate 6), 1-2mm in height. Comparison of various colonies from this one environment indicate that knob development on crust surface is related to the age of the crust (based on the measurement of crust thickness) rather than to any variable environmental factor, as in Lithophyllum (see Plates 6a and b).

* Photophilic - light loving.

** Sciaphilic - shade loving.
a) Crust of *Mesophyllum* sp overgrowing the coral *Madracis* sp. The advancing edge, which is raised off the substrate, is characterised by a smooth glossy surface with ridges parallel to the advancing margin. The older, thicker region at the centre of the crust shows initial development of small knobs.

Small scale divisions: 1mm

b) Older crust on top of *Madracis* sp stick showing extreme development of knobs.

Small scale divisions: 1mm

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**Plate 7**

Frondose *Neogoniolithon* sp colonising *Acropora cervicornis* stick

Initially, crust is closely adherent to the substrate. However, subsequent growth results in leaf-like outgrowths of the crust from the substrate.

Small scale divisions: 1mm
Fig 18  Distribution of *MESOPHYLLUM* in terms of depth & light

Fig 19  Distribution of *LITHOTHAMNIUM* in terms of depth & light
Genus Lithothamnium (Phillippi)

Within the 0-30m depth range, Lithothamnium shows an exponential increase in crustal area with increasing depth and with a decrease in the value of incident light (Fig. 19). Maximum abundance occurs in dim habitats at 25-30m, where it may locally be the dominant encruster. Substrates available for colonisation within this habitat include dead skeletal surfaces and Mesophyllum (Fig. 20), while potential competitors are restricted to similar sciaphilic organisms (Fig. 20).

Crustose Coralline Algae of Restricted Distribution

The crustose coralline algae described in the following sections are of restricted distribution - in all cases, the number of recorded occurrences is less than 10. Consequently, conclusions regarding their distribution and ecology are somewhat speculative.

Genus Neogoniolithon - frondose form

Anatomically, this form is identical to the crustose form of Neogoniolithon. However, crusts are attached to the substrate by their proximal portions only, the distal, spreading regions being raised off the substrate to form pink, leaf-like crusts, up to 0.5mm thick (Plate 7). Shaded undersides of the crusts support colonies of sponges, bryozoans and serpulid worms. Upper surfaces are rarely overgrown. The frondose form is restricted to lighted environments at depths of 13-17m where it forms extensive, dark-blue (when viewed underwater) leaf-like crusts on the dead bases of Acropora cervicornis coral sticks, overgrowth of the fronds often cementing sticks together.
<table>
<thead>
<tr>
<th>ALGAL GENUS</th>
<th>no.</th>
<th>Area sampled (mm)</th>
<th>Area v Depth (metres)</th>
<th>Overgrows:</th>
<th>Overgrown by:</th>
<th>Comments</th>
</tr>
</thead>
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<tr>
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<td>10000 5 1 2</td>
<td>8 16 24 32 40 48</td>
<td>Light/Shadow</td>
<td>Light/Shadow</td>
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<td>5000 2 3 4</td>
<td>16 24 32 40 48</td>
<td>Light/Shadow</td>
<td>Light/Shadow</td>
<td>Sediment with Phyllolix as well as algae, and in deep environments.</td>
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<tr>
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</tr>
<tr>
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</tr>
<tr>
<td>Hymenocalyx</td>
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<td>5000 2 3 4</td>
<td>16 24 32 40 48</td>
<td>Light/Shadow</td>
<td>Light/Shadow</td>
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</tr>
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<td>Light/Shadow</td>
<td>Light/Shadow</td>
<td>Sediment at base of the reef at low tide locations.</td>
</tr>
<tr>
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<td>Light/Shadow</td>
<td>Light/Shadow</td>
<td>Sediment at base of the reef at low tide locations.</td>
</tr>
<tr>
<td>Alcyonaria</td>
<td>7</td>
<td>5000 2 3 4</td>
<td>16 24 32 40 48</td>
<td>Light/Shadow</td>
<td>Light/Shadow</td>
<td>Sediment at base of the reef at low tide locations.</td>
</tr>
</tbody>
</table>

Fig 20 Summary of the Distribution of Crustose Coralline Algae on the reefs at Bellairs, Barbados.
Genus Fosliella (Howe)

Fosliella occurs as individual thalli (2-3 cells thick – Appendix Plate 7) which form loose, leafy crusts of considerable thickness (0.5 cm) by repeated overgrowth.

Habitats are restricted to the dimly-lit sides and tops of the coral Eusmilia fastigiata at depths of 25-30 cm. Crusts are only occasionally overgrown, usually by the crustose coralline Tenarea.

Genus Archaeolithothamnium (Rothpletz)

Crusts of Archaeolithothamnium are only occasionally seen on the reefs at Bellairs. Occurrences were recorded at all depths on dead skeletal substrates in shaded situations. Crusts were only rarely overgrown, usually at their edges by Gypsina plana and by bryozoans (Fig. 20).

2.2.13 Functional Morphology of the crustose coralline Algae and the Factors affecting their distribution off Bellairs

Introduction

Although temperature and salinity are limiting factors in the distribution of crustose coralline algae on a global scale (Johnson 1961, Adey 1973), the range of variation of these factors within the restricted area examined (see Chapter 1, Section 1.3) is insufficient to exceed the limits of tolerance of the crustose coralline algae (Pearse and Gunter 1957, Adey 1973). The coralline algal flora of the Bellairs region is essentially a tropical one of normal salinity requirements, consisting of Porolithon, Neogoniolithon, Lithophyllum, Hydrolithon, Tenarea and Archaeolithothamnium, other forms which are represented, such as
Mesophyllum and Lithothamnium are usually classified as temperate water or arctic in occurrence. However, recent investigations (see Milliman 1974 for summary) have shown that the distribution of these latter two genera is probably related to the intensity of the transmitted light rather than to temperature alone. Consequently, they can be both tropical and arctic in occurrence.

Other potential limiting factors, such as $O_2$, $CO_2$ and nutrients are abundant and are evenly distributed within the area studied (Lewis 1962, Ott 1975). They can therefore be eliminated as limiting factors in crustose coralline algal distribution.

However, factors which are more variable within the waters of the Bellairs region are light and hydrodynamic exposure (both of which are related to depth of water). The limiting effect of each of these factors on crustose coralline algal distribution is discussed below.

Hydrodynamic exposure

As well as being effective in circulating nutrients and dissolved gases throughout the water column, turbulence and wave action are highly variable factors which influence the form and distribution of various encrusting organisms. Thus, crustose corallines found in shallow, turbulent environments are compact, closely adherent forms which are able to withstand exposure to wave action (see Lithophyllum in Section 2.212 above and Plate 5), whereas deeper water forms from sheltered situations are often loosely attached, with a more fragile growth form (see Plate 7).

However, the widespread distribution of most genera of crustose coralline algae in Barbados suggests that turbulence is only effective in the development and distribution of various
phenotypic forms, rather than being a limiting factor in the distribution of the organism or species itself.

**Light**

Crustose coralline algae are autotrophs*, depending on sunlight as a source of energy for growth and reproduction. Light is converted into energy by means of one or more photosynthetic pigments contained within the plants' cells. Each pigment is adapted to absorb light of a particular wavelength, usually that colour complementary to its own (Englemann 1883). Many marine algae contain only chlorophyll, a green pigment and so are restricted in their distribution to shallow water where they can use red light (see Chapter 1, Section 1.37 and Figs. 9 and 10 for sub-surface penetration of visible light). Rhodophyte algae, however, contain a number of photosynthetic pigments, whose absorption ranges cover almost the whole of the visible spectrum. They are therefore potentially capable of flourishing at all lighted depths (Levring 1965, Round 1965, Dixon 1973).

Analysis of the distribution of crustose coralline algae off the Bellairs region indicate that each species has a well defined distribution in terms of depth and amount of incident light (Fig. 20 for summary), and that the crustose coralline algal flora as a whole shows a distinct zonation of species.

In order to understand the mechanisms of coralline algal distribution, representative samples of 3 genera, taken from different depths and from different lighted environments were analysed for both the quantity and type of photosynthetic pigment which they contained. *Porolithon*, *Lithophyllum* and *Neogoniolithon* were chosen.

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* Autotroph - Independent of outside organic sources for provision of its own organic constituents.
for their wide range in distribution in terms of both depth and light and because of the ease of extraction of pigment from their skeletons (see Appendix 5 for methods of pigment extraction). For all 3 genera, the concentrations and light-absorbing properties of both the water-soluble and the '90%-Acetone'-soluble pigments were measured throughout the visible spectrum from 380 \( \mu \text{m} \) to 700 \( \mu \text{m} \). (Figs. 21-24). In the water-soluble pigment extractions, marked peaks in absorbance of light were found at 490 \( \mu \text{m} \) and 560 \( \mu \text{m} \), corresponding to the pigment phycoerythrin, and at 620 \( \mu \text{m} \), corresponding to the pigment phycocyanin (Blinks 1954, Levring 1965, Dixon 1973). Together, these 2 pigments constitute the phycobilins.

Marked peaks* were also found in the 90% Acetone extractions at wavelengths 430 \( \mu \text{m} \), 663 \( \mu \text{m} \), and 680 \( \mu \text{m} \), corresponding to the pigment chlorophyll (a). The combination of peaks in both the water-soluble and acetone-soluble extractions (Figs. 21-23) show that all 3 genera have pigments which are capable of utilising the entire visible spectrum for photosynthesis, each pigment absorbing a different wavelength or band of wavelengths.

The high concentrations of chlorophyll and phycobilin in shallow water algae (Figs. 21-23) suggest that maximum use is being made of incident light for photosynthesis, since the light here is of both high intensity and full spectral quality (see Chapter 1, Section 1.37). However, with increase in depth, concentrations of

* Absorbance, in all cases, is referred to an arbitrary linear scale of 0-3, corresponding to the calibration of the spectrophotometer used in this study (see Appendix 5).
Fig 21  Absorbance of visible light by Phycobilins (a) and Chlorophylls (b) in examples of POROLITHON from various habitats
Fig 22  Absorbance of visible light by Phycobilins (a) and Chlorophylls (b) in examples of NEOGONIOLITHON from various habitats.
Fig 23  Absorbance of visible light by Phycobilins (a) and Chlorophylls (b) in examples of LITHOPHYLLUM from various habitats
both chlorophyll and phycobilins decrease, contrary to theoretical predictions that pigment concentrations will increase with depth in order to compensate for the reduction in the value of total incident light. Although recent investigations (Blinks 1954, Hellebust 1970) have shown that light of high intensity may actually inhibit photosynthesis by breakdown of chlorophyll, other workers (Brody and Emerson 1959, Boney and Corner 1962, 1963) have suggested that at very shallow depth, chlorophyll is protected from adverse levels of illumination by a screening effect produced by phycobilins. The enhanced pigment formation, along with the relative increase in the proportion of phycobilins seen at shallow depth (Fig. 24), may well represent a protective adaptation of the algae to intense incident irradiation.

With increase in depth (and therefore decrease in the level of illumination), the total pigment concentration decreases, until it reaches a minimum value at 15m (Figs. 21-24). Beyond this depth, however, total pigment concentration actually increases until at the maximum depth sampled (30 metres), concentrations often approach their surface value (Fig. 24). Since incident light is much reduced at this depth (Fig. 8), high pigment concentration probably represents an adaptation by the plant to utilise as much of this reduced illumination as possible.

Similar, high concentrations of pigment were found in algae from concealed areas of low light intensity (for example caves and beneath overhangs) at shallow depth (Figs. 21-23) and probably represent a similar adaptation to low light intensity.

The minimum value of pigment concentration at 15m represents an optimal light value at which neither shielding by phycobilins nor enhanced production of pigment is necessary.
Fig 24  Comparison of Pigment Concentrations of 3 Crustose Coralline Algae from Exposed Habitats at Various Depths (conc^n measured at peak absorbance)
Along with a gradual reduction in total intensity, direct incident light also becomes increasingly monochromatic (green) with depth, as both long and short wavelength radiations are absorbed (see Chapter 1, Section 1.37). In addition to an increase in the total pigment concentration at depth, red algae also show an adaptation to this change in the quality of light (referred to as complementary chromatic adaptation – Englemann 1883) in the form of an increase in the relative abundance of phycoerythrin, the only pigment capable of utilising the remnant green light at depth.

Shallow water forms, however, exhibit the opposite effect of counter-complementary chromatic adaptation, whereby increase in both the relative and absolute concentration of phycobilins is used in order to protect chlorophylls from green light (Brody and Emerson 1959, Boney and Corner 1962, O‘h Bocca 1962).

A comparison of the 3 genera of crustose coralline algae analysed from Barbados indicates that algae characteristic (ie most abundant) of well-lit areas (Porolithon) contain proportionately less pigment at a particular depth than those algae characteristic of deeper, less-well lit environments at that same depth (Neogoniolithon) (Fig. 24). Therefore, it appears that, for the 3 algae examined at least, zonation is related to the absolute concentration of pigment (see also Englemann 1883 and Levring 1965). In addition, each species has a range in pigment concentration which can be related to its distribution in terms of depth and light (see also Rabinowitch 1945).

The dark colour of many of the crustose corallines from deeper, less-well lit environments (eg Lithothamnium, Mesophyllum) suggests that complementary chromatic adaptation (in the form of enhanced production of photosynthetic pigments especially phycobilins –
Gaidukov 1903 in: Round 1965) is well developed in this environment. This is most obvious in forms characteristic of crevices and overhangs, which are commonly deep purple in colour at depth, but are of a lighter tone in shallower water.

Whereas all environments at depth, whether exposed or concealed, are illuminated by monochromatic light of low intensity (Chapter 1, Section 1.37), crevices and overhangs in shallow (less than 5m) water are characterized by low levels of ambient light which is of full spectral range (Chapter 1, Section 1.37). Consequently, although concealed environments are illuminated by light of low intensity at all depths, the spectral quality of the light is highly variable. Analyses of crustose coralline algal distribution indicate that a number of genera characteristic of both exposed and concealed environments of low light intensity in deep water are able to exist within concealed environments of similar low light intensity in water of much shallower depth (regional stenosis*).

In support of this, the analyses indicate that maximum crustal area and abundance of crustose coralline algae invariably occurs within an environment characterised by a particular intensity of illumination, whether this environment is an exposed one at depth or is a concealed environment in shallower water. Neogoniolithon, for example, achieves maximum crustal area in lighted/just-lighted

* Regional stenosis - descriptive term used when organisms normally occupying exposed habitats at depth extend their range of occurrence into shallower water environments by colonisation of more protected habitats (see Reidl 1971).
environments at depths of 23-27m (Fig. 20). Although crusts of similar size are also found at much shallower depth, they are invariably restricted to partially concealed environments in which the high level of external incident illumination has been reduced to a lower, just-lighted level. Within any other environment, regardless of depth, the crustal area is markedly reduced. Forms characteristic of concealed environments of low light intensity at depths greater than 25m (e.g. Lithothamnium, Archaeolithothamnium) however, are only rarely found in shallower water environments.

In order to relate pigment types and concentrations to the problems of regional stenosis and zonation of crustose coralline algae, considerable further work is necessary. Nevertheless, the results presented above show that variation in the quantity and quality of light more than any other environmental factor is instrumental in effecting the zonation of crustose corallines.

2.22 Bryozoans

2.22.1 Introduction

The bryozoan fauna inhabiting the reefs off Bellairs consists of 30 species belonging to 24 genera (Table 1). The majority of these species belong to the order Cheilostomata and all (except Reteora sp.) occur as encrusting sheet-like (for example Repadonella sp., Stylopoma sp. and Stegapolarella sp. - Plate 27a) or mound-like (Plate 8) colonies, often with extensive areal coverages (Figs. 25-27).

Although bryozoans were found at all depths examined, the majority of species achieved their greatest abundance in the mid-depth region from 10-30m (Fig. 27). While most bryozoans from the Bellairs region are sciaphilic in nature, certain species, such as
TABLE 1  Classification of the Encrusting Bryozoans found on the Fringing and Offshore Reefs at Bellairs, Barbados.
Thin section, viewed under cross-polarised light, of the heavily calcified, nodular form of the bryozoan *Trematoosea magnifera*, overgrown by and intergrown with the crustose coralline *Lithophyllum* sp.

Two periods during which algal growth rates exceeded those of the bryozoan are evidenced by algal laminae included within the bryozoan colony.

Scale bar: 1mm

Scanning electron micrograph of the cribrate bryozoan *Cribrilina radiata*.

Protective calcification of this bryozoan consists of a porous shield of fused costae above the flexible frontal wall. Elongate spines forming a fence around the oral region are thought to assist in feeding. Avicularia (A) are visible between zooids.

Scale bar: 0.1mm
<table>
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<th>SUB-ORDER</th>
<th>SPECIES</th>
<th>Av. Ax Area</th>
<th>Av. Area v Depth</th>
<th>Av. Area v Light</th>
<th>Substrates:</th>
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<td>Living and dead Bryozoa corallines, Dead skeletal substrates</td>
<td>Reproductive locations in shallower areas, Reproductive locations from 0-10m</td>
<td>Mostly calcified frontal area</td>
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<td>Reproductive locations from 0-10m</td>
<td>Mostly calcified frontal area</td>
</tr>
</tbody>
</table>

Fig 25 Bryozoa Characteristic of EXPOSED Environments

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| ADENOPHYLLA | ariolitica | 20 | 10-20 | 3-5 | Living and dead Bryozoa corallines, Dead skeletal substrates, Dead sponge/plume | Cryptic in shallow areas, Reproductive at depth | Calcified cryptoplat |
| ADENOPHYLLA | nodosa | 20 | 10-20 | 3-5 | Living and dead Bryozoa corallines, Dead skeletal substrates, Dead sponge/plume | Cryptic in shallow areas, Reproductive at depth | Calcified cryptoplat |
| ADENOPHYLLA | simplex | 20 | 10-20 | 3-5 | Living and dead Bryozoa corallines, Dead skeletal substrates, Dead sponge/plume | Cryptic in shallow areas, Reproductive at depth | Calcified cryptoplat |
| ADENOPHYLLA | magnifica | 20 | 10-20 | 3-5 | Living and dead Bryozoa corallines, Dead skeletal substrates, Dead sponge/plume | Cryptic in shallow areas, Reproductive at depth | Calcified cryptoplat |
| ADENOPHYLLA | alpina | 20 | 10-20 | 3-5 | Living and dead Bryozoa corallines, Dead skeletal substrates, Dead sponge/plume | Cryptic in shallow areas, Reproductive at depth | Calcified cryptoplat |

Fig 26 Bryozoa Characteristic of SEMI-EXPOSED Environments
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<th>SUB-ORDER</th>
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<th><strong>Av. Area</strong></th>
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<td><strong>CRYPTIC</strong></td>
<td><strong>Fig 27</strong></td>
<td>Bryozoa Characteristic of CRYPTIC Environments</td>
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Reptadeonella violartia and Trematooeecia turrita occur predominantly in shallow, well-lit waters at depths of less than 10m.

The various environmental factors which are thought to influence the distribution of bryozoans on the Bellairs reefs are discussed individually in Section 2.223. While hydrodynamic exposure appears to be the principal limiting factor controlling this distribution, all of the factors are interrelated and all probably effect distribution to some extent.

2.222 Previous Research

Although there is no comprehensive account of the bryozoan fauna of Barbados, there are descriptions of the bryozoan fauna of the West Indian region as a whole (for example Camu and Bassler 1919), as well as numerous descriptions of faunas from particular areas within this region, such as Florida (Smit 1871, 1872), the Gulf of Mexico (Camu and Bassler 1928) and Puerto Rico (Osburn 1940, Shier 1964). In addition, numerous works deal with fossil and Recent bryozoan faunas of comparable tropical areas (Camu and Bassler 1920, 1923 - North American Tertiary faunas; Osburn 1953 - Pacific coast of N. America; Harmer 1926, 1934 and 1957 - tropical species collected on the Siboga expedition). Many bryozoan species common to Barbados are included in these accounts, with the result that preliminary identifications, at least to the generic level, are possible. Subsequent taxonomic revisions of the Bryozoa, however, have rendered much of the earlier nomenclature obsolete. Table 1 lists the bryozoans encountered in this study in their currently accepted taxonomic form (after P. Cook - personal communication - 1974).
Until quite recently, faunal studies rarely dealt with the ecology, distribution and role of bryozoans on modern reefs, most works being purely taxonomic in nature (see Cuffey 1972 for review). Similarly, descriptions of Recent reefs either fail to mention the bryozoans as ecologically significant or imply that bryozoans are rare and unimportant. Consequently, collections of Recent reefal bryozoans are few and incomplete and do not take account of morphological variability within genera and species.

Cuffey (1971a, 1972, 1973 a and b) however, has recently published accounts of research undertaken on the reef-dwelling Bryozoa of the Bahamas and Florida Keys and of the Pacific island of Eniwetok. This work, although it deals chiefly with the role of bryozoans as frame-builders and sediment producers on the reef, also discusses patterns of distribution including bathymetric zonation.

In a preliminary study of the communities within cavities in Recent reefs of Bermuda, Garrett et Al (1971) dealt briefly with the role of bryozoans and other cryptophilic ('cavity loving') organisms in modifying the reef framework. Jackson et Al (1971) also mention bryozoans as members of the cryptic communities of Jamaica. In the Mediterranean, Reidl (1966) and Gautier (1961) have studied the ecology of sea caves in which they found a zonation of bryozoans which was brought about by variations in the intensity of light and hydrodynamic exposure. In a more recent study, Vasseur (1974) has found that submarine caves off Madagascar support considerable communities of sciaphilic organisms, including bryozoans, whose distribution and zonation could also be related to light and hydrodynamic exposure. Cryptophilic bryozoans have also been described from Jurassic hardground communities by Palmer and Fürsich (1974).
2.223 Factors affecting the Distribution of Bryozoans off Bellairs

General Introduction

The distribution of bryozoans on the West Coast reefs of Barbados is the result of a complex interplay of physical environmental and biotic factors which have acted during settlement and ontogeny. Although it has been necessary to isolate these factors in order to assess their influence on bryozoan distribution, no single factor can be considered responsible for the observed distribution.

Physical factors

Introduction

Physical oceanographic data for the West coast reefs of Barbados is outlined in Chapter 1, Section 1.3. Salinity and temperature are essentially constant throughout the limited geographical and bathymetric ranges examined and so can be dismissed as limiting factors in bryozoan distribution. Light and depth are not, in themselves, limiting factors - they do, however, reflect variations in a number of other physical environmental and some biotic factors (such as turbulence and food) which influence bryozoan distribution on the reefs off Bellairs.

There is, in addition, experimental evidence (Ryland 1960) to show that after an initial period of positive phototactic behaviour (that is; attraction to light), some bryozoan larvae become negatively phototactic, actively swimming away from light to settle in shaded and dark areas. Similar responses probably occur naturally, as most of the bryozoans from the Bellairs region are sciaphilic - they settle and grow only in dark, cryptic habitats.
Moreover, once settlement of these encrusting bryozoans has taken place, colonies show no further growth response to light, being neither positively or negatively phototropic. Behavioural patterns such as these ensure that larval settlement occurs in favourable cryptic habitats in the upper photic layers of the ocean where food supply is plentiful (see following sections).

**Hydrodynamic exposure**

The distribution of bryozoans on the west coast reefs of Barbados is, in part, governed by their ability to withstand (and also to use) hydrodynamic forces. Bryozoans characteristic of high-energy, exposed environments (= Acrophilic forms) (for example Trematoecia sp., Rhynchozoa sp. - Fig. 25) possess heavily calcified colony and zooecial forms, whereas those of low-energy environments (= cryptophilic forms) (for example Escharina sp., Cribrilina sp. - Fig. 27) are delicate forms whose skeletons are adapted to life in the slow-moving waters of these cryptic habitats (see Section 2.224 following).

As bryozoans are sessile, benthonic filter feeders (Cuffey 1971b), they depend on water movements for their supply of food. Turbulence and local current regimes transport food to the colony where actual feeding is performed by tentacular cilia of the zooids (Ryland 1970, Cuffey 1971b). Observations of bryozoan distribution in the Bellairs region suggest that, in the absence of external food transporting currents, certain Bryozoa have developed skeletal structures which modify the flow regime in the immediate vicinity of the zooids. By creating turbulence in the boundary layer above the colony, these structures locally increase the water velocity, so improving the efficiency of the food gathering mechanism (see Figs. 28, 29 and Section 2.224 following).
Turbulent Zone
Buffer Zone
Laminar Sub-layer

Fig 28 Current Regime in vicinity of Organism/Colony of Low Relief
- uninterrupted low velocity laminar flow isolates colony from nutrients suspended in higher velocity region above

length of arrow in boundary layer is proportional to current velocity

Fig 29 Current Regime in vicinity of Organism/Colony of High Relief
- spines etc project into higher velocity regions of boundary layer and disturb flow
Turbidity

In a number of localities in the Bellairs region (opposite river mouths and in inter-reef hollows) where reef substrates are periodically swamped by fine sediment, bryozoans are scarce or absent. The particle size and quantity of settling sediment which a bryozoan can tolerate is not known, but in more turbulent areas, near shore or on the top of the offshore bank reef, fine sediment deposition is not a problem and bryozoan colonies flourish (the decrease in colony number and size seen in the 7-13m depth range in Figs. 25-27 represents fore-reef slope samples in areas of maximum sediment deposition). Both Ryland (1970) and Cuffey (1971b) have reported a restricted distribution of bryozoans to waters which are non-turbid and which are relatively free of settling sediment. The presence of bryozoans on the sides and undersides of corals and dead skeletal substrates which was commonly observed in Barbados will no doubt minimise the risk of burial by sediment.

Small quantities of sediment deposited on the colony surface of cheilostome bryozoans will probably be cleared by the action of specialised heterozooids. The pincer-like and sweeping action of the avicularia and vibracula removes sediment and other foreign matter which settles on the colony surface (Ryland 1970 - see Plates 9 and 10).

Turbidity also impedes the passage of light through the water, so reducing the maximum depth at which the phytoplankton food source can photosynthesise (Wilber 1971). Consequently, bryozoans are restricted in distribution to the upper, photic layers of phytoplankton production. As this extends beyond the maximum depths sampled in Barbados (Ctt 1975), availability of food as a
PLATE 10

Vibraculum on Holoporella tubulosa. This specialised hetero-zoid is moveable and, like the avicularia, has a protective function, clearing the colony of settling sediment and larvae.

Scale bar: 0.01mm (Scanning electron micrograph)

PLATE 11

Scanning electron micrograph of oral spines on a colony of Escharina pes ansoris. Marginal spines at top centre and right are complete and undamaged, whereas older spines at the colony centre are much shorter, possibly as a result of breakage.

Crustose coralline alga (Mesophyllum sp) is overgrowing the colony at lower right.

Scale bar 0.2mm
result of turbidity is probably not a limiting factor in bryozoan distribution off Bellairs.

The effects of abrasion of the colony surface by suspended sediment in turbid environments is a relatively unknown factor in the distribution of bryozoans. Moore (1973) has outlined the effects of heavy sedimentation, stating that, in addition to any physical damage which may be done by suspended sediment, feeding and respiratory mechanisms can be significantly impaired. The heavily calcified skeletons of many of the bryozoans in exposed habitats in the Bellairs region (see Section 2.224 following) may be an adaptation to sediment abrasion, as well as to hydrodynamic exposure.

Substrate

Substrate morphology often determines the pattern of colonisation and colony morphology of the bryozoans examined in Barbados. Species which develop as nodular colonies (Trematoecia magnifera, T. turrita and Schizoporella sp. - Plate 8) characteristically colonise convex surfaces, whilst more laminar colonies are found on planar or concave surfaces (for example Stylodonta informata, Parasmittina sp., Crepidacantha longiseta, Cleidochasma vestita, Steganoporella magnilabris - Plate 28a, c).

In Barbados, the encrusting forms of bryozoan appear to be characteristic of all hard substrates (compare Ryland 1970 p 68 with Stach 1936). However, hard substrate selection itself appears to be very specific, resulting in non-uniform colonisation of the reef surface by bryozoans. On the Bellairs reefs, the most abundant substrates available for colonisation are the crustose coralline algae in exposed, lighted environments and miscellaneous dead skeletal surfaces in protected, cryptic habitats.
Bryozoans colonising crustose coralline algae are found to be heavily calcified forms, suggesting an adaptation to life in a high energy environment, whereas bryozoan epifaunas of dead skeletal surfaces are delicate, poorly-calcified forms which exhibit skeletal adaptations to life in a low-energy environment. (see Section 2.224 following). Although most bryozoans appear to be firmly attached to the substrate, some (for example Steganoporella magnilabris) were often observed bridging cavities and were occasionally raised off the substrate at their distal margins. (Plate 27a).

**Biotic factors**

**Food and Competition**

The availability and supply of phytoplanktonic food to bryozoans on the west coast reefs of Barbados is essentially constant throughout the year (F. Sander - pers. comm. 1973), with the result that availability of food can be dismissed as a limiting factor in bryozoan distribution. Furthermore, there is no evidence to suggest that competition occurs between neighbouring colonies for this available food, even in densely populated habitats. (Ryland 1973).

As growth of encrusting bryozoan colonies appears to be exponential (Stebbing 1973, see also Chapter 2, Section 2.35), competition for space rather than for food is probably more limiting in their distribution.

**Intraspecific competition**

Stebbing (1973) has reviewed the effects of intraspecific competition amongst bryozoans. Competition between approaching crusts can have a number of possible outcomes: both crusts may cease growth at the point of contact and resume growth in another direction or one crust may
overgrow the other, resulting in death of the overgrown zooids. Although examples of both cases have been recorded in Barbados, the latter appears to be more common.

**Interspecific competition**

Bryozoans on the west coast reefs of Barbados compete for space with both sciaphilic and photophilic encrusters. Crustose coralline algae and serpulid worms are the most frequent colonisers of bryozoan surfaces. However, settlement of these encrusters on the actual colony surface is extremely rare, probably because of the irregular surface microtopography of bryozoans and because of the protective action of aicularia and vibracula. More often, bryozoans are overgrown by crustose corallines and serpulid worms which have spread over the colony surface from neighbouring substrates.

Stebbing (1973) has reported that marginal zooids of *Electra pilosa* from the English channel have elongate frontal wall spines. He has suggested that these spines may prevent or hinder overgrowth of the colony by other encrusters. Although similar marginal zooids have also been found by the present study on some bryozoans off Bellairs (e.g. *Escharina pes anseris* (plate 11), *Crepidacantha longiseta*), observations suggest that the spines are restricted to young marginal zooids, since the spines of older, more central zooids are often broken, presumably by abrasion.

A number of bryozoans from the west coast of Barbados secrete a wide calcareous margin which encircles the growing colony. In isolated colonies of *Lichenopora* sp., this margin is usually adherent to the substrate. However, when growth of the colony occurs adjacent to another, attached organism, the margin is often elevated above the substrate (Plate 12 a and b). Stebbing (1973)
a) Colony of *Lichenopora* sp on coral substrate of experimental block. Entire margin of isolated colony (visible as lighter fringing area) is closely adherent to the substrate.

Small scale divisions: 1mm

b) Colony of *Lichenopora* sp on experimental wooden substrate. Entire margin of colony is raised, possibly as a result of threatened overgrowth from neighbouring serpulid worm tubes (*P. multispinosa)*.

Small scale divisions (top centre): 1mm
has described a similar feature in *Disporella hispida* from the English Channel and has suggested that the elevated margin is a response to threatened overgrowth by a neighbouring encruster.

2.22 Functional morphology in relation to the Distribution of Bryozoans off Bellairs

Introduction

With the exception of *Retepora* sp., all of the bryozoans encountered on the west coast reefs of Barbados are closely adherent, encrusting forms. Stach (1936) explained colony form in terms of exposure to wave action and turbulence, stating that the encrusting habit, in particular, developed in exposed, high-energy environments. Ryland (1970), however, has argued that colony form is related to substrate type and not to the degree of hydrodynamic exposure. Although the present study deals only with hard, lithified substrates, the predominance of crustose forms at all depths and in all environments lends support to Ryland's theory. In summary, the encrusting habit of the bryozoans of the Bellairs reefs appears to be related to the lithified character of the substrate and not to any particular value of hydrodynamic exposure.

Order Cyclostomata

The cyclostome bryozoans are represented by 2 genera on the Bellairs reefs. Both *Entalophora* sp. and *Lichenopora* sp. are heavily calcified encrusting forms which possess elongate peristomes but which lack the specialised heterozooids of the cheilostome bryozoans.
Functional morphology and Distribution of the

Cyclostomata

Both Entalophora sp. and Lichenopora sp. were found at mid-depths (10-20m) in protected, cryptic environments, where water movements are considerably reduced (Fig. 27). In these habitats, frictional effects adjacent to the substrate will produce a boundary layer of considerable thickness (up to 0.5 cm - Reidi 1971. See Chapter 1, Section 1.36 and Fig. 7). Any bryozoan of low relief would therefore be totally immersed in such a layer (Fig. 29), with the result that very little food and O₂ would be transported to the colony.

However, both Entalophora sp. and Lichenopora sp. have considerably elongated peristomes (Plates 12 and 13), which project into the boundary layer. The lophophore tentacles, when protruded from the peristome, will therefore be raised above the lowest velocity region immediately adjacent to the colony surface and will be active in higher velocity regimes where the volume of food transported in a given time is much greater (Fig. 29).

The restriction of Entalophora sp. and Lichenopora sp. to 'clean' sides and undersides of substrates off Bellairs is seen as a means of avoiding the problem of burial by fine sediment within these low-energy environments.

Order Gymnolaemata

Introduction

3 sub-orders of the Gymnolaemata (the Anasca, Cribrimorpha and Ascophora) are represented on the reefs off Bellairs (Table 1). The Cribrimorpha are a recent subdivision of the Anasca (see Ryland 1970) but will be treated here together with the Anasca as they appear to have a similar functional morphology.
PLATE 13

Elongate peristomes surrounding the oral region of the Bryozoan *Entalophora* sp.

Scale bar: 0.2mm

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PLATE 14

*Parellisina latirostris*. Only the side walls of this anascan bryozoan are calcified. The frontal wall consists of a flexible chitinous membrane (M). Globose ooecia (O - reproductive bodies) are visible between adjacent zooids.

Scale bar: 0.1mm
Fig 30  Diagrammatic Cross-Sections of Encrusting Cheilistome Bryozoans found off Bellairs, Barbados
The major difference between the Anascan and Ascophoran bryozoans is the degree of calcification of the frontal wall of the zooecia. In the Anascans, only the side walls are initially calcified, leaving the chitinous frontal membrane flexible and unprotected (Bassler 1953, Ryland 1970 (see Fig. 30). The frontal wall of Ascophoran bryozoans is calcified, however, and forms a rigid 'lid' to a strong-sided box (Fig. 30).

**Sub-order Anasca** (including S. order Cribrimorpha)

**Morphology**

Fig. 30 illustrates the types of frontal wall protection possessed by this group. In its most basic form, this protection consists of a thin, flexible chitinous membrane, as seen in *Parellisina* sp. (Plate 14). Additional protection may be provided by marginal or costal spines which develop as outgrowths of the side wall. Fusion at the tips of the opposing spines forms a 'grid' above the frontal wall (for example *Membraninorella aragoii* from Bellairs - Plate 15) while additional fusion of the spines along their length results in a strong, porous sieve-like structure above the frontal wall (for example *Cribrilina radiata* - Plate 9).

An alternative pathway of anascan frontal wall protection is seen in *Labiocorella* sp., *Smitinora* sp. and *Steganoporella* sp. (Plate 16), in which a shelf-like, calcareous layer, the cryptocyst, extends from the marginal wall either wholly or partly beneath the frontal wall. The complete cryptocyst, in particular, provides much greater protection to the soft internal organs than do spines, an important feature in terms of Anascan distribution (see section following).
**PLATE 15**

**Membraniporella aracoi.** Partial protection of the frontal wall against predators is afforded by costal spines, fused at their distal ends only.

*Scale bar: 0.2 mm*

**PLATE 16**

**Steganoporella magnilabris.** Protection of the frontal membrane against predators and hydrodynamic forces is provided by a weakly calcified cryptocyst (C), extending as a complete covering across the frontal region.

*Scale bar: 1 mm*
Significance of Frontal wall calcification and its effect on Ascan Distribution

Non-calcified frontal wall

Parellisia, the only bryozoan on the west coast reefs of Barbados which lacks frontal wall calcification, is restricted to cryptic environments at mid-depth (Fig. 27). This limited distribution suggests that the absence of frontal wall protection prevents colonisation of more exposed habitats.

Marginal spines

Two bryozoans off the west coast of Barbados (Membraniporella aragoii and Cribrilina radiata) possess marginal spines. In both genera, the spines have fused to form a cage or porous pericyst above the frontal wall (Fig. 30 and Plates 9, 15). Although this may afford some protection against predators (such as gastropods and echinoderms), the observed restricted distribution of both genera off the west coast (Fig. 27) suggests that this porous structure is ineffective in protecting the delicate polypide from hydrodynamic forces. Both genera were usually found in protected environments at mid-depths (Fig. 27) and while Cribrilina may be exposed to water movements at greater depths (= regional stenosis), the degree of turbulence which it can withstand at these depths is thought to be small.

Cryptocyst

In contrast to the semi-exposed distribution of bryozoans with marginal spines, it appears from the evidence presented in Fig. 26, that the presence of a calcified cryptocyst allows a potential for colonisa-
tion of more exposed habitats. Although *Steganoporella* sp. and *Smittinora* sp. exhibit regional stenosis and are restricted to protected environments at shallow depth (Fig. 26), the exposed environments which they occupy at greater depths appear to be subject to more extreme hydrodynamic forces than those habitats, at the same depth, occupied by non-cryptocyst-bearing anascans. Nevertheless, the absence of cryptocyst-bearing anascans in shallow, high-energy environments off Bellairs suggests that this structure is inadequate protection against the higher hydrodynamic forces which exist in these exposed environments (compare *Anasca* in Figs. 26 and 27 with *Ascophora* in Fig. 25).

**Sub-order Asconhora**

The frontal wall of all ascophoran bryozoans is strengthened with a layer of calcite. In many Ascophorans, however, external secondary calcification, by way of pores on the frontal wall, results in the development of a layer of aragonite or High Mg-calcite, which increases the thickness of the frontal wall considerably (Rucker and Carver 1969) and often obscures skeletal features (*Schizonorella* sp., *Trematocecia turrita*, *T. magnifera* (Plate 17b) and *Rhynchozoon rastratum* (Plate 17a)). Those Ascophorans which lack secondary calcification (such as *Escharina pes anseria*, * Parasmittinga ophidiana*) often possess long oral spines which develop as a semi-circular fence around the orifice. These spines are rigid and are probably used in feeding (see section following).

Large spherical ooecia are also a characteristic feature of the Ascophora. These reproductive structures, which develop ahead of the orifice, may be significant in modifying water currents in the vicinity of the oral region (see following section).
a) Calcification in *Rhynchozoon rastratum* partially obscures characteristic features of zooids. However, avicularia are still visible.

Scale bar: 0.2mm

b) Calcification in *Trematoecia magnifera* obscures most features and provides protection against predators and hydrodynamic forces in high energy environments.

Scale bar: 0.2mm
Functional morphology of the Ascophora in relation to their Distribution off Bellairs

Secondary Calcifications

All of the bryozoans found in the shallow, exposed high-energy environments off Bellairs are members of the Ascophora and all possess secondary calcification (Fig. 30). In addition, many of these acrophilic (exposed) forms are composed of short erect zooecia which produce small, heavily calcified colonies (Schizonorella sp., Trematoecia turrita and T. magnifera - Plate 8). The adaptations are consistent with life in a high energy environment and may be beneficial in protecting the polypide from hydrostatic damage and sediment abrasion associated with such an environment.

In contrast, ascophoran bryozoans characteristic of low-energy, cryptic environments on the west coast are delicate forms which lack this secondary calcification (for example Chorizonora brogniartii and Crepidacantha longiseta).

Oral spines, secondary pits and oecia

Ascophoran bryozoans of cryptic, low energy environments are laminar forms which normally grow closely attached to the substrate. Because of the thick boundary layers associated with these environments, (Chapter 1, Section 1.36 and Section 2.223 above and Figs. 7, 28), colonies will receive very little food passively by way of water movement. This can be overcome, either directly by active feeding on the part of the zooid (= tentacular movement) or indirectly by improving the flow regime in the boundary layer.
It seems likely that this improvement is brought about by irregularities on the colony surface (such as spines, pits or ooecia) which disturb the laminar flow of the boundary layer, thereby creating vortices on their downstream sides (compare Figs. 28 and 29) (Schultz-Grunow 1956, Reidl 1971). The resultant decrease in current velocity (Shapiro 1941, Allen 1970) allows food particles to settle out of suspension. As the vortices are directed towards the oral region (Fig. 29), they may improve passive feeding by directing settling food particles towards the mouth.

In support of this hypothesis, Ryland (1970) has recorded the presence of elongate tentacles in deep-sea bryozoans. It is conceivable that these tentacles are similar in function to oral spines and ooecia in that they increase the food potential of low velocity currents by disturbing the boundary layer in regions of reduced hydrodynamic flow.

An erect colony form, such as that of Retepora sp. may similarly raise the feeding zooids into regions of high flow velocities in the cryptic low-energy environments in which it is found (Fig. 27).

In conclusion, it appears that bryozoans on the reefs off Bellairs are distributed according to the degree of hydrodynamic exposure. Within each environment, certain morphological adaptations are thought to optimise the food-gathering potential of the colony as a whole.

In general, the simple cyclostome and gymnolaemate (Anascan and Cribirimorph) bryozoans are restricted to cryptic, low-energy environments whereas the more specialised Anascan bryozoans, with their capacity for secondary calcification, are more widespread in their distribution.
2.23 FORAMINIFERANS

2.231 Introduction

The calcareous encrusting Foraminifera of the Bellairs region of Barbados are represented by 7 genera belonging to 5 families (Table 2).

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</table>

Table 2 Classification of the Encrusting Foraminifera found on the Fringing and Offshore Reefs at Bellairs, Barbados.

All of the foraminiferans listed are encrusting in habit, being firmly attached to a solid carbonate substrate throughout their adult life. Encrusting foraminiferans were found at all depths examined off Bellairs, many being of fairly eurybathic occurrence. Most species were found in cryptic habitats where the level of illumination was low. In such habitats, attached foraminiferans were often a significant element of the encrusting fauna. Except for Gysina plana (Parker, 1959) which produced large crusts of up to 3500 mm$^2$ in diameter (Fig. 35), most Foraminifera were small in size (less than 10 mm$^2$).
2.232 Previous Research

No single work deals exclusively with the encrusting Foraminifera of Barbados. Hofker (1969) described foraminiferans recovered from 2 dredge hauls in 100m and 200m depth off Holetown on the west coast, in which some of the reef-dwelling forms were represented (Carpenteria utricularis, C. hassleri, Planorbulina sp. and Biarritzina sp.). As depth plays an important part in the distribution of attached foraminiferans of Barbados (see Section 2.233 following), it is unlikely that dredge hauls from such depths would record many littoral or sublittoral species.

All of the species found at Bellairs have been described from other Caribbean and Atlantic areas. These include Homotrema rubrum from Bermuda and Mexico (Emiliani 1951, Lowenstein 1967, Garrett et al. 1971, Rooney 1970, Logan et al. 1969 and Ginsburg and Schroeder 1973), Gunzina sp. from Mexico (Logan et al. 1969), Planorbulina sp. from the Netherlands Antilles (Hofker 1964), Carpenteria sp. from the north coast of S. America (Carter 1876, Drooger and Kaaschieter 1958, Hofker 1969) and Bdelloidina and Placopsilina from San Andres (Bromley 1970, Voigt 1970 and Bromley and Voigt 1974).

Although there is a great deal of generalised information on the geographical and bathymetric distribution of the foraminiferans, (Pflüger 1960 for review), very little is known of their detailed ecology. This, in part, is a result of the difficulty of laboratory simulation of the marine environment and its micro-habitats.

Much of the available ecological data refers to unattached benthonic examples and deals mainly with substrate preferences and
temperatures of reproduction (Phleger 1960).

The conclusions arrived at in the present section regarding the ecology of the foraminiferans from the west coast of Barbados are based chiefly on observed patterns of distribution of foraminiferans on collected specimens and on published biological data.

2.233 Distribution of Individual Genera

Introduction

In the following section, the distribution of the encrusting foraminiferans on the reefs off Bellairs is described. Detailed morphological and anatomical descriptions of each form are given in Appendix 2 and in Appendix Plates 11-18.

Genus CARPENTERIA

CARPENTERIA UTRICULARIS (Carter)

Two forms of Carpenteria utricularis exist on the reefs off Bellairs: a conical form and a globose form.

Carpenteria utricularis - conical form

(Fig. 31)

Maximum abundance of the conical form of C. utricularis (in terms of number of individuals/unit area) occurs in shallow, semi-exposed shaded-dim areas, often on smooth, unencrusted substrates, such as the under-sides of Agaricia agaricites coral plates or on dead crustose coralline algae (Plate 18). In these restricted habitats, the conical form is rarely overgrown by other encrusters.
Carpenteria utricularis - globose form

(Fig. 32)

Abundance of the globose form increases rapidly at depths greater than 5m. At all depths, abundance is greatest in dim and dark habitats (Fig. 32). The delicate, globose tests found in cryptic habitats (Appendix Plate 12) are normally attached to highly irregular, dead skeletal surfaces which are only otherwise occupied by similar sciophilic encrusters (Fig. 37). Occasionally, in more exposed situations, the test assumes a more conical form of compressed globose chambers which often overgrow crustose coralline algae (Appendix Plate 12b). This form may simply be an intermediary between the more extreme conical and globose forms.

In contrast to the shallow, semi-exposed planar substrates occupied by the compressed, conical form of C. utricularis, the delicate globose form appears to prefer much deeper, more cryptic habitats where crevices and/or surface irregularities afford some degree of protection against hydrodynamic forces and sediment abrasion.

Carpenteria Hassleri

Only 17 examples of C. hassleri were recorded from the west coast reefs. Many were damaged and were, presumably, dead when collected. Most were found in the 16-23m depth range, with only 3 occurring deeper than this at 45m (Fig. 37). All examples occurred on dead skeletal substrates in low energy, dimly-lit habitats. (Appendix Plate 13).
Fig 31 Distribution of **CARPENTERIA utricularis** (conical form) in terms of Depth & Light

Fig 32 Distribution of **CARPENTERIA utricularis** (globose form) in terms of Depth & Light

Fig 33 Distribution of **HOMOTREMA rubrum** (branching form) in terms of Depth & Light

Fig 34 Distribution of **HOMOTREMA rubrum** (encrusting form) in terms of Depth & Light
Genus HOMOTREMA

HOMOTREMA RUBRUM (Lamarck)

Tests of H. rubrum are highly variable in form. Three types were found on the reefs at Bellairs. These are (1) a delicate branching form which develops from small, discrete 'spot-like' tests (Appendix Plate 14), (2) a low, broad closely adherent (= encrusting) form (Appendix Plate 15) and (3) a tall, globose form (Appendix Plate 16) (Fig. 35).

H. rubrum - branching form (Appendix Plate 14)

Although abundance (measured in terms of number of individuals/unit area) slowly decreases with depth (Fig. 33), maximum abundance is seen in dim or dark locations. Both distribution and gross morphology of this form appear to be related to hydrodynamic exposure (see Section 2.234 following).

The branching form is usually found on dead skeletal substrates and is most often overgrown by similar sciaphilic organisms, such as bryozoans and serpulid worms. In more exposed locations, this form both overgrows and is overgrown by crustose coralline algae, such as Mesophyllum.

H. rubrum - encrusting form (Appendix Plate 15)

Maximum abundance of the encrusting form is found in shallow, shaded and lighted environments (Fig. 34) and decreases with depth. In Barbados, the encrusting form of H. rubrum appears to be absent at depths greater than 30 m (see Lowenstam 1967 and Rooney 1970 who both found a similar distribution in Bermuda) and in general, has a more restricted occurrence than either the branching or the globose forms (Figs. 35, 37). Substrates of attachment consist chiefly of living and dead crustose coralline algae (such as Mesophyllum) and dead
skeletal surfaces.

*H. rubrum* - globose form (Appendix Plate 16)

Although data on the distribution of the globose form is limited, it appears to be restricted to dim and dark habitats at depths of less than 24m. Substrates include dead skeletal surfaces and dead crustose coralline algae (Fig. 37), but because of its protruding growth form, it is rarely overgrown, except at its base where it is occasionally overlapped by crustose corallines and bryozoans.

**Significance of the polymorphic forms of**

*H. rubrum*

Previous studies of the distribution of *H. rubrum* on recent Atlantic reefs have produced somewhat conflicting results, despite the fact that research has been confined to a single area (Bermuda). In Bermuda, Emiliani (1951) recognised 5 morphotypes of *H. rubrum*. He suggested that the distribution of these 5 forms was related to some specific (but unnamed) environmental or micro-environmental factor. Both Lowenstam (1967) and Rooney (1970) have explained the distribution of the various forms in terms of hydrodynamic exposure and depth. A zonation, similar to that in Bermuda, was found on the Bellairs reefs (Figs. 3, 37). Here, the low, encrusting form is characteristic of surface, exposed areas, the globose form is usually found in sheltered micro-environments and the delicate branching form is characteristically found in low-energy, protected habitats. In addition, areas of irregular topography on shallow reefs in Barbados provide low-energy micro-environments in an otherwise high-energy environment. Colonisation of these protected micro-environments extends the range of delicate forms into what would
otherwise be inhospitable habitats (= regional stenosis).

With decrease in turbulent energy and/or depth, the number of morphological variants decreases. Fig. 37 indicates that both the encrusting and globose forms decrease in abundance with depth, until only the low-energy environment, branching form remains at depths greater than 25m.

So far in this study, the 3 morphotypes of H.rubrum have all been considered as the same species, following the practice of previous authors (Emilianii 1951, Lowenstam 1967). On this basis, the forms from Barbados are thought to be environmentally produced phenotypes. However, the possibility arises that the various forms are, in fact, sub-species of H.rubrum or even totally different species. If so, then the polymorphic forms may result from differences in genetic constitution and not from environmentally induced variations effected during growth. Similar considerations also apply to the forms of C. utricularis (see above).

Whether or not these various forms from Barbados are genetically or environmentally induced cannot, as yet, be ascertained and will depend on further experimental research on the settlement and growth patterns of each genus in different environments.

Genus GYPSINA

GYPSINA PLANA (Parker and Jones)

Gypsina plana occurs at all depths examined off Bellairs (Fig. 35), although the number of crusts and their average area is greatest at shallow depths. In addition, crust area is proportional to the value of incident light, being greatest in lighted areas (Fig. 35). As Gypsina plana occurs as smooth encrusting sheets (Plates 26b, 39, 42a, 45) at all depths, hydrodynamic exposure appears to have little influence on test morphology.
Fig 35  Distribution of *GYPSINA piana* in terms of Depth & Light

Fig 36  Environmental Distribution of the Various Morphological Forms of *HOMOTREMA rubrum*
Whereas most attached foraminiferans off Bellairs have a constant upper size limit, *Gypsina plana* is more akin to a colonial organism in that chambers are continually added to the circumference to give a crust of considerable lateral extent. While the success of most foraminiferans in a particular habitat has been based on the number of individuals/unit area, success of *G. plana* is assumed to be related to the size of the crust itself. Maximum crustal area of *G. plana* is found at all depths in exposed, lighted environments where crusts may be up to $3500mm^2$ in area. Microscopic examinations undertaken on a number of specimens of *G. plana* from Barbados reveal the presence of unicellular organisms contained within the protoplasm (Plate 19). Since most foraminiferans are slow-growing heterotrophic organisms which do not require sunlight for food, the abundance and areal extent of *G. plana* within lighted habitats suggests that these unicellular organisms may be symbiotic and may aid in the growth and calcification of *G. plana* (in much the same way as zooxanthellae in scleractinian corals), allowing it to compete successfully with other photophilic organisms, such as crustose coralline algae, in lighted environments.

*G. plana* is rarely overgrown. Apart from crustose coralline algae which frequently overlap its margin, very few organisms from the reefs off Bellairs appear to be capable of colonising the surface. While the well-lit, exposed habitats occupied by *G. plana* may exclude some of the more sciaphilic organisms from competing with it, it seems that the irregular surface micro-topography of *G. plana* discourages attachment of settling larvae of other photophilic encrusters (see Chapter 4, Section 4.31).
Foraminiferan assemblage on the underside of the coral Agaricia agaricites. Of the four conical forms of Carpentaria utricularia (C), visible at the upper right, two have undergone secondary calcification, resulting in a reticulate surface patterning.

Two colonies of Bdelloidina sp (B) are visible encircling sponge papillae at the centre of the plate. Small examples of the branching form of Homotrema rubrum (H) are visible at top centre.

Scale bar: 5mm

Photomicrographs of squashes made of Gypsina plana. Protoplasmic cell contents of the foraminiferan are visible as circular drops of variable dimensions and are brown in colour. Circular and oval dark objects (green in colour) are thought to be symbiotic algae contained within the protoplasm of the foraminiferan.

Scale bar: 0.01mm
Genus *BDELLIOIDINA* (Carter)

**BDELLIOIDINA** sp.

The present study recorded *Bdelloidina* sp. from a variety of depths off Bellairs. Tests are usually confined to the smooth, unencrusted undersides of corals (for example *Agaricia agaricites*) which have been bored by the sponge *Cliona* sp. and are characteristically found encircling the respiratory papillae of the sponge (Plate 18). While similar associations of sponge borings and foraminiferans have been reported from the Cretaceous (Bromley 1970, Voigt 1970, Bromley and Nordman 1971), it is only recently that living examples have been described. Bromley and Voigt (1974) have found large numbers of *Bdelloidina aggregata* on material from the Recent reefs of San Andres, Columbia. Environments of occurrence in Colombia appear to be similar to those occupied by *Bdelloidina* in Barbados.

Several other attached foraminiferans were found on the fringing and offshore bank reefs off Bellairs. However, as they occur in insufficient numbers to permit accurate interpretation of their distribution and ecology, the following notes are restricted to brief descriptions of localities of occurrence.

Genus *BIARRITZINA* (Loeblich and Tappan)

**BIARRITZINA** sp.

Only one specimen was found, encrusting a very thin layer of crustose coralline algae on the dimly-lit underside of a *Porites* coral stick at 20m depth.

Genus *PLANORBULINA*

**PLANORBULINA MEDITERRANEENSIS** (d'Orbigny)

*P. mediterraneensis* was found only on the shaded undersides of coral plates (such as *Porites astreoides*) in the 15-25m depth range. Tests were
restricted in occurrence to planar even substrates such as the crustose coralline *Mesophyllum* and the smooth bases of branching corals such as *Eusmilia fastigiata* (*Planorbulina* sp. has also been recorded by the present study from small internal cavities within rhodoliths from the exposed, high-energy east coast lagoon at Bath, Barbados).

2.234 Functional morphology of the Foraminiferans and the Factors affecting their distribution on the reefs off Bellairs

**Introduction**

The factors which affect the distribution of the foraminiferans on the reefs at Bellairs are outlined below. Interpretation of the ecology of encrusting foraminiferans is extremely difficult, largely because of a lack of published data on their biology and ecology. As no experimental ecological work was undertaken in their present study, many of the conclusions outlined below are tentative and are based chiefly on a comparison of foraminiferan distribution and known environmental factors. Special emphasis is given to those factors which have a direct effect on distribution.

**Physical factors**

**Depth**

Since the purely hydrostatic (= pressure) effect of depth has little influence on foraminiferan distribution (Haynes 1965), the zonation in response to depth, observed both on the west coast reefs of Bellairs (Fig. 37) and elsewhere (Phleger 1960) probably results from variations in other factors brought about by a change in depth. As temperature and salinity are constant on the Bellairs reefs (Chapter 1, Section...
<table>
<thead>
<tr>
<th>SPECIES</th>
<th>No. of Samples</th>
<th>Abundance v Depth</th>
<th>Substrates</th>
<th>Habitats</th>
<th>Skeletal Characteristics</th>
</tr>
</thead>
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<td>20</td>
<td>4</td>
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<td>In unencrusted substrates in exposed locations at shallow depth.</td>
<td>Heavily calcified low skeletal test</td>
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<tr>
<td>C. striolaris</td>
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<td>10</td>
<td>Living and Dead Crustose Corallines, Dead Skeletal substrates, Dead Gypsina</td>
<td>Cryptic, low-energy environments</td>
<td>Delicate gypsina forms in low-energy environments, low skeletal forms where exposed</td>
</tr>
<tr>
<td>C. striolaris</td>
<td>17</td>
<td>1</td>
<td>Dead skeletal substrates</td>
<td>Restricted to irregular surfaces in cryptic localities</td>
<td>Expansive tests or low relief</td>
</tr>
<tr>
<td>C. crassula rubrum</td>
<td>1250</td>
<td>10</td>
<td>Living and Dead Crustose Corallines, Dead Skeletal substrates</td>
<td>Shallow water high-energy environments</td>
<td>Semi-encrusted forms in exposed localities</td>
</tr>
<tr>
<td>C. crassula rubrum</td>
<td>12</td>
<td>1</td>
<td>Living and Dead Crustose Corallines, Dead Skeletal substrates</td>
<td>In both high- and low-energy environments</td>
<td>Semi-exposed forms in exposed localities</td>
</tr>
<tr>
<td>C. crassula rubrum</td>
<td>250</td>
<td>50</td>
<td>Living and Dead Crustose Corallines, Dead Skeletal substrates, Living and Dead corallines</td>
<td>Co-dominant with Crustose Corallines in Lighted locations at shallower depths</td>
<td>Plate, sheet-like shapes in all habitats</td>
</tr>
</tbody>
</table>

Fig 37 Summary of the Distribution of Encrusting Foraminifera on the Reefs off Bellairs, Barbados
1.3), factors such as the amount of light, turbulence, turbidity and availability of food are probably critical in foraminiferan distribution. The depth related effects of each of these factors is discussed below.

**Turbidity**

The effect of settling sediment on the growth of encrusting foraminiferans is apparently unknown. Turbidity indirectly affects their distribution by way of its curtailing effect on the transmission of light underwater and therefore the availability of phytoplanktonic food. The implications of this are further discussed below (light).

**Light**

As foraminiferans are holozoic organisms, depending on external organic sources of food (Myers 1943), their distribution, in theory, should not be directly dependent on the value of incident light. However, the evidence presented in Fig. 37 indicates that some encrusting foraminiferans from exposed and semi-exposed locations on the west coast off Bellairs are zoned according to the value of incident light. As their main food source, phytoplankton, is directly dependent on light for photosynthesis, the foraminiferans are restricted to the upper photic layers of the oceans (Myers and Cole 1957, Phleger 1960, Loeblich and Tappan 1964). As this layer extends below the maximum depth sampled in Barbados, however, (Ott 1975), the availability of food and therefore the amount of incident light, is unlikely to affect distribution significantly.

Many tropical foraminiferans are known to contain unicellular algae within their tissues (Cushman 1922, 1947; Loeblich and Tappan 1964; Logan et Al 1969). Whilst the
relationship between the alga and foraminiferan has been questioned by many authors (for examples Myers and Cole 1957), it is commonly assumed that the algae are symbiotic in nature (Cushman 1947). If this is so, then the host foraminiferan will probably be zoned according to the value of incident light and will be restricted to depths at which the contained algae can photosynthesise.

On the mid-west coast reefs of Barbados, two foraminiferans, *Gypsina plana* and the conical form of *Carpenteria utricularis* are thought to contain symbiotic algae. Both foraminiferans show photophilic trends in their distribution (Fig. 37) and both are green or brown in colour. In addition, microscopic examination of squashed specimens of *Gypsina plana* have revealed the presence of unicellular organisms which may be symbiotic in nature (Plate 19).

Haynes (1965) has summarised the symbiotic relationship of algae and foraminiferans and has suggested that the perforate radial high Mg-calcite walls of many hyaline (= glassy) tests (such as those of *G. plana* and *C. utricularis*) will permit the transmission of incident light and will probably aid symbiosis by providing a 'natural greenhouse' for the contained algae.

The expansive crusts of *G. plana* will also be beneficial to any symbiotic relationship by providing a large surface area for algal photosynthesis. In return, the algae may liberate certain metabolites which will, in turn, aid calcification and growth of the foraminiferan, in a manner similar to that suggested for corals and zooxanthellae by Yonge (1931) and by Goreau (1969).

In addition to this direct influence of light, the distribution of foraminiferans in relation to other environmental factors (such as hydrodynamic exposure and substrate type) is often reflected in the value of incident light. (see below).
**Hydrodynamic exposure**

The turbulent inshore waters of the Bellairs region (Chapter 1, Section 1.3) promote the growth of holozoic organisms by transporting food supplies and $O_2$ to the organism and by removing waste metabolic products (Loeblich and Tappan 1964, Lowenstam 1967).

Hydrodynamic exposure exerts a considerable influence on the form of the test of many encrusting foraminiferans. For example, each of the 3 forms of *Homotrema rubrum* from Bellairs can be correlated with a habitat characterised by a particular degree of hydrodynamic exposure. (See Section 2.233 - *H. rubrum* and Fig. 35).

In general, low compressed forms (such as the encrusting *H. rubrum*, *G. plana* and the conical form of *C. utricularis*) are found in exposed turbulent environments whereas erect or branching forms (Branching and Globose *H. rubrum*, globose *C. utricularis*) are restricted to low-energy, cryptic environments. (See Section 'food' below).

**Substrate type**

Substrate is an important limiting factor in the distribution of benthonic foraminiferans and is often thought to be of greater importance than temperature or salinity (Phleger 1960, Loeblich and Tappan 1964). Since the present study is restricted to encrusting foraminiferans of reef-occurrence only, gross character of the substrate (that is, whether sand, mud or rock) has little influence on distribution.

However, the microtopography of the substrate does influence settling patterns. Small-scale irregularities on the substrate surface at shallow depth, in high-energy environments provide sheltered micro-cavities in which delicate forms from low-
energy environments can survive, thereby extending their range of habitats into otherwise unfavourable areas. (See Section 2.233 - Homotrema rubrum - above and section 2.3 following).

**Biotic Factors**

**Food**

Foraminiferans are suspension feeders which feed on dead organic matter, usually phytoplankton (Myers 1943). They therefore depend on water movements for their supply of food which is captured externally by means of a pseudopodial net* or reticulum (Marsalek et Al 1969).

In moderately high-energy environments characterised by thin boundary layers (Chapter 1, Section 1.36) no great skeletal modifications are needed to raise the filtering apparatus into the moving water layers above. However, in the thick boundary layers of lower energy environments, small foraminiferans will probably be immersed within a slow-moving water layer (Chapter 1, Section 1.36) and consequently, will receive very little water-borne food. However, many of the foraminiferans found within the low-energy environments of Barbados (Branching form of H. rubrum, Globose form of C. utricularis) are elevated forms whose tests probably have sufficient relief to raise the pseudopodial reticulum into the higher energy waters above the substrate boundary layer.

It appears that the size of an individual filter feeder is related to the amount of food available, since the largest foraminiferans from the reefs off Bellairs are those from exposed, high-energy environments where the rate of transport of food in

* Part of cell contents are extruded from the test to form a net-like feeding apparatus above the test.
a given area is high (for example the encrusting form of *H. rubrum*, *G. plana*). However, in low-energy environments where water movements and therefore the amount of food transported per unit area in a given time is considerably less, encrusting foraminiferans are considerably smaller (for example, the globose form of *C. utricularis* and the branching form of *H. rubrum*).

Bromley and Voigt (1974) have suggested that the relationship between *Bdelloidina* sp. and the boring sponge *Cliona* sp. is a commensal one. *Bdelloidina* sp. frequently grows around the inhalent and exhalent sponge papillae (Plate 18) and so is ideally situated to obtain food from currents generated by the sponge. Similar xenorheophilic* responses of other encrusting organisms have been described by Reidl (1971).

2.235 Conclusions

In conclusion, it appears that the overall distribution of the encrusting foraminiferans off Bellairs is effected by water movements within the marine environment, either directly as a result of food supply or feeding restrictions which they impose or indirectly as a result of morphological variations which they may induce. In addition, the distribution of some of the larger foraminiferans may also result from the beneficial influence of associated unicellular organisms contained within the animal.

* Xenorheophilic - adaptation or preference for microhabitats which are under the influence of water currents produced by other animals (Reidl 1966).
2.24 SERPULID WORMS

2.24.1 Introduction

The calcareous encrusting worms of the Bellairs region of Barbados are all members of the sedentary polychaete family serpulidae (Table 3).

![Phylum Classification Diagram](image)

Table 3 Classification of the Encrusting Serpulid Polychaetes found on the Fringing and Offshore reefs at Bellairs, Barbados.

Of the nine species which have been recognised, only four (Pseudovermilia multispinosa, P. fuscostriata, Vermiliopsis annulata and Serpula (lobiarcoi)) occur in sufficient numbers to permit quantitative investigation.

Although serpulid worms were recorded from all depths examined, maximum abundance usually occurred at mid-depth in cryptic environments. Locally, a single species was often abundant, with individuals overgrowing one another to form an elevated or laminar mass of tangled tubes (Plate 23). The majority of serpulids, however, occur as solitary tubes composed of either calcite or aragonite (Bornhold and Milliman 1973 for compositional data) which are attached to the undersides of coral plates or to the walls of cavities and overhangs.
Although serpulids readily overgrow dead skeletal substrates and crustose coralline algae, they are also frequent colonisers of normally 'inhospitable' substrates such as the surfaces of bryozoans and foraminiferans.

Since the animal itself is entirely contained within the calcareous tube and only emerges at the distal end to feed, colonisation of the inert, external surface of the tube by other encrusters is extremely common. Feeding occurs passively by means of ciliated tentacular crowns (Barrington 1967, Plate 20a) or by mucus nets. Serpulids are therefore dependent on water movements for their supply of food, and, on the reefs at Bellairs, are generally restricted to surfaces free of sediment in moderately high energy environments.

In Section 2.243 following, the more common serpulids are described in terms of their distribution. Illustrated morphological descriptions of all species are given in Appendix 3 and in Appendix Plates 19-22. Limiting environmental factors are discussed in Section 2.244.

2.24.2 Previous Research

Very few accounts deal comprehensively with the serpulid fauna of Barbados. Both Mullin (1923) and Treadwell (1924), and later Marsden (1960) described the polychaete faunas of Barbados, but in all cases, the genus Spirobranchus was the only serpulid identified from the coastal waters.

In a study of Caribbean Serpulinae, ten Hove (1970, 1973, 1975) has described 3 genera (Spirobranchus, Solerostylia and Pseudovermilia) which are common in Barbados. Other serpulids
PLATE 20
SPIROBRANCHUS GIGANTEUS

Left-hand plate illustrates the twin conical tentacular crowns used in food capture. Fine, hair-like filaments on the lophophores trap food which they then transfer to the oral region below.

Scale bar: 2mm

Right-hand plate illustrates the partially buried tube of *S. giganteus* when the tentacular crown is retracted.

Scale bar: 5mm

PLATE 21

*Hydroides* sp on the underside of the platy coral *A garicia* sp overgrowing both living and dead colonies of the bryozoan *Reptadeonella violartia*. Associated encrusters on the plate include *Edelloidina* sp (top right), the bryozoan *Gemelliporidra* sp (lower centre) and an encrusting sponge (lower left)

Small scale divisions: 1mm
related to those encountered in the present study are described in accounts of the polychaete faunas of Venezuela (Weisbord 1964) and of Brazil (Zibrowius 1970).

Whilst the composition of the tropical Atlantic polychaete fauna is known in considerable detail (see Weisbord 1970 for review), their ecology and distribution remains largely unknown. Specific references to serpulid distribution are few and are chiefly confined to descriptions of depths of occurrence. The interpretations of serpulid distribution are therefore based chiefly on existing accounts of serpulid biology and on their patterns of distribution as observed in the present study.

2.24.3 Distribution of Individual Genera

Genus PSEUDOVERMILIA

Pseudovermilia multispinosa (Monro)

Tubes of *P. multispinosa* were recorded from all depths examined and from habitats which ranged from shaded to dim/dark in degree of illumination (Fig. 38). Although maximum abundance (measured as number of tubes / unit area) occurred in dim habitats at shallow depth, there appears to be no correlation between the dimensions of *P. multispinosa* tubes and the depth of occurrence or degree of illumination of the habitat on the west coast reefs. *P. multispinosa* is most commonly found in protected habitats on substrates which consist chiefly of dead skeletal surfaces and bryozoans. Abundances may be quite high locally where intense overgrowing of tubes has taken place.

Previous accounts of Monro (1933) and Zibrowius (1970) have noted a restricted distribution of *P. multispinosa* in depths of 30-37m off the coasts of South America.
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<th>No. v Light</th>
<th>Substrates</th>
<th>Habitats</th>
<th>Skeletal Characteristics</th>
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<td>50-25</td>
<td></td>
<td>Dead Skeletal substrates</td>
<td>Occasionally semi-exposed, Usually</td>
<td>Thick-walled, linear tube, often clustered</td>
</tr>
<tr>
<td>multisetae</td>
<td></td>
<td></td>
<td></td>
<td>Dead Crustose corallines</td>
<td>cryptic</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Dead Crustose corallines</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Dead Gypsina</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Vermiliopsis</em></td>
<td>0.6 0</td>
<td>20-10</td>
<td></td>
<td>Dead Skeletal substrates</td>
<td>Low-energy environments at all depths</td>
<td>Perisome usually well developed in the environments - Intraspecific variation</td>
</tr>
<tr>
<td>annulata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Serpula</em></td>
<td>0.4 0</td>
<td>40-30</td>
<td></td>
<td>Dead Skeletal substrates</td>
<td>Semi-exposed locations at mid-depth</td>
<td>Max, tube length in lightest environments</td>
</tr>
<tr>
<td>(Cheloniella)</td>
<td></td>
<td></td>
<td></td>
<td>Dead Crustose corallines</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig 38  Distribution of the more common SERPULIDS off Bellairs, Barbados
Pseudovermilia fuscostriata (ten Hove)

Occurrences were restricted to depths greater than 14m and were most abundant in the 14-30m range, in habitats which ranged from shaded to dim/dark in degree of illumination (Fig. 38). Greatest abundance was found in dim habitats. There appears to be no correlation between the size of P. fuscostriata tubes and the depth or degree of illumination of the habitat. Substrates include dead skeletal surfaces and bryozoans in cryptic environments and crustose coralline algae (such as Mesophyllum) and the foraminiferan Gypsina plana in more exposed situations. A comparison of the relevant sections of Fig. 38 suggest that P. fuscostriata is generally more cryptic in occurrence than P. multispinosa.

Genus VERMILICOPSIS

Vermilioniosia annulata (Schmarda)

V. annulata occurs at all depths examined, in habitats which range from shaded to dim/dark in degree of illumination (Fig. 38). The bimodal distribution of V. annulata suggests that two morphological forms or sub-species may be present. The simple, 5-ridged form (see Appendix 3) is most abundant at shallow depth, in shaded and shaded/dim environments and may represent a different species or form to the peristome-bearing tubes (Appendix 3) which are most abundant in dim, protected environments at depths greater than 20m (Fig. 38). In all cases, V. annulata is restricted in occurrence to dead skeletal substrates.

Genus SERPULA

Serpula lobiancoi (Rioja)

S. lobiancoi is found at depths of 14-45 metres in habitats which range from shaded to dim/dark in degree of illumination. Although greatest
abundance was found in dim/dark localities at mid-depth, no correlation was found between tube size and the depth or degree of illumination of the habitat.

*S.(lobiancae)* frequently encrusts dead skeletal substrates and crustose coralline algae and is often found associated with solitary corals on the shaded undersides of coral blocks (Plate 22). On many crustose coralline algae substrates, there is a zone of dead algae surrounding the tube. It is conceivable that the worm may prevent overgrowth by the algae by secretion of some toxic or inhibiting substance.

The following serpulids occur in insufficient numbers to permit accurate quantitative determinations of their distribution. Descriptions are therefore restricted to generalised statements of environments of occurrence.

**Genus SCLEROSTYLA**

*Scleroctyla ctenactis* (Morch)

It appears, from the few specimens which were found, that *S.ctenactis* is restricted in occurrence to dimly-lit habitats at depths greater than 25m. Open, porous substrates such as the skeleton of the corals *Porites porites* and *Agaricia agaricites* seem to be the most suitable substrates for its embedded mode of growth.

Similar occurrences of *S.ctenactis* from other Caribbean areas have been described by ten Hove (1973). Neither the present study, nor those of ten Hove have found any correlation between tube morphology and the environment of occurrence.

**Genus PSEUDOVERMILIA**

*Pseudovermilia occidentalis* (McIntosh)

*P.occidentalis* was most commonly found at shallow and mid-depths in dim
PLATE 22

Association of *Serpula ?lobiancoi* and solitary coral sp A (unknown).

Scale bar: 2mm

---

PLATE 23

Colonial aggregations of *Filograna* sp on an artificial perspex substrate. Intergrown with and associated with *Filograna* sp are the crustose coralline *Mesophyllum* sp (lighter patches beneath tubes) and the bryozoan *Lichenopora* sp. Circular nail head used to attach plate to the mounting block is visible at top centre.

Small scale divisions: 1mm
localities. Although Bush (1910) reported P. occidentalis on Agaricia fragilis coral plates in the infralittoral zone of Bermuda, Zibrowius (1970) reported P. occidentalis from all depths off the coast of Brazil.

**Genus HYDROIDES** (Gunnerus)

*Hydroides* sp.

*Hydroides* was usually found at mid-depth off Barbados in dimly-lit habitats on dead skeletal substrates and occasionally on bryozoans.

**Genus FILOGRANA** (Oken)

*Filograna* sp.

Semi-colonial aggregations of *Filograna* are usually found on dead skeletal substrates in dimly-lit habitats at most depths.

**Genus SPIROBRANCHUS**

*Spirobranchus giganteus* (Pallas)

*S. giganteus* is found on the upper surface of most species of corals at all depths off Bellairs. The proximal part of the tube is commonly embedded within the coral skeleton (Plate 20b).

Similar occurrences from the coast of Barbados have been reported by Mullén (1923), Treadwell (1924) and Marsden (1960).

### 2.24.4 Functional morphology of serpulid worms and the Factors affecting their distribution off Bellairs

**Introduction**

There appears to be no single work which deals exclusively with the ecology of serpulid worms. Apart from the fairly specific works of Hartmann Schroeder (1967, 1971) most references to serpulid ecology are brief
and are usually contained within systematic works (such as Zibrowius 1970).

Therefore, the conclusions arrived at in the following section regarding serpulid ecology are based almost entirely on observations of their distribution on the west coast reefs of Barbados and on what little physiological and biological data exists.

Individual species on the reefs off Bellairs show very little morphological variation in different habitats. As most worms occupy fairly cryptic habitats, factors such as hydrodynamic exposure and sediment abrasion will probably have little effect on skeletal morphology. Most worms are fairly eurybathic in distribution and so are unlikely to be limited in occurrence by hydrostatic pressure. Temperature and salinity variations for the west coast of Barbados are discussed in Chapter 1, Section 1.3 and can probably be eliminated as limiting factors. Environmental factors relating to larval settlement and to food supply (such as depth, light and water currents) are probably more significant in limiting serpulid distribution. These factors are briefly discussed below.

Depth and Light

Most serpulid species have a fairly widespread depth-and light-related distribution on the reefs off Bellairs (Fig. 38). 2 species, however, Pseudovermilia fuscostriata and Serpula lobiancoi, exhibit strong sciophilic tendencies and both are found in dim and dark habitats at depths greater than 14m. As there is no obvious physiological explanation for this distribution, it may be the result of a negative phototactic response of the larva at the time of settlement.

Hydrodynamic exposure and food supply

Serpulid worms are impingement filter feeders which depend on external water currents for their supply of food (Nichol 1960). As a result, they
are restricted to well-flushed habitats and on the Bellairs reefs are often found on sediment-free substrates, either in semi-exposed situations or in cavities. Many of the larger serpulids will obviously occur only in more exposed habitats because of the lack of space and food within cavities.

**Competition**

**Interspecific**

Serpulid worms compete with other sciaphilic filter feeders (such as bryozoans and foraminiferans) for suspended detrital and planktonic food. Although each of these groups may be fairly specific in its food requirement (which would reduce competition for food) they are all found to occupy similar habitats on the Bellairs reefs. Competition for space between various filter feeders will therefore be a critical factor in serpulid distribution. As serpulids were often found overgrowing these other filter feeders, it is assumed that they are fairly successful encrusters within this habitat.

Whereas overgrowth of many filter feeders prevents feeding and may result in death by starvation, overgrowth of all but the oral region of the inert serpulid tube appears to have little effect on the activity of the organism and may even be beneficial in reinforcing the protective function of the calcareous tube.

Within the cryptic, medium-low energy environment, in which serpulids are found, initial settlement is normally restricted to relatively smooth substrates, such as the undersides of coral plates and crustose coralline algae. Subsequent growth of the tube may lead to colonisation of a variety of other, irregular substrates (such as bryozoans) by way of lateral overgrowth (Plate 21).
In more exposed (that is, lighted) environments, serpulids are less successful and are seen in places to be completely overgrown by crustose coralline algae.

Intraspecific

Dense, mono-specific clusters of serpulids occur frequently off Bellairs. Filograna sp. in particular, is often found in semi-colonial aggregations of sub-parallel tubes (Plate 23), an association which most likely results from the asexual mode of reproduction of Filograna (see Nichol 1960 for details). Although availability of food will obviously be a critical factor in the survival of worms within these dense associations, most examples of serpulids off Bellairs occur in well-flushed environments where the volume of suspended food material is probably quite high.

Summary and conclusions

While physical environmental factors probably determine the settlement patterns of most serpulid larvae, the ubiquitous distribution of adult worms in most habitats on the reefs of Bellairs suggests that the distribution of the majority of serpulids is effected by biological rather than by physical environmental factors during growth. Within most habitats, competition for space for both larval settlement and for adult growth and for food appear to be the principal limiting factors in serpulid distribution.
2.25 CORALS

2.251 Introduction

While the majority of corals (both Scleractinians and hydrocorals) are massive forms which can be considered as primary frame builders*, certain species are only found colonising this primary frame, either as encrusting sheets or knobs or as attached, bract-like plates. Because of their small size, however, and because they often act as a substrate for a considerable population of other, much smaller encrusters, these attached corals transgress the boundary between primary and secondary (ie encrusters) framebuilders*. As such, they are only considered briefly as elements of the encrusting fauna.

2.252 Scleractinia

Favia fragum (Oken)

Colonies of F.fragum occur as small knobs, 1-4 cm in diameter in shallow, well-lit and lighted environments on the fringing reefs at Bellairs (Plate 26a). Generally, colonies overgrow and are overgrown by Crustose coralline algae such as Porolithon, Lithophyllum and

* Primary framebuilders are those corals, whether massive or branching, which make up the initial framework of the reef and which constitute the greater part of the massive reef rock formed during later growth.

Secondary framebuilders are those encrusting and fragile branching organisms which live on or in the primary frame. Although unable to contribute significantly to the overall bulk of the reef, certain secondary framebuilders, such as the crustose coralline algae, are important in cementing together both primary and secondary framebuilders thereby consolidating the reef structure.
Neogoniolithon.

**Aparicia agaricites** (including *A. agaricites v. purpurea*)

(Pallas)

(*A. agaricites*) occurs either as encrusting box-like colonies 5-10 cm in diameter on horizontal or gently inclined reef surfaces or as plate-like colonies 10-20 cm in diameter growing out from the steeply-sloping sides and overhangs of coral spurs and from other, dead coral colonies. Both forms are usually attached to dead primary framework or to a crustose coralline algal, secondary, framework. The inert, shaded undersides of the platy form, in particular, provide a habitat for a variety of shallow-water sciaphilic encrusters, such as the coralline alga *Mesophyllum*, the encrusting form of *Homeo trema rubrum*, the conical form of *Carpenteria utricularia* and the bryozoans *Rentadecellia violartia* and *Trematoecia turritae*, as well as to some serpulid worms. Similar environments and similar encrusters are also found on the undersides of platy primary framebuilders such as *Montastrea annularis*, *Colpophyllia* sp. and *Manicina* sp.

**Mandracis sp. - Deepwater form**

An encrusting form of *Mandracis* sp. occurs as extensive thin laminar sheets 2-5 mm in thickness at depths greater than 10 m in shaded and shaded/dim environments where it is often associated with the crustose coralline alga *Mesophyllum* (Plates 27c, 28c and 40).

**Astrangia solitaria** (Lesueur) and Solitary coral sp. A (Genus and species unknown).

Both solitary corals found on the reefs at Bellairs were restricted in distribution to shaded/dim cryptic cavities at all depths examined. *A. solitaria*, in particular, generally occurs in clusters, associated with
bryozoans, serpulid worms and foraminiferans (Plates 22, 29b, c.).

2.253 Hydrocorals

*Millepora* sp. (Linneus)

Only one of the 4 forms of *Millepora* found on the reefs at Bellairs can be considered as encrusting in habit (Stearn and Riding 1973). Whereas the 3 erect species, *M. complanata*, *M. alcicornis* and *M. squarrosa* are encrusting at the point of attachment only, the encrusting form (possibly a variety of one of the other species) occurs as an extensive, laminar colony which is entirely attached to the substrate (Plate 43). Colonies are only occasionally found and generally achieve their greatest crustal area on expansive but inert substrates, such as dead coral heads (Plate 43) and on artefacts such as wrecks and harbour constructions. In addition, living and dead gorgonian corals are frequently encrusted by *Millepora*, the living gorgonian being separated from the hydrocoral by a zone of dead tissue (Plate 46).

Serpulid worm tubes (especially *Spirobranchus giganteus*) are frequently overgrown by and included within the hydrocoral skeleton. Occurrences of all species of *Millepora* are restricted to lighted and just lighted surfaces at depths of less than 20m. With decrease in depth, the most fragile branching and bladed species disappear, until only the box-like and encrusting forms remain in shallow, high-energy environments (Stearn and Riding 1973). Stearn and Riding (op cit.) considered that the encrusting form of *Millepora* is an environmentally-induced phenotype of the other 3 species and will probably give rise, either by vertical accretion or by branching, to one of the other 3 forms.
SECTION 2.3

GROWTH AND DISTRIBUTION OF ENCRUSTING ORGANISMS ON ARTIFICIAL SUBSTRATES

- EXPERIMENTAL EVIDENCE
Experiments involving the use of natural and artificial substrates in the study of sedentary organisms provide information on both the biology of the organisms themselves and on the structure of the community in general. By planting a variety of substrates in different environments underwater, it is possible to monitor the growth and distribution of encrusting organisms and also to determine the sequences of colonisation and therefore the succession of organisms in a community. During the initial stages of colonisation, it is possible to trace the development of plant and animal colonies in the absence of competition for space from neighbouring organisms. By providing settling encruster larvae and spores with a variety of substrates in a number of different orientations, it is possible to infer the behavioural responses of the larvae in relation to substrate type and orientation, at the time of settlement.

In the present study, 14 experimental substrate blocks were planted in a variety of locations on the Bellairs reefs. Individual experimental blocks consisted of 6 substrate types in a variety of orientations, providing in all, some 33 surfaces for colonisation (Plate 24 and Section 2.33 below). The blocks were placed in a variety of habitats and were left in position for periods of time ranging from 3 to 13 months. In this way, it has been possible to monitor the sequences of colonisation (and therefore the community succession) of the various blocks.

In most cases, the growth and distribution of encrusting organisms on the substrate blocks is very similar to their distribution on the reefs at Bellairs.
Experimental substrate block prior to immersion. Glass and perspex substrates, mounted on wooden stakes are visible at top right. Coral and brick substrates (here part of a brick pipe) are visible at lower left. All substrates are mounted in a concrete base.

Grazing scratches made by the sea-urchin *Diadema antillarum* on the foraminiferan *Gypsina plana*.
2.32 Previous Investigations

In general, investigations of the settlement and growth of encrusting organisms on artificial substrates have been conducted in temperate water environments. The total number of such experiments is small and they are, in most cases, restricted to observations of a single species or to a small group of related species (for example, the studies of Pomerat and Reiner 1942, Crisp and Ryland 1960 and Ryland 1960). In a number of such studies, laboratory experiments involving bryozoan and barnacle larvae, have provided valuable information on behavioural responses of the larvae at the time of settlement (Ryland 1960, Crisp and Ryland 1960). The present study has adopted methods and materials similar to those used by previous workers (Tandy and Colman 1931, Coe and Allen 1937, Pomerat and Reiner 1942), whereby substrates of different materials and of different surface characteristics are placed in the sea in a variety of orientations and then left for known periods of time. Glass plates, mounted in concrete or wire, have usually been chosen for experiments in both the natural environment (Coe and Allen 1937, Pomerat and Reiner 1942) and in the laboratory (Ryland 1960, Crisp and Ryland 1960).

Although most studies have found that settlement of heterotrophic organisms takes place on the shaded undersides and on the roughened surfaces of experimental substrates, Crisp and Ryland (op cit) have shown that some bryozoan larvae actually prefer upper, lighted and often very smooth, surfaces. All of the sessile filter feeders encountered in the present investigation, however, have preferentially colonised the roughened undersurfaces of substrates, where the influence of settling sediment (and of light in some cases) is minimal.

Coe and Allen (op cit) found that larval settlement on cement blocks in the sea off the coast of California, U.S.A. was heaviest near to the top of substrates and on outward-facing surfaces. Similar
distributions have been found by the present study on many of the blocks in cavity habitats on the Bellairs reefs and are thought to result from the greater supply of nutrients and settling larvae, as well as freedom from settling sediment, which exists near to the top of exposed substrate faces.

2.33 Construction of Experimental Substrate Blocks and Materials

2.331 Introduction

A total of 6 substrate types were utilised in the construction of the experimental blocks used in the present study. Of these, only coral was of natural, reef origin. The remainder (glass, perspex, brick, wood, concrete) were chosen as controls to monitor the process of encrustation of the coral block. Their inert nature also proved beneficial in that coral substrates (and their adherent biota) were more often grazed by echinoderms (and fishes) than were artificial substrates, with the result that much of the evidence of community succession on the coral was lost. Two of the inert substrates, wood and concrete, were used as mounting media for the other 4 substrates.

The area of each substrate type and the total area of the block available for colonisation are given in Table 4.

2.332 Individual Substrate Types

Glass

3 glass microscope slides were mounted in a wooden block in the arrangement shown in Fig 39. One face of the vertical glass slide was ground using a coarse abrasive and the other left smooth. Of the 2 horizontal slides, one slide was ground on both upper and lower surfaces, while both surfaces of the
Fig 39  Character & Orientation of Glass & Perspex Substrates
other horizontal slide were left smooth. In this way, a total of 6 glass surfaces, each of different characteristics and of different orientation were available for colonisation. Each slide was mounted in a wooden block, which was itself mounted in the concrete base (Plate 24).

**Perspex**

3 perspex 'petri'-dishes were mounted on a wooden stake in the arrangement shown in Fig 39. Half of the surface of each dish was roughened with an abrasive. Each vertical dish was mounted such that the junction between the roughened and smooth areas was vertical (Fig 39). In this position, the slight shade afforded by the horizontal dish would affect both surfaces of the vertical plate to an equal extent. In all, a total of 6 perspex substrates of different surface characteristics and of different orientations were available for colonisation.

**Coral**

Dead coral blocks were removed from the living reef, were washed in fresh water for 48 hours and were then oven dried at 60°C for 24 hours. In this way, any organisms attached to the block or living within it would be removed prior to planting on the reef. The coral blocks were then trimmed into cubes of uniform dimensions (Table 4) and were mounted vertically in the concrete base (Plate 24).

**Brick**

Baked clay housing bricks and pipes were chosen as experimental substrates because of the nature of their surfaces, which superficially resembled the rough, porous surfaces of the natural coral substrates. This enabled comparisons to be made between the patterns of colonisation of inert substrates and of natural coral substrates of similar surface characteristics.
Wood was chosen as a convenient medium on which to mount the glass and perspex substrates. It also provided an additional inert substrate for attachment of encrusters.

Concrete

All experimental substrates were embedded in a shallow concrete base, weighing approx. 10 kg (Plate 24).

2.34 Location of Experimental Substrate Blocks

Table 5 lists the various experimental blocks used, their locations and periods of immersion on the reef. A total of 14 blocks were planted on the reefs at Bellairs in locations which ranged from 1.5 to 50m in depth. Availability of materials limited the number of blocks which could be constructed and therefore the number of reef environments which could be exploited. Where possible, blocks were located at regular depth intervals in a variety of habitats (Table 5). In order to monitor the sequences of colonisation of the various substrates, blocks from shallow depth were removed from the reef after various periods of immersion.

Within each depth range, both concealed and exposed habitats were chosen. In exposed locations, blocks were placed horizontally on top of the reef surface, away from the sheltering or shading effect of neighbouring corals or surrounding reef topography. In this position, blocks were evenly illuminated from above. Horizontal surfaces on the blocks received maximum illumination, while vertical surfaces and the undersides of substrates were shaded from direct illumination and thus provided information on cryptic and cavity encrusters at that location.
<table>
<thead>
<tr>
<th>SUBSTRATE TYPE</th>
<th>AREA OF EACH SURFACE (cm²)</th>
<th>NUMBER OF SURFACES</th>
<th>TOTAL AREA OF SUBSTRATE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glass</td>
<td>15.0</td>
<td>6</td>
<td>90.0</td>
</tr>
<tr>
<td>Perspex</td>
<td>63.6</td>
<td>3</td>
<td>190.8</td>
</tr>
<tr>
<td>Brick</td>
<td>42.0</td>
<td>5</td>
<td>210.0</td>
</tr>
<tr>
<td>Coral</td>
<td>42.0</td>
<td>5</td>
<td>210.0</td>
</tr>
<tr>
<td>Wood</td>
<td>28.0</td>
<td>8</td>
<td>224.0</td>
</tr>
<tr>
<td>Concrete</td>
<td>140.0</td>
<td>2</td>
<td>280.0</td>
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<tr>
<td></td>
<td>115.0</td>
<td>2</td>
<td>230.0</td>
</tr>
<tr>
<td></td>
<td>644.0</td>
<td>1</td>
<td>644.0</td>
</tr>
<tr>
<td></td>
<td>600.0</td>
<td>1</td>
<td>644.0</td>
</tr>
</tbody>
</table>

Total Area Available For Colonisation - 2678cm²

**Table 4** Areas of Experimental Substrates Available for Colonisation

<table>
<thead>
<tr>
<th>BLOCK</th>
<th>PERIOD OF IMMERSION (months)</th>
<th>LOCATION</th>
<th>DEPTH (m)</th>
<th>INCIDENT LIGHT</th>
<th>ENVIRONMENT</th>
<th>HYD. EXP</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>4</td>
<td>Cavity</td>
<td>8</td>
<td>Dim</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>4</td>
<td>Exposed</td>
<td>6</td>
<td>Lighted</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>4</td>
<td>Exposed</td>
<td>1.5</td>
<td>Well Lit</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>4</td>
<td>Cavity</td>
<td>1.5</td>
<td>Shaded</td>
<td>Mod./High</td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>4</td>
<td>Exposed</td>
<td>6</td>
<td>Lighted</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>4</td>
<td>Cavity</td>
<td>6.5</td>
<td>Shaded/Dim</td>
<td>Low/Mod.</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>3</td>
<td>Cavity</td>
<td>3.3</td>
<td>Dim</td>
<td>Low/Mod.</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>4</td>
<td>Cavity</td>
<td>3.3</td>
<td>Shaded/Dim</td>
<td>Low/Mod.</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>4</td>
<td>Exposed</td>
<td>15</td>
<td>Just Lighted</td>
<td>Low/Mod.</td>
<td></td>
</tr>
<tr>
<td>J</td>
<td>4</td>
<td>Exposed</td>
<td>50</td>
<td>JLighted/Shaded</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>K</td>
<td>10</td>
<td>Exposed</td>
<td>1.5</td>
<td>Well Lit</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>11</td>
<td>Cavity</td>
<td>5</td>
<td>Shaded/Dim</td>
<td>Low/Mod.</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>9</td>
<td>Exposed</td>
<td>3.3</td>
<td>Lighted</td>
<td>Moderate</td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>18</td>
<td>Exposed</td>
<td>33</td>
<td>Just Lighted</td>
<td>Low</td>
<td></td>
</tr>
</tbody>
</table>

Table 5 Location, Environmental Setting and Periods of Immersion of Experimental Substrate Blocks used in the present study.
The undersides of ledges and overhangs and the interior of reef cavities were chosen as suitable locations for the experimental study of cryptic habitats. Most cavities were small, only extending 1-2m into the reef interior. As a result, cavities, especially those at shallow depth, were partially illuminated by scattered horizontal light. The resultant zonation of photophilic and sciaphilic encrusters on experimental blocks is outlined in Section 2.35 below. Blocks in both exposed and cavity locations were, whenever possible, placed on irregularities of the substrate, such that the base was raised above the reef surface. The small cavity so formed beneath the block was flushed by water and provided an additional habitat for the settlement of sciaphilic organisms.

2.35 Patterns of Encrustation
2.351 Exposed Blocks

Introduction

The upward-facing, lighted surfaces of all exposed blocks were, in every case, colonised by crustose coralline algae. Those blocks from shallow and mid-depths were colonised by Porolithon and Leptoheliolithon, while blocks from depths greater than 30m were dominated by Lesophyllia. Vertical faces, which were less densely populated, supported smaller crusts of crustose coralline algae, bryozoans (such as Lichenopora) and some serpulid worms (such as Pseudoverrillina multispinosa). Undersides of blocks developed a rich, sciaphilic fauna of bryozoans, foraminiferans and serpulids (Appendix Table 32).

Marked distinctions were often seen between the type and degree of colonisation of the various substrate types. Glass and perspex were often heavily colonised by crustose corallines, whereas brick, coral and wood supported much sparser algal populations.
Coral substrates, in particular, supported a reduced growth of encrusters. Grazing by the echinoid *Diadema antillarum*, as evidenced by scratch marks on the substrate (see Plate 25), appears to be responsible for the removal of considerable quantities of attached biota. In some cases, as much as 1.5mm of rock has been removed from each face. Only on artificial substrates, such as brick and glass, is the succession of encrusters complete.

Photophilic and sciaphilic encrusters found on exposed blocks are listed in Appendix Table 32.

### Colonisation of Exposed Glass Substrates

Of the 6 glass surfaces available for colonisation, upward-facing horizontal and vertical glass slides received the greatest encrustation of algae (Appendix Table 1). In all cases, colony size and number was greatest on upward-facing rough and vertical rough surfaces. Upward-facing smooth, vertical smooth and downward-facing surfaces were much less heavily colonised (Appendix Table 1). In many cases, smooth surfaces were only colonised as a result of overgrowth of crustose corallines from an adjacent roughened surface.

### Colonisation of Exposed Perspex Substrates

Perspex, like glass, often supported extensive growths of crustose coralline algae in exposed locations. Unlike the patterns of colonisation on glass, however, there was no distinction, in terms of density of colonisation, between rough and smooth perspex substrates - both supported similar populations of crustose corallines.

Horizontal plates, although in theory, ideally oriented for algal growth, tended to receive heavy sedimentation on their upper surfaces, preventing algal growth. Because of this overlying sediment,
the undersides of horizontal plates were frequently shaded. Consequently, they supported a population of sciaphilic encrusters, similar to those found on the underside of the block (for example, the bryozoan *Lichenopora* sp. and serpulid worms such as *Pseudovermilia multispinosa* and *Vermilisions annulata*) (see Appendix Table 32).

**Colonisation of Exposed Brick and Coral Substrates**

The horizontal tops of both brick and coral substrates were also subject to some degree of sedimentation, with the result that colonisation was restricted to the less-well lit vertical faces. The effect of grazing on the population of coral substrates is outlined above. Encruster populations on brick and ungrazed coral were in most cases identical.

**Colonisation of Exposed Wooden Substrates**

Colonisation of wooden mounting stakes was usually confined to a limited number of crustose coralline algae or bryozoan colonies. As a result, there was very little competition for space and colonies were often of considerable size (2300 mm$^2$ in the case of *Stylopora informata*).

**Colonisation of Exposed Concrete Substrates**

Except in a few cases, the upper surface of the concrete base was covered in sediment, often to a depth of 3-4 mm. On those blocks where settling sediment was not a problem, there was extensive algal and foraminiferal (*Grypsina plana*) colonisation of the concrete surface. Shallow water sciaphilic encrusters on the underside of the block include the branching and encrusting forms of *Homotrema rubrum*, the bryozoans *Lichenopora* sp. and *Parasmittina ochidiana* and the worms *Pseudovermilia multispinosa* and *Pilograna* sp. Sciaphilic encrusters of deeper water, exposed blocks were similar to those found on cavity blocks in shallow water (App. Table 32).
2.352 Concealed, Cavity Blocks

The pattern of colonisation of substrates within cavities depends very much on the shape and size of the cavity and its depth. Large, shallow water cavities are illuminated with scattered light from the bright exterior, while deeper water cavities, receiving less light, are usually darker with no directional illumination. Consequently, substrate blocks in shallow cavities which were illuminated on the side facing the exterior developed a zonation of encrusting organisms - vertical surfaces which faced the exterior supported encrusters of intermediate photophilic/sciaphilic affinities (for example, *Mesophyllum*, *Lichenopora* sp. and *Pseudovermilia multispinosa*), whereas vertical surfaces which faced the interior supported typical sciaphilic encrusters (Appendix Tables 27 and 32).

Heavy sedimentation within most cavities prevented colonisation of horizontal surfaces. Consequently, glass and perspex substrates were only colonised on their sides and undersides, while colonisation of brick and coral substrates was restricted to vertical faces. Furthermore, encrustation of both coral and brick substrates was often confined to the upper region of the vertical face, where the influence of settling sediment is least.

2.36 Growth and Distribution of Individual Encruster Species

(see also Appendix 4)

2.361 Introduction and Methods of Analysis

In order to determine the growth rates, distribution and patterns of colonisation of the various encrusting species, it was necessary to record for each substrate type, the total number of individuals of a species colonising the substrate, their size, their location on the substrate and the characteristics of their immediate environment (depth, amount of light, degree of hydrodynamic exposure). The maximum and the average
size of each encruster species on a particular substrate was then determined. The largest individual of each species was assumed to be both the oldest and the most successful colony on that substrate. In the descriptions following and in Appendix 4, it is assumed that the age of this specimen is equal to the period of immersion of the block. As this period varied considerably for different blocks, it was decided that the growth rate of each colony would provide a more reliable indicator of success in a habitat than colony size alone. The growth rate of the largest colony of a particular species on each substrate was calculated using the formula:

\[ R = \frac{\sqrt{A}}{2T} \]

where \( R \) is the mean radial growth increment (m.r.g.i.) of the colony expressed as mm/month, \( A \) is the area (mm\(^2\)) of the largest individual and \( T \) is the period of immersion of the block (months). The value of the mean radial growth increment assumes that the colony is circular in form and grows at an equal rate in all directions. Most of the crustose corallines, bryozoans and foraminiferan species examined on the experimental substrates were, in fact, circular in form or very nearly so. Consequently, the difference between actual radial growth rates and those expressed by the formula above is minimal.

Some colonies, such as the bryozoans *Hipponodina irregularis* and *Parellisina latirostris*, as well as most of the serpulid worms grow linearly. Growth rate in this case, was based on the length of the individual and its age - this assumes that the growth rate is linear in function. On most substrates, the percentage cover by each individual species, whether circular or linear, is proportional to its growth rate (that is, the higher the growth rate, the greater the area of substrate covered.

For some encruster species, such as the foraminiferans
Homoetema rubrum and Carpenteria utricularia, individuals, being of a limited, small size, do not expand as colonies. Success in a habitat, in this case, is based on the density of colonisation of a substrate by that species, measured as settlement rate per unit area (number of individuals/dm²).

In Appendix 4, each encruster species is described in terms of its distribution and growth rate, as indicated by examination of the various experimental substrates. Where possible, comparisons are made with the distribution of that species in the natural environment. Appendix Tables 2-24 summarise the information obtained from the various substrates. Specimens are ranked according to their mean radial growth increments or density of colonisation and not by crust/colony size alone. Light values correspond to those given in Fig 8.

2.37 Succession of Encrusters on Experimental Substrates

Appendix

Tables 25-27 list the various encrusters found on experimental blocks from similar environments after various periods of time. In most cases, the number of species present is proportional to the period of immersion of the block. Because of slight differences in the micro-environment of similar blocks, encruster species which are found on short-term blocks may be absent from similar blocks submerged for longer periods.

Because of the limited number of substrate blocks used at depth, comparisons of the populations of these blocks, which were in a variety of habitats, have not been undertaken.

Appendix Tables 28-30 list the various encrusters found on the experimental substrates in terms of their succession. Table 28 lists the initial colonisers - those organisms which were already established after a period of 3-4 months. Table 29 lists those encrusters which became established between 4 and 11 months (in depths of 3-5m only), while Table 30 lists those late stage or secondary
encrusters which were only found on substrates which had been underwater for periods greater than 11 months (33m depth only). Again, the limited number of experimental blocks restricts the number of comparisons which can be made. Appendix Table 31 lists those encrusters which were present on the Bellairs reefs themselves, but which were absent from the experimental substrates. In most cases, these encrusters were also of limited occurrence on the reefs. Exceptions include the bryozoans Schizoporella sp., Steganoporella magnilabra, Trematoecia magnifera and Reptadeonella violartia which are extremely abundant on the reefs (see Section 2.22 this chapter and Figs 25 and 26) but are entirely absent from the experimental substrates.

2.38 Summary

Appendix Tables

2-34 summarise the information presented in Appendix 4. Table 33 lists the various encrusters, their range of occurrence on the experimental substrates and the environment in which their maximum growth rate is attained. Table 34 ranks each group of encrusters in terms of maximum radial growth rates and, where applicable, rates of colonisation. It is interesting to note that both photophilic encrusters and sciaphilic encrusters (especially bryozoans) have similar growth rates on experimental substrates. In all but a few species, growth rates of colonies and individuals were found to be exponential — the initial high rate of growth seen in developing crusts (those on blocks of short periods of immersion) gradually decreases to a slower rate in larger, more mature crusts on blocks of long-term immersion. (this assumes that, in all cases, the largest colonies on blocks of long period of immersion represent growth since initial immersion of the block).
2.39 Conclusions

In general, the distribution of calcareous encrusting organisms on experimental substrate blocks is similar to that of organisms on the reefs themselves. In addition, the maximum growth rate of most experimental substrate colonisers occurred in environments similar to those in which the organism was found to be most abundant in the natural environment. On any one substrate, the area overgrown by a particular encruster was generally proportional to the growth rate of that species.

In most cases, blocks which had been underwater for less than 9-10 months were only sparsely colonised. All of the encrusters on these blocks (Appendix Table 28) were attached directly to the experimental substrate and only in a few cases were they overgrown. These initial or primary colonisers represent approximately half of the total number of encruster species recorded on the Bellairs reefs themselves. Experimental blocks immersed for periods greater than 10 months supported additional species (Appendix Tables 29 and 30). Since many of these species on long-term blocks were only found on surfaces already colonised by primary colonisers, they are assumed to be late-stage or secondary encrusters. Similarly, encrusters known to be present on the Bellairs reefs but which were absent from the experimental substrates (Appendix Table 31) may also be secondary encrusters.

On many blocks and especially on those which supported primary encrusters only, colonies had developed in the absence of competition for space from other encrusters. As a result, their form and growth rate probably represents the maximum attainable in that habitat. Except on exposed, roughened glass substrates where space available for colony expansion was limited, all crustose coralline algae and bryozoans on short-term (4 month) blocks developed as isolated circular or elliptical colonies. On blocks immersed for longer periods, however, colonies
frequently competed for space from their neighbours, resulting in crusts of irregular shape.

Comparisons of crustose coralline algal crust dimensions on natural (coral) and artificial experimental substrates emphasises the effect which predation can have on colony growth. On most exposed coral substrates, grazing by echinoids and fish had removed considerable amounts of both adherent crustose coralline algae and the substrate itself. Neighbouring artificial substrates, however, generally supported entire ungrazed crusts. This reduced population on natural substrates, which results from the opposing processes of growth and destruction is probably a more accurate reflection of the overall (net) process of encrustation as it exists on the reefs themselves, than are the densely colonised, but relatively ungrazed populations on the various artificial substrates. Nevertheless, the latter are significant in reflecting the patterns of settlement and distribution of organisms in the absence of competition for space and in the comparative absence of predators.

The overall similarity of the patterns of distribution of encrusting organisms on experimental substrates (where space for settlement and growth is relatively unlimited) and on the reefs themselves suggests that biotic factors such as competition for space and food and predation do not play a significant part in effecting the distribution of either the larvae/spores or adults of the various encrusters in the natural environment. More important factors in this distribution appear to be the nature and orientation of the substrate and the character of the physical environment (for example, the amount of light, the depth or degree of hydrodynamic exposure) in the immediate vicinity of that substrate.
In general, the influence of environmental factors on the growth and distribution of encrusters is related to the physiology of the particular group or species. For example, crustose coralline algae are autotrophic plants whose distribution is determined by the requirement of light for photosynthesis. Conversely, bryozoans are sessile animals which require an external organic source of food and, as a result, are restricted in their distribution because of the need for food-transporting currents.

Thus, within each encruster group, certain environmental factors are more critical in the distribution of the organism than others. While distribution probably cannot be attributed to one single factor, it is these limiting factors, as determined by the physiology of the organism, which affect the distribution of an organism most significantly.

2.42 Effects of Inter- and Intra-specific Competition

Competition for food and space is only found between organisms occupying similar habitats or ecological niches. Success or dominance within a habitat basically depends on the feeding ability of the individual, which, in turn, affects its growth rate - organisms of high growth rate usually overgrow those of slower rates. In general, photophilic organisms of high growth rate (such as the crustose corallines Porolithon and Neogoniolithon) predominate in exposed, illuminated environments, while colonial organisms of high growth rate (such as certain species of bryozoans) predominate in more cryptic environments (see Section 2.3 and Appendix 4 for individual growth rates).
2.43 Distribution of Individual Encruster Groups

2.431 Introduction

Although the overall distribution and zonation of a species of encrusting organism can be explained in terms of physiological responses to environmental stimuli (such as light, water movement and turbidity), the final form of an individual organism is governed by its mode of growth during development. In addition to being environmentally controlled, the mode of growth of an individual is affected by the nature of the underlying substrate (Chapter 4) and by competition and predation from other organisms.

However, factors such as competition and predation can be considered as random in their action and their specific effects on an individual can be eliminated by examination of a number of individuals from one particular environment. This will indicate the specific effect of environmental and physiological factors which, in turn, can be related to crust area and/or density of colonisation, and the success of an organism within an environment.

2.432 Crustose Coralline Algae

As autotrophic plants, crustose coralline algae are limited in their distribution by the requirement of adequate light for photosynthesis. As a result, colonisation by crustose corallines invariably occurs on exposed, upward-facing horizontal and vertical surfaces on the reef. Analyses of the distribution of the crustose corallines at Bellairs indicates that, although different genera may occupy similar environments, maximum crust area of each genus is achieved in different habitats, each characterised by a particular value of incident light. Within its optimum habitat, growth of an individual crustose coralline is prolific, resulting in rapid colonisation of the substrate. Other,
neighbouring photophilic encrusters of slower growth rate (including crustose corallines growing outside their optimum habitat) will be overgrown and will therefore be effectively excluded from that habitat.

2.433 Bryozoans

Except for certain bryozoans such as *Reptadeonella* sp., *Tronmotoeacia* sp. and *Schizoporela* sp. which colonise the surfaces of photophilic crustose corallines, the majority of bryozoans occur within sciaphilic environments. Such a distribution may result either from a negative phototactic response of the larvae at the time of settlement and initial growth (Chapter 2, section 2.32) or may be the result of exclusion from environments of greater illumination by the prolific growth of crustose corallines. Initial settlement (as indicated by experimental substrates) normally occurs on sediment-free, dimly illuminated sides and undersides of substrates characterised by a small amount of surface micro-relief (for example, roughened glass slides and dead skeletal substrates), rather than on the surfaces of other bryozoans, serpulid worms or foraminiferans.

Although mature crusts of bryozoans may achieve an area similar to that of crustose coralline algae in more exposed environments, growth proceeds by the addition of new individuals to the colony, rather than by radial expansion of the individual itself.

Bryozoans rely on external water currents, both for their supply of food and removal of waste, and for the distribution of the free-living larval stage. A zonation of forms develops in response to variations within the hydrodynamic regime, as a result of the ability of the individual to withstand and to use water movements for feeding.

2.434 Foraminiferans

With the exception of the photophilic foraminiferan *Gypsina plana*, all foram-
iniferans are sciaphilic encrusters which colonise dimly-lit, usually dead skeletal substrates. Most foraminiferans are capable of limited growth only, probably to a size at which the interior of the unicellular organism can just be supplied with diffused gasses and nutrients. Because only limited radial expansion can take place away from the point of larval settlement, substrates are generally confined to those surfaces suitable for larval settlement, such as dead skeletal surfaces and some sciaphilic crustose coralline algae (such as _Mesophyllum_ and _Lithothamnium_).

The anomalous photophilic distribution and the large size of crusts of _Gypsina plana_ is thought to result from the beneficial effect on growth of symbiotic algae contained within the protoplasm. The high growth rates which result allow colonisation of a variety of exposed and cryptic substrates.

2.435 **Serpulid Worms**

Serpulid worms are sciaphilic encrusters which normally colonise dimly-lit, dead skeletal substrates. Analyses of their distribution on both natural and artificial (experimental) substrates indicates that colonisation normally occurs on rough substrates of slight to moderate micro-relief. Although linear expansion of the tube during growth results in colonisation of a number of otherwise unsuitable substrates such as bryozoans and foraminiferans (see Chapter 4), growth rarely occurs outside of cryptic habitats. Because the worm itself is entirely contained within its tube (except at the distal end), there is no means of protecting the external surface of the tube from overgrowth, and consequently, serpulid worms are colonised by most of the encrusters occupying the same habitats.
2.44 Model of Encruster Distribution

Table 6 summarises the distribution of the more common encrusters within various environments on the reefs at Bellairs. Although each environment is characterised by a number of encruster species, in general, the population can be summarised in terms of those species which are either common or abundant within that environment. Species which are only rarely found within a habitat (less than 5% of the total encruster population within that habitat) have been omitted from the relevant section of the table.

2.441 Shallow Water Environments (0-10m depth)

In the shallow water zone occupied by the fringing reefs off Bellairs, exposed, lighted surfaces are characterised by crustose coralline algae, the foraminiferan Gymnana plana and various encrusting corals. In the inshore area (zones a and b of Figs 3 and 4), active growth of primary frame-builders is restricted to patches of the branching coral Porites porites and to massive coral heads of P. astreoides and Montastrea annularis. Approximately 70% of the exposed well lit and lighted surfaces within this zone are occupied by three genera of crustose corallines, Porolithon, Neogoniolithon and Lithophyllum. Porolithon and Lithophyllum are dominant in the shallowest (less than 1.5m), well lit areas, while Neogoniolithon and Lithophyllum are dominant in lighted areas in depths of 1.5 - 5m. The remaining 30% of exposed surfaces in the inshore zone are colonised by encrusting corals Favia fragrana, Ivaricia agaricites and the bladed, box-like and encrusting forms of the hydrocoral Hillepora sp. (Plates 1 and 26a).

Semi-exposed, shaded and dim cavities and overhangs in the inshore zone are characterised by encrusters of intermediate sciaphilic-photophilic affinities, such as the crustose coralline Mesophyllum, the
Table 6: Model of Encrustee Distribution within various habitats on the reefs at Barbados

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<tr>
<th>Depth</th>
<th>HIGH</th>
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OCCURRENCE: AMPLITUDE
Common: Occurrence
foraminiferans *Hematrya rubrum* (encrusting and branching forms) and *Carpenteria utricularis* (conical form) and by the heavily calcified bryozoans *Ruptadonella violartia*, *Schizonorella* sp and *Trematoecia turrita* (Plate 27c).

Seaward of the inshore zone, the spur and groove zone (zones c and d in Fig. 3 and 4) is characterised by an increase in the percentage cover by living coral. Spur tops are dominated at their seaward end by *Porites porites* (Plate 2a), while the leeward (shoreward) tops of spurs, as well as their sides and seaward faces are dominated by massive corals such as *Siderastrea* sp. and *Montastrea annularis*, as well as by numerous partially encrusting corals such as *Agaricia* sp., *Porites astreoides* and various forms of *Millepora* sp. (Plate 2b). Because of the abundance of coral within this zone, exposed surfaces available for colonisation by encrusters are reduced to 15-20% of the total surface area.

On spur tops, encrustation by *Neogoniolithon*, *Lithophyllum* and *Mesophyllum* is restricted to the partly shaded, dead bases of *Porites*. Exposed surfaces on spur sides are colonised by *Lithophyllum*, *Porolithia*, *Neogoniolithon* and *Cynopsa plana* (Plate 26a). Crevices and the shaded undersides of platy growth forms of corals on spur sides are inhabited by the crustose coralline *Mesophyllum*, by foraminiferans (*Hematrya rubrum* and the conical form of *Carpenteria utricularis*), by bryozoans (*Schizonorella* sp., *Trematoecia turrita*, *Lichenopora* sp., *Ruptadonella violartia*, *Crepidacantha longiseta* and *Holoporella tubulosa*) and by serpulid worms such as *Pseudovermilia multissimosa*, *P. fuscostriata* and *Hydroides* sp. (Plate 27b).

Other encrusters found within these shallow water cavities include solitary corals (*Astrangia solitaria*, unknown sp A,) and the erect branching coral *Stylaster roseus*. 
a) Thick, compact crusts of *Porolithon* sp overgrowing living coral *Favia fragum*. Inshore zone of the Bellairs fringing reefs. Depth 1.5m, Well Lit environment.

Small scale divisions: 1mm

d) Thick, compact crusts of *Cypsina plana* overgrowing dead coral (*Siderastrea* sp) substrate. Inshore zone, Bellairs fringing reefs. Depth 2-3m. Lighted environment.

Small scale divisions: 1mm

c) Shallow water encruster assemblage consisting of the coral *Agaricia agaricites*, the crustose corallines *Porolithon* (P), *Lithophyllum* (L) and *Neogoniolithon* (N) and the foraminiferan *Cypsina plana* (C)

Small scale divisions: 1mm
a) Dead skeletal substrate from a depth of 10m, reef top at Nurses Jetty, overgrown by a large colony of Steganoporella magnilabris (S) which is associated with and overgrown by the bryozoan Stylopoma sp. S. magnilabris exhibits a raised growing margin characteristic of encrusters which bridge irregularities in the substrate.

Small scale divisions: 1mm

b) Underside of a platy growth of Acardia sp from the fringing reef off Bellairs (3m depth) showing associations of the bryozoan Lichenopora sp (L), the worms Pseudovermilia multispinosa (P) and Sclerochyla ctenactis (S), the crustose coralline Mesophyllum sp and various encrusting foraminiferans (globose form of Carpenteria utricularia (G) and the branched form of Heteromera rubrum (H)) and solitary corals.

Scale bar: 1cm

c) Shaded side of coral substrate from the Bellairs fringing reef, 4m depth. Encrusting Radiacis (H) and the bryozoan Pentadeonella violarvia (R) are overgrown by an extensive crust of the alga Mesophyllum sp.

Scale divisions: 1mm
2.442 Mid-Depth Environments (10-25m)

Exposed surfaces at depths of 10-25m (zones h, i and k of Figs 3 and 4) at the edge of the Bellairs shelf and on the tops of the offshore bank reefs consist of dead sides and undersides of coral heads and of coral debris. Encrusters of these lighted and just lighted substrates consist chiefly of crustose coralline algae (such as Neogoniolithon - massive and frondose forms, Neoponyporolithon, Tenarea, Posiella, Hydrolithon and Mesophyllum), of the foraminiferan Cypina plana and of encrusting corals such as Agaricia sp. and Millepora spp. (Plates 3, 28a and 43).

Shaded and dim cavities and overhangs in these environments are colonised by the crustose coralline Mesophyllum, by the foraminifers Homotrema rubrum (branching and globose forms), Carpenteria utricularis (globose form), Carpenteria hassleri and Planorbulina sp., by numerous bryozoans (such as Lichenopora sp., Steganoporella magnilabris, Parasmittina ophidiana, Rhynchozoon rastratum, Trematoecia magnifera and Chleidochaetia vestita) and by the majority of encrusting serpulid worms (Plate 27a).

2.443 Deep Water Environments (25-50m)

At depths greater than 25m, exposed surfaces increase in area as the proportion of living coral cover decreases. Surfaces range from just lighted to dark in their degree of illumination and are colonised by crustose coralline algae (Neogoniolithon, Hydrolithon, Mesophyllum, Archaeolithothamnium and Lithothamnium), by bryozoans (Parellisina latirostris, Trematoecia magnifera and Schizoporella sp.) and by serpulid worms. Other, less common encrusters within this environment include Cypina plana and the encrusting, deep water form of the coral Madracis sp. (Plates 28b, c).

Shaded and dark cavities at depth are colonised by a number of cryptic bryozoans (Table 6 and Fig 27) and serpulid worms (Table 6, Fig 38 and Plate 29).
ENCURSTERS AND SUBSTRATES CHARACTERISTIC OF EXPOSED SURFACES AT DEPTH

a) Assemblage of massive coral heads on top of the offshore bank at Nurses Jetty. Montastrea cavernosa (centre) exhibits overgrowth of living tissue by crustose corallines (Neogoniolithon and Porolithon) and by the foraminiferan Gypsina plana.

Scale divisions: 5cm

b) Totally encrusted plate of Meandrina sp from the exposed surface of a pillar-growth form, inner slope of the outer bank at Nurses Jetty. 30m depth, Just-Lighted environment. Encrusters include the corals Acaricia sp, Porites astreoides and Madracis sp, the crustose corallines Neogoniolithon, Neopolyporolithon and Tenarea and the foraminiferan Gypsina plana.

Small scale divisions: 1mm

c) Part of an encrusted plate from the inner slope at Nurses Jetty, 25m depth. Encrusters include Hesophyllum sp (G), Gypsina plana (G), the deep-water, encrusting form of Madracis sp (m) and the bryozoan Schizoporella sp (S)

Small scale divisions: 1mm
PLATE 29

SCIAPHILIC ENCROUCHERS CHARACTERISTIC OF CONCEALED HABITATS AT DEPTH

a) Serpulid worms (*Sclerostyla ctenactis* - S and *Pseudovermilia multispinosa* - P) and crustose coralline algae (*Mesophyllum* - M) encrusting dead skeletal substrate. Dim environment, 40m depth. Outer bank, Nurses Jetty.

Small scale divisions: 1mm

b) Solitary corals and bryozoans (*Steganoporella mammilabris*) on a dead skeletal substrate from the inner bank of Nurses Jetty, 35m depth, Dimly-lit environment.

Small scale divisions: 1mm

c) Serpulid worms (*P. multispinosa* - P and *P. fuscostriata* - F), bryozoans (*Cribrilina radiata* - C), solitary corals (-S) and encrusting barnacles, colonising the underside of a coral plate from a Dim-Dark habitat on the outer bank of Nurses Jetty reef at 50m.

Scale bar: 5mm


2.444 Discussion

The maximum diversity of species and the greatest abundance of individual encrusters is found in mid-depth (10-20m), lighted-dim habitats. Within shallower and deeper habitats, diversity decreases. Although abundance usually decreases with increase in depth, the number of individuals of many species remains high in shallow water, where a considerable area of the reef is occupied by crustose coralline algae. Maximum thickness of individual crusts and of encrustations also occurs in shallow, inshore environments, where composite crusts of *Porolithon* and *Lithophyllum* may achieve a thickness of 1-2cm.

Crusts formed on both exposed and concealed substrates in deeper, less well lit environments are considerably thinner (less than 0.5cm) as a result of the slower growth rates of crust components. In the absence of cementing and stabilising layers of crustose coralline algae in dim and dark habitats, other crust components on death are rapidly eroded from the unstable substrate. Consequently, sciaphilic crusts in deep water environments are only preserved when growth is followed by rapid burial by sediment.

2.445 Significance of Distribution Model in Crust Analysis

Within any one environment, colonisers of experimental substrates and components of Recent crusts were found to be similar to those living encrusters found on the actual surface of the reef. Although experimental substrates suggested that certain foraminiferans and other encrusters were late-stage colonisers, many of which required substrates to be previously colonised, no where was any marked succession of encrusters found, other than in constantly changing environments. This absence of a well-defined succession justifies the use of the Recent model in the interpretations of the conditions of growth and formation of the Pleistocene reefs (see Chapter 3 following).
CHAPTER 3

THE PALAEOECOLOGY OF SOME UPLIFTED PLEISTOCENE REEFS OF BARBADOS
3.1 INTRODUCTION AND PREVIOUS RESEARCH

The uplifted

Pleistocene reefs of Barbados, which constitute over 80% of the total land area of the island, are exposed as a series of terraced outcrops which rise from sea level to a maximum height at Mt. Hillaby of 340 metres (Figs 40, 41 and Plate 30). The geological significance of the terraced coral cap has attracted considerable attention in the past and numerous theories have been advanced to explain its origin (for example, Jukes-Brown and Harrison 1891, Spencer 1902, Harrison 1907 and Trechmann 1937). The application of radiometric dating techniques by Ku (1968) and by Essolella (1968) confirmed the original theory of Jukes-Brown and Harrison (op cit) that the terraced nature of the coral cap resulted from the superimposition of sea level fluctuations on the gradual tectonic uplift of the island. The age of the terrace is therefore related to its height above sea level (Essolella et al 1969) (Fig 41).

Facies analysis and environmental interpretations of the Pleistocene reef tracts were undertaken by Essolella (1967, 1968) and by James (1972). Both investigators found a well-defined faunal and sedimentological zonation within the Pleistocene reefs which was quite distinct from that of the present day reefs off the west coast of Barbados (Chapters 1 and 2 of the present study, Lewis 1960 and Stearn et al (in press)). Essolella (op cit) and James (op cit) concluded that each terrace unit represents a reef complex composed of an offshore 'barrier' reef facies of deep water coral heads and shallow water corals (Acropora palmata and A. cervicornis), a back-reef lagoon of sparse coral heads and sand; and a discontinuous fringing reef system of mixed faunal composition growing adjacent to the shore (Fig 42). The overall structure and faunal composition of this reconstruction compares closely with that of reefs growing at the present time in other areas of the Caribbean (for example, Florida (Ginsburg 1956),
Fig 40 Areal Distribution of Major Reef Terraces on Barbados. Localities illustrated are those where terraces show extensive encrustation.
Fig 41  General Stratigraphy of Barbados, with ages of major uplifted reef terraces.
Fig 42  3-Dimensional Model of a Pleistocene Reef Tract at the Time of Growth. (based on field evidence & on fig 11 of Mesolella et Al 1970)
the Bahamas (Newell and Rigby 1957), Jamaica (Coreau 1959), the Alacran Reef complex, Mexico (Kornicker and Boyd 1962, Shinn 1963) and the Netherlands Antilles (Scatterday 1974).

However, despite their detailed nature, Pleistocene facies analyses give, what is essentially, a static picture of the reefs at the time of burial and uplift. In general, little mention is made of the conditions of growth on and within the reefs, nor of the fate of coral colonies in the various zones after death, except that the colonies are either welded together by crustose coralline algae or are broken and transported by wave action from their place of growth. Because of the differences in structure and coral composition of the Recent and Pleistocene reefs of Barbados, the history of growth and preservation of the Pleistocene reefs cannot be investigated using a model based on the growth and distribution of Recent corals from Barbados. However, the distribution of encrusting organisms which inhabit the surfaces of primary frame builders is environmentally controlled on both a large and small scale and is independent of overall reef structure and coral zonation. Analysis of encruster distribution provides an alternative means of investigating the palaeoecology and sedimentology of fossil reefs which is not based on the overall structure of the reef.

Many of the massive corals in the Pleistocene reefs of Barbados are overgrown by a thick organic encrustation. Previous investigators (such as Tesolella 1967, 1963 and James 1972) have used this crust, which was assumed to have developed on the upper, lighted surface of the coral, as a criterion for its 'in-situ' nature. James (1972) described the crusts found on corals from reefs on the North Point Shelf (Fig. 40) as consisting of the crustose coralline alga Lithophyllum with up to 10% of Lithometrella. Analyses carried out in the present study, however, reveal that the crusts are composed of a variety of organisms, all of which are represented on the living reefs of Barbados. In addition, encrustations not only indicate
the life orientation of the coral, they also document the entire history of growth and burial of that coral. By referring to the model of encruster distribution derived from investigations of the Recent reefs (Chapter 2, section 2.44), it can be shown that initial encrusting layers were formed while the coral was in growth position. Analyses of later-formed crusts often indicate removal from the original environment of growth - in many cases, crusts continue to grow long after death and break-up of the coral colony, suggesting that the process of burial is somewhat protracted.

The processes of growth and development of the Pleistocene reefs of Barbados, as suggested by patterns of encrustation, compares favourably with those known to be operating on similar, Recent reefs which have been investigated (Shinn 1963, Ginsburg et al. 1971, Land and Goreau 1971).

3.2 PATTERNS OF ENCRUSTATION AND COMPOSITION OF CRUST

In general, the sequences of colonisation by encrusters on living reefs is dependent upon the environmental location of the substrate (in terms of physical factors such as depth, amount of light, hydrodynamic exposure and abundance of sediment). On this basis, two types of encrustation can be recognised on the uplifted Pleistocene reefs. These are: (1) crusts of Mixed Composition composed of encrusters characteristic of a number of diverse environments and (2) crusts of Constant composition composed of encrusters characteristic of one particular environment.

Each type can be further subdivided (as outlined below) on the basis of species association, as determined by the particular environment or range of environments in which growth occurred.
3.21 Crusts of Mixed Composition

3.211 Environmental Setting and Facies Distribution

The majority of well-developed reef terraces on Barbados consist, in part, of a thick (up to 10m) accumulation of both in-situ and broken and transported colonies of *Acropora palmata* set in a matrix of reef-derived sediment (Plates 31 and 32). Both Besolella (1967, 1968) and James (1972) suggested that this assemblage resulted from the breakup and accumulation of *A. palmata* fronds which grew on the crest of an offshore barrier reef (Fig 42). In most cases, these fronds support thick (up to 8 cm), laminar encrustations on one or more surfaces (Plate 32).

3.212 Composition of Crusts

Except for those examples described in Section 3.22 following, all crusts of mixed composition found on corals in the *A. palmata* facies were of the type described below. (See Appendix 6 for localities of crust-bearing corals).

Fig 44 illustrates diagramatically the composition of a mixed crust found on *A. palmata*. Initial encrusters on the upper surface of the coral immediately adjacent to the skeleton consist of crustose coralline algae such as *Porolithon*, *Neogoniolithon* and *Lithophyllum* (only *Lithophyllum* is illustrated in Fig 44. See Fig 43 for Key to symbols used). Individual crusts are often of considerable thickness (0.5-1.5mm) and repeated overgrowth leads to a thick crust composed either of a single species or of regular alternations of different species.

Successive encrustations above this thick initial layer consist of thinner laminae of crustose coralline algae, such as *Mesophyllum* and *Tenuarea* (and *Lithophyllum*) which are often interlaminated with the chambered foraminiferan *Planorbulina* sp. Later formed crusts of *Mesophyllum*, which are often thin and highly contorted, support various forms of encrusting foraminifers (such as the encrusting and branched forms of *H. rubrum*,
Uplifted reef terrace forming the 530,000 yr Second High Cliff at Gay's Cove, N.E. Barbados.

Sea caves and the undercut sea stack are evidence of a marine origin of the flat land in the foreground, which forms the upper surface of the 83,000 yr North Point Shelf reef complex.

PLATE 31

a) 83,000 yr sea cliffs at The Tides (locality TT), N.E. coast of Barbados. The cliffs are composed of both broken and in-situ colonies of *Acropora palmata* embedded in an uncemented lime sand.

b) Part of the cliff-face in (a) showing *A. palmata* plates with a thick algal crust of mixed composition on both upper and lower surfaces. The crust below the lens cap cements together two separate plates - evidence for continued crust growth after break-up of the original coral colony.
CRUSTOSE CORALLINE ALGAE

Porolithon

Neogoniolithon

Lithophyllum

Tenarea

Hydrolithon

Fostiella

Mesophyllum

Lithothamnium

Archaeolithothamnium

Scale (mm)

Upper crust

Lower crust

FORAMINIFERA

Planorbulina sp.

Homotrema rubrum - encrusting & branched

Carpenteria utricularis - conical & globose

SEDIMENT TYPE

Reef-derived Biomicrite

Internal cement

Infilled boring

CORAL SUBSTRATES

Acropora palmata

Montastrea annularis

Fig 43 Key to Figs 44-52 & 55
Diagrammatic cross-section of a crust of mixed composition on a plate of *Acropora palmata* from the barrier reef facies of the 83,000 yr reef tract, Animal Flower Bay. Arrows indicate the direction of growth of the crust.

An initial, thick photophilic crust on the upper surface is gradually replaced by a layer of thinner, contorted crustose corallines and foraminifera.

The thin photophilic crust on the lower surface is soon overgrown by similar sciaphilic algae and foraminiferans.

(For key to symbols, see Fig 43)

Diagrammatic cross-sections of crusts of mixed composition on *Acropora palmata* (Fig 45a) and *Montastrea annularis* (Fig 45b) from concealed, shaded environments on the living reef at Bellairs. Arrows indicate the way-up nature of crusts (i.e. growth was downwards away from the *A. palmata* substrate in (a) and from the *M. annularis* substrate in (b)).

The initial, thick photophilic algal layers near to the coral substrate are replaced gradually by thinner laminae of sciaphilic algae and foraminiferans. Growth of (a) has been terminated by biomicrite sediment.

(For key to symbols, see Fig 43)
the conical and globose forms of *Carpenteria utricularis* and *Planorbulina sp.*). In all cases, this outer foraminiferan layer is overlain by a biomicrite (Fig 44).

Thin crusts on the underside of many fronds of *A. palmata* lack this thick initial layer of crustose coralline algae. Instead, crusts consist of a thin, basal layer of *Lithophyllum* or *Neoconiolithon* which is immediately overlain by laminar crusts of *Mesophyllum* (Fig 44). successive crusts of *Mesophyllum* form in much the same way as those on the upper surface, becoming increasingly thinner and more contorted towards the outer surface of the crust. The outermost layers of *Mesophyllum* are interlaminated with and overgrown by encrusting foraminifers (for example, *H. rubrum*, *C. utricularis* and *Planorbulina sp.*) which, in turn, are overlain by biomicrite (Fig 44, Plate 32).

### 3.2.13 Environmental Conditions of Formation

Analysis of encruster distribution on the living reefs of Barbados (Chapter 2) has provided a model of encruster distribution which can be used to interpret the conditions of growth of uplifted Pleistocene reefs. The thick initial layers of *Porolithon*, *Neoconiolithon* and *Lithophyllum* on the upper surface of *A. palmata* are all associated, at the present day, in shallow, well-lit environments (Chapter 2, section 2.21, Fig 20). The coralline algae overlying this photophilic layer are more typical of shaded environments at shallow and mid-depths, while those algae and foraminifers (such as *Mesophyllum* and *Hormotrama rubrum*) forming the outermost layers of the crust are only associated at the present time on the sediment-free undersides of shaded and dim cavities and overhangs at shallow depth (Chapter 2 and Figs 20 and 37). Thus, a transition exists from photophilic algae characteristic of shallow, well-lit environments to sciaphilic encrusters typical of cryptic environments.
Numerous descriptions of Recent reefs (for example, Ginsburg 1956, Goreau 1959) indicate that growth of *A. palmata* is most prolific at, or near the water surface in exposed environments. Apart from the investigations of Shinn (1963), Ginsburg (1971) and Land and Goreau (1970) into the internal structure of *A. palmata* reefs, no detailed account exists of the fate of *A. palmata* upon death and/or breakup of the coral colony.

Analysis of encrustations on Pleistocene colonies of *A. palmata*, however, reveal a history of burial which is both long and complex. Initial encrusting layers of photophilic algae are assumed to have formed on the coral whilst in growth position near the reef crest, in a shallow, well-lit environment. Thickness of this initial crust is related to the time spent in that environment and to the degree of illumination and hydrodynamic exposure to which the coral is subjected (see Chapter 2, section 2.2). During vertical and lateral expansion of the coral colony, however, the lower (often dead and encrusted) areas become shaded from direct illumination by higher branches and by other colonies. Growth of *A. palmata* in this manner results in extensive cavities and voids beneath the living reef surface. Wave surge and other water movements within this high energy environment will circulate throughout these voids, preventing any reef-derived sediment from settling out of suspension. Crustose coralline algal laminations of intermediate photophilic/sciaphilic affinities (such as *Mesophyllum*) which overlie the initial photophilic layer suggest that these water movements within shaded cavities promote the growth of crusts by the addition of sciaphilic coralline algae.

With continued upward growth of the coral colony, however, the amount of light reaching the lower voids and branches will be progressively reduced. Additional layers added to existing crusts will reflect this environmental change, in that they will become increasingly sciaphilic in nature. Thus, the relatively thin crusts of *Mesophyllum* which succeeded the photophilic crust on initial shading will, in turn, be succeeded by
thinner, often highly contorted laminae of *Hesophyllum*, formed in response to a reduction in water velocity (Zankl and Schroeder 1972) and growth rate in shaded and dim environments.

At some stage in this burial process, there is insufficient light for the development of crustose coralline algae. Their place is taken by fully sciaphilic organisms such as foraminifers and serpulid worms. *Planorbulina* sp. and delicate branching forms of *H. rubrum* characterise shaded, shallow-water reef environments at the present day (Table 6) and their presence in the Pleistocene crusts indicates that voids at this stage must still have been open to circulating water. However, this encrusting foraminiferan layer is usually thin and is overlain by and interlaminated with biomicrite sediment. This suggests that, by this stage of burial, water movements were so reduced that reef-derived sediment could settle out within voids, thus effectively terminating crust growth.

The absence of a thick initial photophilic algal component in crusts on the underside of *A. palmata* fronds suggests a shaded position on the colony during growth. Shading of the coral colonies probably continued after breakup, with the result that thinly laminated crusts of sciaphilic algae were established in advance of those on the upper surface. A long history of growth of sciaphilic organisms on the underside would account for the proportional increase in thickness of the sciaphilic layer of the crust often seen on the underside of fronds (Fig 44).

Fig 46 summarises these stages in the growth, burial and preservation of *A. palmata* and its adherent crusts. Fig 45 and Plate 33 illustrate two crusts from the roof of a shaded/dim cavity on the living reef at Bellairs. Both are transitional in nature, from initial photophilic crusts of *Porolithon* and *Lithophyllum* through to completely sciaphilic crusts composed of *Hesophyllum* and *Lithothamnium* and the globose form of *Carpenteria utricularia*. Although this particular cavity was closed progressively by lateral overgrowth of primary framebuilders, rather than
Summary diagram of the environment of growth of mixed crusts in the reef-crest facies of a Pleistocene offshore barrier reef.

Inserts a-d illustrate crust development during the gradual burial of the *Acropora palmata* colony and broken plates.

a) Development of initial thick photophilic crust of *Porolithon*, *Neogoniolithon* and/or *Lithophyllum* on the upper surface of the frond and of thinner photophilic crust of *Neogoniolithon* and *Lithophyllum* and initial sciaphilic crust of *Mesophyllum* on the lower surface.

b) Crust on upper surface of intermediate photophilic-sciaphilic affinities, composed of *Tenearea, Mesophyllum* and *Lithothamnium*, gradually succeeds the photophilic crust.

The lower surface shows the development of layers of sciaphilic foraminiferans (*Carpenteria utricularia* - conical form and *Planorbulina* sp).

c) Final sciaphilic crust of *Mesophyllum, Lithothamnium* and *Archaeolithothamnium* with inter-laminated foraminiferans (*Carpenteria utricularia* - conical and globose forms and *Hematotrema rubrum* - all forms). Growth of the lower crust has already been terminated by burial in sediment.

d) Complete burial of frond and encrusters by sediment.

(For key to symbols, see Fig 43)
Fringing Reef  Lagoon  Barrier Reef

WELL LIT
LIGHTED
LIGHTED/SHAD ED
SHAD ED
DIM
DARK

fig 46
Heavily encrusted fronds of *Acropora palmata* (A) from Animal Flower Bay, seen in cross-section. Crusts (C) are of mixed composition and are thickest on the upper surface of the frond.

**PLATE 33**

Thin sections of crusts of mixed composition from the living reefs off Bellairs.

a) *A. palmata* substrate (right) encrusted by thick initial crust of *Lithophyllum* (I). Subsequent crusts consist of highly contorted laminae of *Mesophyllum* (II) and individual foraminiferans (*Carpenteria utricularis* - C). Crust growth is terminated by sediment.

See also Fig 45a. Crossed polars. Scale bar: 1mm

b) *Montastrea annularis* (right) encrusted by thick initial crust of *Lithophyllum* (I). Successive crusts consist of *Mesophyllum* (II) and the encrusting form of *Homo-trema rubrum* (III).

Final algal laminae are thin and consist of *Mesophyllum*, *Lithothamnium* and *Archaeolithothamnium*. Extensive boring, especially in the inner layers of the crust, results from the slow growth rate in a Shaded-Dim environment. See also Fig 45b. Plane polarised light

Scale bar: 1mm
by burial beneath an accreting frame, the process of gradual reduction in the intensity of light is reflected by the transitional nature of the encrusting community and is the same as that envisaged for the Pleistocene reefs.

The development of this transitional or mixed type of crust on both the Recent and Pleistocene reefs is the result of the growth form of the coral and its environment of growth. The open framework structure of the A. palmata zone of the barrier reef, combined with a location in a shallow, high energy environment promotes the growth of encrustations long after breakup and/or overgrowth of the coral colony and results in thick crusts which record a long and complex history of deposition prior to final burial.

3.22 Regional Variation within Crusts of Mixed Composition

In general, most crusts from the A. palmata facies exhibit this transitional photo-philic to sciaphilic structure. However, depending on environmental conditions, considerable variation in encruster composition exists within crusts on A. palmata. Examples of such a variation can be found within the 125,000 yr reef tract described below.

3.221 125,000 yr Reef Complex - First High Cliff

Location

The first high Cliff reef complex is one of the more prominent reef terraces on Barbados. It outcrops as a seaward-facing cliff approximately 25-30m in height, which can be traced from Harrison Point, North of Speightstown to Crane Beach on the S. coast of the island (Figs 40, 41).

The faunal structure of this and other uplifted reef terraces has been described by Tesolella (1967, 1969) and by Tesolella et al (1970).

Composition of Encrustations

Encrustations on corals exposed in numerous road cuts, ravines and quarries along the reef tract were
examined in order to refine the barrier reef - lagoon - fringing reef model of Resolella (op cit). Although most fronds of A. palmata in west coast exposures support thin (1 cm) laminar encrustations similar to those described in section 3.21 above, they are nowhere as thick as those on broken and in-situ colonies exposed along the south coast portion of the reef tract. Crusts examined at locality BJ (Fig 40) were frequently 3-4 cm and occasionally up to 8 cm thick on the upper surface. In all cases, the excess thickness of the crust could be accounted for by the increased development of the initial photophilic algal layer in which individual laminae of Porolithon, Neogoniolithon and Lithophyllum were often 2-3 mm in thickness.

The outer 2-3 mm of all crusts was composed of encrusters of intermediate and fully sciaphilic affinities. Initial sciaphilic layers of Mesophyllum within this outer layer were subsequently overgrown by encrusting foraminiferans, such as the compressed, encrusting form of Monotreta rubrum and the low, conical form of Carpenteria utricularis.

Environmental Conditions of Growth

The transition from photophilic to sciaphilic encrusters resembles that found on A. palmata in the barrier reef facies described in section 3.21 above. However, crusts on the upper side are considerably thicker and are composed predominantly of photophilic crustose coralline algae overlain by a thin layer of encrusting foraminiferans. Similar algal species on the Recent reefs of Barbados achieve their greatest thickness and abundance in shallow, well-lit high energy environments (Chapter 2, section 2.21). Since crusts in west and south coast localities of this reef tract differ only in thickness and not in composition, it is concluded that the south coast reefs of the 125,000 yr reef complex must have grown in higher energy, shallower water environments than their west coast counterparts.
3.21 Crusts of Constant Composition

3.231 Environmental Setting and Facies Distribution

Massive coral heads are found in a number of localities in the Pleistocene reefs of Barbados. Most commonly, large hemispherical heads of *Montastrea* sp., *Diploria* sp. and *Siderastrea* sp. occur in front of and below the *A. palmata* facies (Plate 34), an association interpreted by Lesolella (1967, 1968) as a deep water community which grew at the base of the fore-reef slope of an offshore barrier reef (Fig 42). Massive coral heads are also sparsely distributed behind the *A. palmata* facies in a shallow water, lagoonal environment (Lesolella - op cit). In the 83,000 yr reef complex of the North Point Shelf (Fig 40), tall (3-10m) 'organ-pipe' colonies of *Montastrea annularis* are found immediately behind the *A. palmata* facies in the coral knob zone (James 1972)(Plate 35). In most outcrops examined, both massive coral heads and other growth forms in fore- and back-reef environments possessed thick (1-2cm) laminar encrustations on their upper surfaces. Sediment content within this zone is everywhere much higher than that of the coral-dominated *A. palmata* facies.

3.232 Composition of Crusts

Figs 47 and 48 and Plate 36 illustrate the composition of crusts found on massive (Fig 47) and platy (Fig 48) growth forms of coral in the coral head zones. On both growth forms, encrustations consist almost entirely of crustose coralline algae (such as *Neogoniolithon*, *Tenarea*, *Hydrolithon*, *Mesophyllum*, *Posidella* and *Archaeolithothamnium*). Occasionally, examples of other encrusting organisms are found (for example, the foraminifers *G. flava*, *Planorbulina* sp. and the encrusting form of *H. rubrum*). These encrusters are only associated at the present time in just lighted/shaded mid-depth (25-30m) zones of the Bellairs reefs (see Table 6). No transition in composition from photophilic to sciaphilic organisms was found.
PLATE 34

Massive coral head facies in front of the Acropora cervicornis zone, First High Cliff, Mullins, Barbados. Massive heads consist of Siderastrea (S) and Diploria spp (D), embedded in a matrix of broken coral fragments, mostly A. cervicornis.

PLATE 35

Organ-pipe colony of Montastrea annularis at River Bay, N.E. coast of Barbados (locality RB). Camera bag scale 20cm in height.

PLATE 36

Thin-section of crust of constant composition growing on top of an 'organ-pipe' Montastrea annularis substrate (extreme right). Crusts consist of alternate laminae of Neopolyborolithon (N), Lithophyllum (L) and Mesophyllum (M). Scale bar: 2mm
Diagrammatic cross-section of a crust of constant composition on Montastrea annularis from the back-reef facies of the 33,000 yr barrier reef at River Bay.


Arrow indicates way-up and direction of growth of crust.

Diagrammatic cross-section of a crust of constant composition on an A.palmata plate from the back-reef facies of the 33,000 yr reef tract at River Bay.

Initial crusts of Mesophyllum and later crusts of Archaeolithothamnium are inter-laminated with reef-derived sediment.

Arrows indicate that crust growth was away from both sides of the substrate. The upper crust is at the top.
Summary diagram of the environment of growth of crusts of constant composition in the back-reef facies of a Pleistocene offshore barrier reef.

Inserts a-c illustrate the development of sciaphilic crusts of constant composition.

a) Initial growth of *Archaeolithothamnium* which is subsequently overgrown by *Mesophyllum*

b) Regular alternations of similar sciaphilic crustose corallines (*Archaeolithothamnium*, *Mesophyllum*, *Poslicella* and *Lithothamnium*) increases thickness of crust.

c) Crust is eventually terminated by burial beneath sediment as colony breaks up or sediment level rises.

For key to symbols used, see Fig. 43.
fig 49
in this crust type. Instead, crusts were either composed entirely of
one species of crustose coralline or else they consisted of regular alter-
nations of two or more algal types (Figs 47 and 48). In all examples,
algal crusts were overlain by sediment of reef origin. Where colon- 
isation had taken place on the sides of corals, crusts were considerably
thinner and contained a greater proportion of sciaphilic species than
those on the upper surface.

3.233 Environmental Conditions of Formation

Both Mesolella
(1967, 1968) and James (1972) stated that the massive coral head zones
were located in deep water, sediment-dominated environments. Encrustations
on both massive and platy corals in this zone suggest a depth of origin
of more than 20meters, considerably deeper than that of the A. palmata
zone and similar to the fore-reef slope and back-reef lagoonal environ-
ments found on present day reefs of similar structure in the Caribbean
(see Goreau 1959).

Whereas encrusting organisms on A. palmata of the barrier reef
facies suggest that growth of crusts continued even after breakup and
overgrowth of colonies, the crusts on coral heads in the Pleistocene
show no such transitional trend, being terminated by sediment while
still supporting growths of photophilic crustose coralline algae.

Fig 49 illustrates the history of growth and deposition of
Montastrea annularis in the back-reef lagoon of the 83,000 yr reef
complex at locality RD, as indicated by the composition of attached crusts.
Tall 'organ - pipe' colonies of Montastrea annularis, 10m or so high,
grow up from a solid substrate base, probably of A. palmata plates (James
1972). Encrustation of the exposed tops and sides of dead colonies results
in thick accumulations of crustose coralline algae, whose composition
suggests that water depth was of the order of 25-30m. The massive nature
of this type of substrate resists immediate breakup on death, with the
result that dead areas continue to be exposed in the same environment.
for considerable periods of time. Algal crusts which form are composed of similar photophilic genera and show no transition from photophilic to sciaphilic types (Figs 47-49). Eventually, however, the destructive activity of boring organisms and/or a rise in the level of surrounding sediment will result in burial of the coral. In the absence of light and circulating water beneath the sediment, crust growth ceases, resulting in a massive coral colony, either in growth position or on its side, which supports a thick crust of crustose coralline algae (showing no transition from photophilic to sciaphilic types) which is overlain by reef-derived sediment.

Localities where coral heads with well-developed crusts are exposed are listed in Appendix 6

3.24 Regional Variation within Crusts of Constant Composition

The composition of algal crusts on massive coral heads in reefs with a well-defined zonation is relatively constant, regardless of the age or location of the reef tract. However, minor reef tracts which lack a well-defined zonation, are often composed of massive and platy corals, possessing crusts of anomalous composition.

3.241 220,000 yr Reef Complex

This particular reef complex outcrops at an elevation of 60-66m as a discontinuous terrace of low relief which can be traced from the vicinity of mole-town north into the Speightstown area (Fig 40). The terrace, which lies immediately above the First High Cliff (Fig 41), is exposed in a series of low road cuts (localities H3 and D1 illustrated in Fig 40 and described in Appendix 6), which are composed of isolated, broken fronds of A. palmata with some coral heads, set in an extensive sandy matrix (Plate 37). Fronds of A. palmata at locality H3 support thin algal encrustations.
Exposure of poorly developed 210,000 yr reef tract near Mt. Standfast (locality MS). Oval fronds of *A. palmata* are sparsely distributed in a matrix of coral debris and sand. Colonies have undergone considerable solution, their outlines being preserved by thick (1-2cm) white encrustations (E) of crustose coralline algae.

**PLATE 38**

**MIXED CORAL ASSEMBLAGE AT LOCALITY CU IN THE 310,000 yr REEF TRACT**

a) Heavily encrusted fronds of *Acropora palmata* interbedded with coral debris.

Scale as for (b) below.

b) Immediately adjacent to the *A. palmata* facies is the massive coral head facies consisting of heads of *Montastraea* sp and *Siderastrea* sp with thin organic crusts, embedded in a matrix of coral debris.
Composition of Encrustations

Crusts on A. palmata are composed entirely of thin algal laminations of Tenarea, Lithophyllum, Neogoniolithon, Posidiella, Hydrolithon and Mesophyllum (Fig 50), and show no evidence of transition from photophilic to sciaphilic organisms. All crusts are overlain by reef derived sediment.

Environmental Conditions of Formation

The lack of any well-defined photophilic - sciaphilic transition in the composition of algal crusts on A. palmata suggests that upon breakup, fronds were immediately buried by sediment. The seemingly anomalous distribution of a non-transitional algal crust on A. palmata (see Section 3.21 above) can be explained in terms of depth of growth of the reef complex. The semi-photophilic nature of the crustose coralline algae forming the crust suggests a depth of growth of 15-20m (see Fig 20 and Table 6). At this depth, the growth rate of A. palmata is considerably reduced (Goreau 1959), with the result that colonies are small and fragile. The A. palmata facies so formed was probably of low relief, which was surrounded by and probably overgrew reef-derived sediment. Because of the slow rate of growth, thick accumulations of A. palmata fronds, such as those found in the barrier reef facies (Section 3.21 above), would be unlikely to form. Consequently, on the breakup of A. palmata colonies, fronds would be immediately buried in surrounding sediment, with the result that crust growth would be terminated without a transitional, sciaphilic layer.

In this particular reef tract, analysis of crust composition indicates a depth of growth for A. palmata which is considerably deeper than that known at the present time. The locality may represent a drowned reef tract where vertical growth failed to keep pace with a rise in sea level (see Bresolella et Al 1970, p. 1910).
Diagrammatic cross-section of a crust of mixed composition from locality MB in the 210,000 yr reef tract.

An initial crust composed of Tenarea, Neogoniolithon and Lithophyllum of deep-water, photophilic affinities is overgrown by an increasingly sciaphilic crust of Neogoniolithon, Mesophyllum and encrusting foraminiferans (Planorbulina sp).

Diagrammatic cross-sections of crusts of constant (a) and mixed (b) composition from locality CJ in the 310,000 yr reef tract.

a) Upper crust consists of intermediate photophilic-sciaphilic algae (Neogoniolithon and Mesophyllum). Lower crust consists of sciaphilic layers of Hydrolithon, thinly laminated Mesophyllum and Homotrema rubrum.

b) Mixed crust on H. annularis substrate consists of initial photophilic-sciaphilic crust of Neogoniolithon, Hydrolithon and Planorbulina sp which is gradually replaced by irregular sciaphilic layers of Fosliella, Hydrolithon and Mesophyllum.

For key to symbols, see Fig 43.
3.25 Individual Reef Facies with Crusts of both Constant and Mixed composition

3.251 Introduction

A number of localities in different reef terraces consist of a mixture of *A. palmata* and massive coral heads which possess crusts of both constant and mixed composition. These localities do not show the typical zonation of other reefs in which platy growths of *A. palmata* overlie the zone of massive coral heads. Localities in the 275,000 yr reef complex (locality DNQ in Fig 40), the 310,000 yr reef complex (locality CU in Fig 40 and Plate 38) and in certain areas of the Second High Cliff (530,000 yr reef complex - locality HM in Fig 40) exhibit this mixed coral zone. Crusts are confined to the upper surface of massive coral heads but often occur on both surfaces of platy *Acropora palmata*. On both types of coral, crusts are either of 1) constant composition, consisting of thick alternating laminae of similar photophilic algae (such as *Lithophyllum*, *Neogoniolithon* and *Tenarea*) (Fig 51a) or are 2) of mixed, transitional composition consisting of a thick initial layer of photophilic algae (such as *Porolithon*, *Lithophyllum* and *Neogoniolithon*) which is succeeded by thinner algal and foraminiferal layers of increasingly sciaphilic affinities (Fig 51b).

3.252 Environmental Conditions of Crust Formation and Reef Growth

Fig 52 illustrates the environments of growth and deposition of corals in this particular type of reef. Since a well-defined zonation of *A. palmata* and massive coral heads is absent, it is concluded that both growth forms were closely associated at the time of growth. *A. palmata* being of faster growth rate, would be predominant at the top of the reef. The thick, initial photophilic crusts on all corals suggests that growth of the reef took place in a shallow, moderately high energy environment.
Summary diagram of the environment of growth of crusts of both constant and mixed composition on a Pleistocene offshore bank/patch reef of low relief.

Inserts a-c illustrate development of crusts within different environments.

a) Initial growth of crusts takes place above sediment level and consists chiefly of photophilic algae (*Neogoniolithon*, *Tenarea* and *Lithophyllum*) of mid-depth environments.

b) Continued growth of either massive or platy corals above the sediment level results in crusts of mixed composition. Irregularly laminated crusts of *Mesophyllum* with foraminiferans overlie initial photophilic crust as shading of the coral by other colonies takes place.

c) Growth of crusts on substrates exposed on the lower slopes continues by the addition of photophilic algae (*Tenarea*, *Neogoniolithon* and *Hydrolithon*) until a rise in sediment level or detachment of the coral results in burial by sediment and abrupt termination of crust growth.

For key to symbols, see Fig 43.
Since many of the crusts on both massive and platy heads are of mixed composition, crust growth must have continued long after death of the coral colony. The reef itself must therefore have been an elevated feature, the upper part of which consisted of an open framework of broken and in-situ corals which was open to circulating sea water. However, since many crusts are composed solely of photophilic algae which are overlain by sediment, some corals, on death and/or breakup must have been immediately buried within sediment. The close association of the two types of crust suggests that the reef, although an elevated feature, must have been closely associated with and in some places, probably overgrew reef-derived sediment (Fig 52).

3.3 Summary and Conclusions

In his study of the Pleistocene reefs of Barbados, Nesolilla (op cit) made comparisons with some of the Recent reefs of Jamaica and Florida and on the basis of faunal similarity, defined depths of growth for the various Pleistocene zones. However, because comparison studies such as these are restricted to reefs of similar structure and faunal composition, they are of limited value in the interpretation of reef palaeoecology. Moreover, once corals have died, they are no longer able to reflect environmental conditions on and within the reef complex. Reefs are rarely preserved with corals in life associations and generally, the picture of reef palaeoecology which emerges is a static one which does not account for the dynamic processes operating on and within a reef.

Analysis of the composition of encrustations on dead corals, however, provides an alternative, and perhaps, a more accurate means of determining reef palaeoecology. The encrusting community, which forms during the growth of the coral colony, is not affected by the death
of the coral, and often continues to grow during overgrowth and initial burial. Environmental conditions and dynamic processes operating within the reef are reflected in the faunal and floral composition of this community. Analysis reveals that corals often undergo a period of initial burial which is both long and complex (= crusts of mixed composition). Conversely, crusts of constant composition suggest that substrates were exposed for long periods during which thick crusts developed. Final burial beneath sediment is indicated by the termination of crust growth.

Investigations based solely on the composition of crusts on corals in the *A. palmata* zone of Pleistocene reefs indicate an internal structure of anastomosing, sediment-free voids similar to those found in Recent reefs which have been sectioned with explosives (Shinn 1963, et al., Ginsburg 1971, Land and Goreau 1971).

The abundant, thick crusts of photophilic crustose coralline algae which are found on *A. palmata* (for example, at locality BJ in the 125,000 yr reef tract) support the hypothesis of Mesoella et al. (1969) that the more extensive reef tracts reflect the degree of climatic warmth - the development of well-defined zones and abundant algal crusts within these reef complexes probably indicates a climax community (for definition, see Goreau 1959) which grew very near sea level. Conversely, poorly-developed reef tracts, which often support only thin algal encrustations (for example, locality MS) probably represent depauperate communities which did not reach a climax succession because of their depth of growth.

Encrusters also play an important role in the construction of Pleistocene reefs in that coral fragments are often welded together by overgrowth of crusts. This is most commonly seen in the high energy environments where coral debris is abundant. Broken fronds of *A. palmata* and to a lesser extent, broken sticks of *A. cervicornis*, are frequently found welded together by a continuous crust of coralline algae in the
reef crest zone of many uplifted reefs (Plate 31b). Algal encrustations in the A. palmata zone of present day West Indian reefs (for example, see Ginsburg 1956, Kornicker and Boyd 1962, Shinn 1963 and Scatterday 1974) play a similar role and frequently form an exceedingly wave-resistant, rigid framework.
CHAPTER 4

METHODS OF SUBSTRATE COLONISATION BY ENCRUSTING ORGANISMS
4.1 INTRODUCTION

The manner in which an encrusting organism overgrows a particular substrate is determined by the mode of growth of that individual and by its growth rate. In addition, the nature of the substrate (whether smooth or irregular and whether living or dead) and its own mode of growth can profoundly affect the final form of an encruster.

4.2 FORM AND GROWTH RATE OF ENCRUSTER

The encrusters on the reefs at Bellairs can be subdivided, on the basis of their growth form, into three types: (1) those which grow by radial expansion of the colony or crust and develop as a laminar form, (2) those whose growth is predominantly linear and (3) those whose growth, although radial, is limited in size.

With each of the above groups, growth rates of individual encrusters is highly variable. However, within group (1), growth rates of circular crusts (such as the crustose corallines, bryozoans and the foraminiferan Cypsina plana) usually exceed those of organisms in the second and third groups (such as serpulid worms and individual foraminiferans), whose limited growth results in low growth rates.

While the specific substrate selection by settling larvae will restrict the initial distribution of encrusters, growth of colonies of high radial and linear growth rates may extend the distribution of the colony/individual to otherwise unsuitable substrates.

Crusts may either be closely adherent to the substrate throughout their growth or, if the substrate is irregular (see Section 4.3), crusts may be raised off the substrate at the growing margin, so forming a bridge over any irregularity (Plate 27a).
4.3 Nature of Substrate

Whatever the mode of growth of an encruster, the method of colonisation and the final form of the individual is directly influenced by the nature of the underlying substrate.

4.3.1 Inert Substrates

Analyses of the patterns of colonisation of experimental blocks indicates that the basic growth form of any encruster is found on an inert substrate where active competition between the substrate and the encruster is at a minimum. On such a substrate, an encruster will develop to its maximum size and will usually exhibit its characteristic shape and form. This is most obvious on inert substrates with only a small degree of surface relief (such as dead crustose coralline substrates). Here, algal spores and the larvae of bryozoans, foraminiferans and worms settle and develop into colonies and individuals which are attached to the substrate over the whole of their basal surface. (Although colonies and crusts are able to expand in the absence of competition from the substrate, there may be competition for space from neighbouring encrusters occupying the same substrate).

The actual process of cementation and attachment of encrusters is unknown but it may occur by way of mucopolysaccharide cementation as suggested for bryozoans by Soule and Soule (1974).

On inert substrates of irregular surface relief, colonisation is usually restricted to dead skeletal substrates of corroded coral skeletons. Other high relief substrates such as dead bryozoans, dead Gypsina plana and heavily ornamented serpulid worm tubes are only rarely settled by larvae and spores. Whether this is due to the irregular surface micro-topography or because of some other inhibiting factor, either chemical or biological, is not known.

More often, colonisation of high-relief substrates takes place from a neighbouring, low-relief substrate. Colonisers are generally those
of laminar form with a high radial growth rate, such as crustose corallines some bryozoans and *Cypsina plana*.

Once overgrowth has taken place, encrusters attach to planar areas of the high relief substrate and proceed over irregularities either by bridging (Plates 27a, 41) or by deposition of basal cells and chambers within the irregularity (Plate 42b). In general, crusts proceed as an advancing layer of uniform thickness, which eventually conceals underlying surface features (Plate 39). Whereas laminar colonies and crusts of foraminiferans and crustose corallines overgrow substrates either by bridging or by chamber fill, bryozoans and serpulid worms employ only the bridging method on irregular substrates. In terms of security of attachment, the bridging of surface irregularities is much less secure than chamber fill of irregularities which 'roots' the crust to the substrate.

Individual encrusters which are of limited size attach themselves by means of cementation of either the chamber margins (such as the conical form of *Carpenteria utricularis* - Appendix Plate 11) or of the entire basal region (such as *Homotrema rubrum* - Appendix Plates 14-16). In most cases, the substrate occupied by the adult organism is the same as that colonised by the larva at the time of settlement.

4.32 Living Substrates

Growth and accretion of living substrates can occur either vertically (for example, corals) and/or laterally (for example, encrusting corals, crustose coralline algae, bryozoans and serpulid worms).

4.321 Substrates of Vertical Accretion

Substrates such as corals which grow by vertical accretion do so in a direction which
Living *Montastrea annularis* (M) showing initial overgrowth by *Gypsina plana* (G). Both *G. plana* and *M. annularis* are subsequently overgrown by an extensive crust of *Mesophyllum*. In this case, both the crustose coralline and the foraminiferan are dominant over the coral. Underlying substrate features are gradually obscured by crust growth.

Small scale divisions: 1mm

**PLATE 40**

Deep water form of *Hadracis* sp overgrowing and being overgrown by *Mesophyllum* (C). The association suggests that the crustose coralline and the coral are co-dominant. *Hadracis* sp (M) also exhibits overgrowth of and colonisation by serpulid worms.

The alga spreads across the substrate as a layer of uniform thickness.

Small scale divisions: 1mm

**PLATE 41**

Thin section of *Montastrea annularis* exhibiting gradual overgrowth by *Neoconiolithon*, which spreads across the coral substrate as a layer of uniform thickness with a convex growing margin (m). Growth of most crustose corallines follows a similar pattern. Although crust accretion, which is predominantly lateral, occurs around the perimeter, the entire upper surface of the crust participates in photosynthesis. Partially enclosed intraskeletal voids beneath the crust will eventually be infilled by cementation and/or sedimentation. Thin section, crossed polars.

Scale bar: 1mm
is either normal to or away from the direction of spreading of an encruster (Plates 45 & 46). Consequently, competition for space in a horizontal plane is not a limiting factor in the growth of the encruster. Since living coral will ingest settling encruster larvae and spores (Yonge 1940), overgrowth of a living substrate usually proceeds by way of laminar spreading of the encruster from a neighbouring dead substrate, rather than by direct settlement and colonisation of the substrate. Whether by bridging over the living coral or by gradual advancement of the attached crust, laminar encrustations can usually overgrow living coral tissue (see Plates 39 and 42-46).

4.322 Substrates of Lateral Accretion

Overgrowth and colonisation of a substrate growing predominantly by lateral accretion results in competition for space in a horizontal plane between the substrate and the encruster. In general, substrates of lateral accretionary growth are secondary, rather than primary frame builders. Examples include the crustose coralline algae, the bryozoans, the encrusting foraminiferan *Gypsina plana* and encrusting corals such as *Hillenorn* sp. and the deep-water form of *Madracis* sp. Unless protective mechanisms exist against overgrowth (see below) or unless potential substrate and coloniser are of similar growth rates, the organism with the slower growth rate is generally the one which is overgrown. Since growth rates are environmentally as well as genetically controlled, one particular organism may act as a substrate for another encruster in one environment, while itself overgrowing the same encruster in a different environment.

When both encrusters in the same environment are of similar growth rates, neighbouring margins of one encruster may show simultaneous overgrowth of and colonisation by the second encruster (Plate 40). Regular alternations of overgrowth in this situation result in a complex
a) Multiple crusts of *G. plana* overgrowing *Acaricia* sp. Crusts originate at discrete points on the substrate and spread radially until mutual interference restricts growth.

Small scale divisions: 1mm

b) Thin section of crust of *G. plana* advancing over *Montastrea annularis* coral substrate. Crust behind advancing convex margin is of uniform thickness. Basal layer (B) of non-organised chambers fills irregularities in bored substrate (S). Outer chambers in crust are more highly organised and produce an overall smooth crust surface.

Scale bar: 1mm

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Overgrowth of head of living *Siderastrea* sp by the encrusting form of the hydrocoral *Millepora* sp. Serpulid worms are visible within and beneath the crust.

Scale divisions: 5cm
Eusmilia fastigiata from the reef crest at Nurses Jetty showing progressive overgrowth by crustose coralline algae (Porolithon, Neogoniolithon and Lithophyllum). Underlying skeletal features are gradually obscured by crust growth.

Small scale divisions: 1mm

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Eusmilia fastigiata from the reef crest at Nurses Jetty showing progressive overgrowth by the foraminiferan Cypina plana. Encrustation of the polyps at the extreme right and lower centre is restricted to the base and sides and extends to the living edge zone. Encrustation of the upper centre polyp, however, has taken place across the edge zone and is progressing towards the centre of the polyp across the septa.

Small scale divisions: 1mm

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Gradual overgrowth of the sea fan Gorgonia flabellum (top right) by the hydrocoral Millepora sp (centre and lower left on main stem). The zone of dead tissue which precedes encrustation is clearly visible between the coral and the gorgonian.

Small scale divisions: 1mm
junction between crusts showing periodic interlaminations of the respective crusts (Plates 8, 47 and 48). One encruster will eventually dominate the association and will entirely overgrow the second organism.

Protective mechanisms which may have evolved to prevent overgrowth are evident in the encrusting bryozoans. Normally, peripheral margins of *Lichenopora* sp. are closely adherent to the substrate (Plate 12a). However, when growth occurs in the vicinity of a neighbouring encruster, the margins are raised off the substrate, thereby imposing a barrier which will prevent overgrowth (Plate 12b).

Certain other encrusting bryozoans possess specialised organs, the vibracula and avicularia which act, in part, to prevent attachment of settling larvae and spores (see Chapter 2, section 2.2.4). Similar deterrents in the form of extracellular extensions of the protoplasm may exist in the foraminiferans, since living representatives are rarely settled upon or overgrown by other encrusters.
Neogoniolithon on coral substrate being gradually overgrown by Porolithon (P). Scale bar: 0.2mm

Lithophyllum showing progressive overgrowth, from bottom left to upper right, by the bryozoan Schizoporella sp. Scale bar: 1mm.

In both plates, colonisation of one organism does not proceed by simple overgrowth by the other. In each case, the pattern of overgrowth suggests that both the substrate organism (i.e. that which is overgrown) and the colonising organism have similar growth rates and are co-dominant within that environment. At regular intervals in the overgrowth process, the substrate organism has attempted to overgrow the coloniser, as suggested by the upturned, wedge-shaped sections of crust at the interface. However, in each case, the colonising organism has dominated and has succeeded in blocking and overgrowing each attempted overgrowth by the substrate organism.
CHAPTER 5

GROWTH, DIACENESIS AND PRESERVATION OF ORGANIC ENCRUSTATIONS
A number of interrelated processes are responsible for the formation of a reef (Schroeder and Zankl 1974, Scoffin and Garrett 1974). Constructional processes, such as the growth of corals (primary frame builders) and encrusting organisms (secondary frame builders) combine to form a framework which acts as a host for further processes which are both constructional (for example, internal cementation and sedimentation) and destructional (such as boring, rasping and grazing) in nature. The operational sequence of these processes is often highly complex and is related to the environment of growth of the reef (see Section 5.3 below).

As an integral part of the reef framework, encrusting organisms are themselves subject to modification by various processes. While environmental conditions basically determine the composition of the secondary framework, processes such as boring, cementation and sedimentation interact with and affect its final form. Although the processes of growth and destruction occur simultaneously, crust development and preservation depends ultimately upon the relative rates at which the various processes operate. Thus, in well-lit areas where crusts are composed predominantly of rapidly growing crustose coralline algae, rates of growth are considerably higher than rates of destruction—consequently, organic encrustations are well developed, and, providing burial takes place within the same environment, crusts will be preserved without substantial alteration. However, in deeper and less-well lit areas where crusts are composed of slower growing, sciaphilic organisms, rates of growth and destruction are similar. Numerous processes interact with and modify crust growth in this environment, resulting in a complex, secondary framework which consists of multiple generations of boring, cementation and sedimentation (Plates 49, 50. Fig 53 illustrates the interrelationships of these processes which begin with primary frame growth. Solid lines indicate the directions in which the sequence of
Fig 53  Summary of Processes Operating On and Within a Reef

INTRASKELETAL VOIDS

Coral
Crustose Coralline Algae
Bryozoans
Forams
Serpulids

INTERSKELETAL VOIDS

between various crust components

INTER- & INTRASKELETAL BORED CAVITIES

Interskeletal Pelecypod
Inter & intraskeletal Sponge
Intraskeletal Polychaete
Intraskeletal Algal & Fungal

Fig 54  Typical Reef Frameworks which result from Constructive and Destructive Processes.
processes can operate. Broken lines indicate infrequent occurrences of a particular processes. Absence of directional lines between processes indicates that this particular sequential stage is absent).

Generally, primary and secondary frame growth is terminated by burial beneath sediment. The subsequent fate of the reef depends both on the diagenetic environment and on the mineralogy of the various framework components.

5.2 PREVIOUS RESEARCH

The concept that growth is the result of a number of interacting processes is a relatively recent one which has resulted from investigations of the internal structure of living reefs (Scoffin 1972, Zankl and Schroeder 1972, Ginsburg and Schroeder 1973, Schroeder and Zankl 1974 and Scoffin and Garrett 1974). The present study deals with the specific process of secondary crust growth on the Bellairs reefs and the manner in which other processes interact with and affect its formation and preservation.

Related studies (outlined below) deal with the specific processes of boring and cementation within the reef framework. The boring activity of sponges (Goreau and Hartman 1963, Neumann 1966 and Cobb 1969), pelecypods (Otter 1937), polychaetes (Ebbs 1966, Blake 1969), algae (Duerden 1902, Dethurst 1966), fungi (Kohlmayer 1969) and other organisms (see Yonge 1963 and Bromley 1970 for review) within the primary and secondary framework results in a variety of both open and closed cavities (Fig 54). Along with the non-bored, intra- and interskeletal voids, (Fig 54), these cavities provide a suitable environment for the precipitation of carbonate cement and the accumulation of reef-derived sediment. Studies of Recent reefs (Jand and Goreau 1970, Ginsburg et al 1971, Zankl and Schroeder 1972) have shown that synsedimentary cementation is
currently taking place within the marine environment, often within millimetres of the living surface of the framework (Hubbard 1972, Hooper 1973, Schroeder and Zankl 1974. See Fig 55 and Plates 50, 51 in the present study). Alexandersson (1974) has found cements within intraskeletal voids in the crustose coralline algae of Recent rhodoliths. Although anomalous in that they occur in the carbonate-undersaturated, temperate waters off the Scandinavian coast, the cements are similar to those currently forming within intraskeletal cavities of crustose coralline algae from Barbados (see section 5.32 below).

Macintyre et al (1963) found that patches of sand on top of the offshore bank (barrier) reef on the west coast of Barbados were cemented by high-Mg calcite. The close association of a sponge and pelecypod with the cemented sediment led Macintyre et al (op cit) to suggest that organic processes are involved in cementation. A similar, organic origin is postulated for much of the in-filling sediment found in many of the cavities within the skeletal framework of the reefs off Bellairs (section 5.33).

5.3 PROCESSES OCCURRING WITHIN THE RECENT MARINE ENVIRONMENT

5.31 Introduction

The initial process in any dynamic sequence of reef formation is growth of a framework, both primary (coral) and secondary (encrusting framework overgrowing primary frame). The type and composition of the secondary encrusting framework is related to physical factors within the environment of growth (such as light, hydrodynamic exposure - see Chapter 2). In well lit environments, the secondary framework is composed predominantly of laminar encrustations of crustose coralline algae and foraminiferae and develops as a result of lateral spreading and vertical accretion of the various
components (Chapter 4, section 4.2). Crusts in less-well lit areas, however, are composed of slower growing, sciaphilic organisms whose mode of growth results in irregular crusts composed of contorted, thin sheets of crustose coralline algae and bryozoans, overgrown by and interlaminated with individuals of a discrete and upright nature. As a result, organic encrustations are diverse in both form, composition and mineralogy. Subsequent processes, such as boring, cementation and sedimentation, will therefore have a variety of substrates with which to interact. This, in turn, creates a new framework in which the whole sequence of processes can be repeated.

5.32 Cementation

The mode of growth of primary and secondary frameworks and the skeletal structure of the framework builders themselves results in inter- and intraskeletal voids within the framework which not only act as suitable habitats for encrusters, but also provide micro-environments for the formation of internal cement. Voids range from large, irregular, sheet-like interskeletal voids which form between overgrowing crusts, to much smaller, intraskeletal voids, often a few microns in diameter, which form as a result of growth processes within the organism itself (for example, chambers within corals, foraminiferans and serpulid worms and cells and conceptacles within crustose coralline algae) (Fig 54 and Plates 49-54).

A variety of cements are found within the Recent submarine environment. These are described below.

5.321 Aragonite Cements

The aragonite cements found within the Recent reefs of Barbados are similar to those from other tropical areas (Friedman 1964, Friedman et al. 1974, Land and Goreau 1970, Sibley and Murray 1972, Ginsburg and Schroeder 1973, Hoberley 1973, Schroeder 1974 and see Bricker 1971 for general review) and also temp-
-erate water regions (Alexandersson 1972, 1974).

Typically, aragonite cements occur as fringes of fine, needle-like crystals (Plate 49) within intra- and interskeletal voids and as spherulitic clusters of radiating fibres (Plate 51), the latter occurring most often in sheet-like, interskeletal voids.

5.322 High Mg-Calcite Cements

On the basis of previous descriptions (Chave 1954, Hoherley 1970, Bricker 1971 and Milliman 1974), three types of High Mg-calcite cement have been recognised in the Recent reefs off Bellairs. These are: (1) a blocky cement of equant crystals which occur as a cavity or void infill (Plate 51) (2) a fringe cement of scalenohedral crystals and (3) a micrite-grade cement which is restricted to intraskeletal borings (Bathurst 1966) and voids where its precipitation often obliterates fine skeletal structure (Wolf 1965, Hoherley 1970, 1973, Sibley and Murray 1972).

5.323 Discussion

Both aragonite and High Mg-calcite cements on the reefs at Bellairs are of Recent, marine origin and are found immediately (1-2mm) beneath the living surface of the reef framework (Plate 51). Both cements form simultaneously, often in adjacent voids and cavities within the same substrate (Plate 51). More often, however, the form of the initial cement suggests that it is of the same composition as the substrate, the cement often occurring as a syntaxial overgrowth. This is most common in fringe cements of aragonite which occur within voids in corals such as Acropora sp. and Montastrea sp. (Plate 49). A number of authors (for example, Wilbur and Matabe 1962, Suess and Futterer 1972) have suggested that this substrate control of cement type results from the organic matrix of the host substrate acting as a template for syntaxial cement precipitation. Successive cements, however, can be of different form and mineralogy.
Shallow water coral and sciaphilic crust assemblage (left-hand frame), illustrating the various processes which are operating.

The coral substrate (lower half, white areas) has undergone extensive boring near its surface with subsequent sedimentation within the bored cavities (S). The inner region of the coral skeleton has suffered less boring and intraskeletal voids are either empty (v) or are infilled, either wholly or partly, with syntaxial aragonite cement (A) (see insert, lower right).

The encrustation on the coral substrate consists of irregular laminae of *Mesophyllum*, with interlaminated foraminiferans (*Homotrema rubrum* - see insert upper right) and serpulid worms. The outer zone of the crust, in particular, exhibits extensive boring but no internal sedimentation. Both foraminiferans and crustose corallines have undergone secondary, internal cementation (insert, upper right). The outer chambers of *Homotrema rubrum* have been infilled with High Mg calcite cement (C), while the perithallus of *Mesophyllum* has been subject to micritisation (H). Generally, the underlying hypothallus is unaffected by cementation, cell structure, in this case, still being visible.

All scale bars: 1mm
Shallow water coral and sciaphilic crust.

The original skeletal framework can be seen as a reticulate white structure in the lower part of the left-hand frame. Intraskeletal voids and bored cavities within this framework have been infilled with sediment ($S_1$ - lower right frame) and both have subsequently been bored. These second generation borings ($B_2$) have themselves been partially infilled with a second generation of sediment ($S_2$).

The sciaphilic crust complex (upper half of left-hand frame) consists of crustose coralline algal laminae and an encrusting coral (*Agaricia* sp - white framework). Both coral and crust have undergone extensive boring (upper right insert) but no internal sedimentation or cementation within the resultant cavities.

All scale bars: 1mm
Cements occur within crusts of both high (that is, those from well lit environments) and low (dimly lit environments) accretion rates. Their distribution appears to be related more to the mineralogy of the substrate and to microenvironmental conditions within the skeletal void, than to physical environmental factors, such as depth and hydrodynamic exposure (Alexandersson 1974).

5.33 Sedimentation

While cements are forming within skeletal voids, adjacent cavities within the primary and secondary framework, which are formed by boring, as well as some skeletal voids, are being filled with sediment. This sediment consists of sub-angular, 10-100μ-sized fragments of coral, coralline algae and benthonic foraminiferans, which are embedded in a matrix of brown micrite (Plate 50). Although this biomicrite infill is occasionally found in crusts of high accretion rates from shallow, exposed environments, it is most common within primary and secondary frameworks from more cryptic habitats. Infilling of skeletal voids and cavities is greatest on the underside of the coral/crust framework.

Ginsburg and Schroeder (1973) have suggested that the biomicrite sediment found in Bermudan reefs is of reef origin, derived from organic breakdown of the frame. They concluded that wave action probably creates a venturi effect within the open skeletal framework, the waves sucking water out of cavities and voids, while the resultant turbulent inflow transports suspended sediment back into the frame. However, sea conditions on the leeward, west coast of Barbados are much calmer than those around the exposed boiler/cup reefs of Bermuda and it is unlikely that wave surge is sufficient to produce extensive cavity infilling, especially on the underside of the frame where sediment-filled voids are most numerous. Furthermore, the sharp outline of sponge and polychaete borings...
within the void and cavity filling sediments suggests that early syn-
sedimentary cementation of the sediment is taking place (Fig 55 and Plate
50).

In many examples of infilled reef frame examined in the present
study, boring sponges, probably of the genus *Cliona*, were found associ-
ated with internal sediment (Plates 52 and 53). In some examples, sponge
tissue containing isolated coral and foraminiferal fragments identical
in shape and size to those in the biomicrite can be seen to merge into
internal sediment (Plate 53). This intimate association suggests that
deposition and cementation of the sediment is brought about by metabolic
activity of the sponge. It is conceivable that alteration of the partial
pressure of the CO₂ within the boring and/or the liberation of metabol-
ites would result in cementation of both locally derived and foreign
particles of which the sediment is composed.

Internal cement in cavities and voids where boring activity is
absent is probably derived from superficial sediments produced by organic
breakdown of the framework by bivalves, polychaetes, sponges, echino-
dermats and fishes in the manner described by Ginsburg and Schroeder (1973-
see above).

In a number of specimens examined, internal cement was found
overgrowing sediment in partially filled cavities.

5.34 Discussion and Summary

Although

cruster growth, cementation and sedimentation are constructional pro-
cesses which reduce porosity by the addition of a secondary framework,
the simultaneous activity of boring organisms destroys this and older
frameworks, thereby creating new surfaces on which the sequence of pro-
cesses can be repeated.

Whereas constructional processes dominate on the upper, lighted
surface of the frame, the underside often reflects the delicate balance
Adjacent conceptacles, 2mm below the outer, living surface of the crustose coralline *Hydrolithon* exhibiting both fibrous ?Aragonite (A- showing radial extinction patterns) and blocky High Mg calcite cements (B).

Scale bar: 1mm

**PLATE 52**

Thin sections under plane-polarised (left) and cross-polarised light (right) showing the association of boring sponges (B), internal sediment (first generation - S), coral skeleton (C) and intraskeletal void/cavity (V).

Internal sediment shows boring by the sponge.

Scale bar: 0.5mm

**PLATE 53**

Association of boring sponge and internal biomicrite sediment. Left-hand plate shows sponge (B), coral skeleton (C) and internal sediment (S) under plane polarised light. Under crossed polars (right hand plate), although the sponge skeleton is isotropic, the particles (P) contained within the tissue can be seen to merge gradually into internal biomicrite sediment (S).

Scale bar: 0.5mm
which exists between the opposing processes of growth and destruction. Examination of this sciaphilic crust from the fringing reefs of Barbados illustrates the whole developmental history of reef formation, from primary framework with initial encrusting layer (Fig 55a), through stages showing the interaction of various constructive and destructive processes (Fig 55b-d), to the stage of virtual destruction of the primary and often secondary frame by boring, cementation and sedimentation (Fig 55e-f). The sequence continues until boring either completely destroys both primary and secondary frame or until the frame is removed from the environment of growth by burial and/or uplift.

5.4 PROCESSES OCCURRING WITHIN THE PLEISTOCENE REEFS OF BARBADOS

The location and nature of the Pleistocene reefs of Barbados (Chapter 3) suggests that reef growth was terminated before complete breakdown by destructional processes. Furthermore, the excellent state of preservation of both the primary and secondary framebuilding elements suggest that, during reef growth, constructional, rather than destructional, processes were dominant for these particular reefs. Secondary framework growth is considerable, especially in those reef tracts interpreted as growing in shallow, high energy environments (Chapter 3, section 3.22).

In shallow water areas, polychaetes, pelecypods and clionid sponges are responsible for most of the boring activity, while in deeper water, borings are chiefly those of clionid sponges.

Internal sediment is identical in composition to that found within Recent reefs and has a similar distribution within the skeletal framework. Whereas a large number of borings within the primary and secondary framework of Recent reefs were empty, many of the borings within the Pleistocene reefs were infilled with sediment (suggesting
Diagrams, reproduced after examination of thin sections, illustrating the gradual process of internal sedimentation, cementation and boring operating in corals and their crusts. All examples are from shaded-dim cavities at depths of 3-5m on the fringing reefs off Bellairs.

a) Initial development of algal crust (*Neogoniolithon*) on unaltered coral (*Montastrea annularis*) skeleton.

b) Crust growth of 3-4 layers of unaltered sciaphilic algae (*Archagolithothamnium* and *Mesophyllum*) on a *M. annularis* substrate showing evidence of boring (cavity labelled C) and internal sedimentation (First generation).

c) Sciaphilic crust on *M. annularis* substrate of *Mesophyllum* and *Lithothamnium*. An earlier crust of *Mesophyllum* shows partial micritisation of the perithallus.

The outer zone of the underlying coral substrate shows evidence of two generations of boring (*C_1, C_2*) and one generation of internal sedimentation.

Primary voids (V) within the coral skeleton show extensive growth of ?Aragonite fringe cement.

Symbols not illustrated in key are described in Fig 43.
KEY

- Primary skeletal framework with intraskeletal void (v)
- Secondary encrusting frame with interskeletal void
- Framework with bored cavity (c, figure denotes generation of boring)
- Sediment-filled void or cavity (figure & ornament denotes generation of infill)
- Aragonite fringe cement
- High Mg-Calcite cement
- Micritised crustose coralline algal perithallus
- Living Clionid sponge & associated cavity

SCALE mm

Fig 55
d) Thick sciaphilic crust of crustose corallines (*Mesophyllum*), foraminiferans (*Homotrema rubrum*) and serpulid worms. Micritised layers of *Mesophyllum* show first generation borings ($C_1$) but no sedimentary infill. Primary voids between crusts (interskeletal) and within foraminiferans (intraskeletal) show cementation by ?High Mg-calcite (see upper insert of Plate 49).

Underlying coral substrate (*M. annularis*) shows extensive boring (3 generations) and two generations of internal sediment. Primary voids exhibit syntaxial fills of aragonite fringe cement, in addition to internal sediment (see lower insert of Plate 49).

e) Sciaphilic crust of heavily micritised layers of *Mesophyllum* showing two generations of boring ($C_1$, $C_2$) and a single generation of sedimentation.

The underlying *M. annularis* substrate has undergone 3 generations of boring and 2 generations of sedimentary infill. The few remaining primary voids exhibit aragonite fringe cements.

f) Thick crust of sciaphilic algae (*Mesophyllum*, *Lithothamnium*) showing some micritisation of the *Mesophyllum* skeleton and extensive boring (4 generations) and internal sedimentation (?2 generations). The large open cavity (labelled $C_{3-4}$) is colonised by the globose form of *Carpenteria utricularis*.

The underlying substrate has suffered extensive alteration by boring (4 generations) and internal sedimentation (4 generations), obscuring original skeletal features.
Fig 55 (cont.)
Shallow-water coral (*Montastrea annularis*) overlain by thick (3mm) crust of *Porolithon*. The coral shows no evidence of boring and internal sedimentation, all voids (v) being primary intraskeletal voids. Some syntaxial aragonite cement was found on septa and tabulae.

Similarly, the crust of *Porolithon* shows very little evidence of boring. Conceptacles show some internal cementation just below the living surface (left).

Scale bar: 1mm

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Peel of a polished and etched section of a mixed crust from the 83,000 yr reef complex at Animal Flower Bay. Coral skeleton (right) shows no evidence of boring or internal cementation or sedimentation. Other than the micritised perithallus (M) of *Mesophyllum*, crustose corallines are preserved with very little evidence of alteration.

Scale bar: 1mm

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Peel of polished and etched section of mixed crust from the 530,000 yr reef complex, locality IR.

Coral skeleton (right) has undergone solution and replacement by sparry calcite. Borings within the coral skeleton are preserved as dark areas. The majority of algal laminae have undergone micritisation with some boring (?polychaete/hivalve boring - B).

Scale bar: 1mm
that sediment infilling was a late-stage process (Plate 56).

Many of the Pleistocene reefs of Barbados are in the process of diagenetic alteration from Recent marine to fresh water (vadose) mineralogies (Matthews 1967, Pingitore 1970, James 1972). Primary frameworks consist of unstable aragonitic corals and in many of the older reefs, alteration to Low Mg calcite is taking place via a partial or complete void stage, resulting in a loss of skeletal structure (Friedman 1964, Matthews 1967, James 1972). In contrast, the greater part of the encrusting secondary framework of the uplifted reefs consists of High Mg-calcite which forms the skeletons of crustose coralline algae and foraminiferans. Alteration of the secondary High Mg-calcite frame takes place without a void stage by exsolution of Mg from the crystal lattice (Chave 1954, Friedman 1964). The skeletal framework as a result, undergoes little or no structural alteration (Winland 1969) (Plates 55 and 56) and is preserved as the stable polymorph, Low Mg calcite. The effect of diagenesis on different framework mineralogies is most obvious in older Pleistocene reefs of Barbados where the secondary encrusting framework of well-preserved crustose coralline algae and foraminiferans frequently overlies a primary framework, which after diagenesis, consists of solution voids and sparry, Low Mg calcite limestone (Plate 56).

Cements are also affected within the fresh water, vadose environment. Although aragonite needle cements are occasionally preserved in the younger Pleistocene reefs (James 1972), its unstable nature usually results in early alteration within the diagenetic environment. Cavities and voids within both the primary and secondary framework, which were presumably once filled with aragonite cements, now consist of a sparry calcite infill (Plate 56).

High Mg calcite cements (scalenohedral fringes and micrite envelopes) alter by exsolution of Mg. Consequently, they are preserved with little or no structural alteration. In many cases, High Mg calcite
fringes are the only indication of skeletal structure, both skeleton and void being replaced by sparry calcite.

Although bryozoans are a common element of superficial crusts in shaded and dim environments on Recent reefs (Chapter 2, section 2.22), they are rarely preserved within Recent sciaphilic crusts and are absent in all Pleistocene crusts examined. Their absence may result from the delicate nature of many skeletons and from the mixed, unstable mineralogy of the skeletons (Rucker and Carver 1969), neither of which will favour preservation within bored and diagenetically altered crusts.

5.5 SUMMARY AND CONCLUSIONS

Studies of the internal structure of Recent reefs have shown that numerous processes, both constructional and destructional, operate during the growth and formation of a reef. Although the present study deals with the constructional processes of secondary framework growth, all other processes interact with and affect secondary crust growth.

The type and composition of organic encrustations depends upon the environment of growth. Because they are late-stage in the constructional history of the reef and because they frequently inhabit those environments unsuitable to primary framebuilders, organic encrusters often comprise a greater proportion of the reef framework than primary framebuilders. However, the likelihood of this imbalance being preserved in the fossil record is determined by the rates of processes operating, and thus, by the environment of growth. If growth of the secondary encrusting framework exceeds the destructive activity of boring organisms, then the potential for preservation is high. This can be found in those crusts formed in shallow, well-lit environments. However, in shaded, deep water areas, crust growth is slower and destructive processes assume a greater importance.
The preservation potential of the secondary framework is also related to the length of exposure of crusts to these processes. The longer the exposure, the greater the alteration of crusts by boring, cementation and sedimentation.

Finally, the mineralogical composition of the crust determines its fate during diagenesis. Organisms and cements of High Mg calcite have a higher chance of preservation without textural and structural alteration than those composed of the aragonitic polymorph.
CHAPTER 6

SUMMARY OF STUDY AND OVERALL CONCLUSIONS
The present study is an attempt to document the distribution, ecology and geologic significance of calcareous encrusted organisms on the living reefs off the west coast of Barbados and to further elucidate the conditions of growth and burial of the uplifted Pleistocene reefs of the island using preserved encrusting organisms.

On the Recent reefs, each major physical environment is characterised by a particular assemblage of encrusters. In high-energy, shallow water environments, surfaces which are exposed to direct incident illumination of high intensity are characterised by crustose coralline algae such as *Porolithon*, *Neoegoniolithon*, *Lithophyllum* and *Tenarea* spp. These and other encrusters such as foraminiferans (*Gypsina plana* and the encrusting form of *Homotrema rubrum*) and bryozoans (*Trematoecia turrita*, *T. magnifera*, *Reptadeonella* sp. and *Rhynechozoon* sp.) generally found within this environment exhibit morphological and anatomical adaptations (such as compact skeletal form and increased skeletal calcification) for life in this relatively hostile environment. In lower energy, deeper water environments, exposed surfaces which are illuminated by light varying from 10-30% of the total surface illumination are encrusted by crustose coralline algae such as *Neoegoniolithon* and *Hydrolithon*, by foraminiferans (*Gypsina plana* and the encrusting and globose forms of *H. rubrum*) and by a variety of serpulid worms.

In contrast, concealed shaded environments at all depths which are characterised by light intensities varying from 0-20% of their surface incident value are characterised by shade-loving encrusters such as the crustose corallines *Archaeolithothamnium*, *Mesophyllum* and *Lithothamnium*, the foraminiferans *Homotrema rubrum* (branching form) and *Carpenteria utricularis*, serpulid worms such as *Pseudovermilia* sp., *Serpula* sp. and *Vermiliopsis* sp. and by a variety of bryozoans (*Crepidacantha* sp., *Cribrilina* sp. and *Parasmittina* sp.). Most of these sciaphilic encrusters
are delicate forms which exhibit varying degrees of structural and behavioural adaptations to this extreme, low energy environment.

Examination of encrusters living on the Recent reefs and colonising experimental substrates planted during the course of this study indicate that the overall distribution of encrusters on the reefs at Bellairs results from the influence of physical environmental factors (for example: light, hydrodynamic exposure). The zonation of encrusters results from the differing ability of individual species to withstand and to utilise variations within these environmental factors.

For each encruster group, however, distribution can usually be related to the influence of one specific (or limiting) environmental factor. For example, light is a controlling factor in the distribution of crustose coralline algae but has little influence on the distribution of serpulid worms or bryozoans. The mechanisms by which limiting factors effect distribution of the various encruster groups has been investigated in the present study.

Pigment analyses of three genera of crustose coralline algae have shown that their distribution in relation to incident light can be correlated with the type and quantity of photosynthetic pigment which they contain. Algae from shallow, well lit environments have both a high pigment concentration and also a high ratio of the pigments phycobilin:chlorophyll. While a priori arguments suggest that shallow water plants should contain a high level of the red-absorbing chlorophyll in order to maximise their potential for photosynthesis, it is suggested that the relatively high level of phycobilins acts as a filter to protect the chlorophyll from possible denaturing by excessive sunlight. This argument is supported by analytical evidence which indicates that both the total pigment content and the ratio of phycobilins:chlorophylls decreases to a minimum value at 15m where levels of illumination are much lower (approx. 30% of their surface incident value).
Beyond this depth, however, incident light becomes increasingly monochromatic in composition and it is suggested that the second increase seen in the total pigment concentration and in the phycobilin:chlorophyll ratio results from an increase in the quantity of phycobilin, allowing maximum utilisation of the remnant green light at depth.

Microscopic examinations of living examples of the foraminiferan Gypsina plana have suggested the presence of symbiotic algae, an association which could explain the anomalous photophilic distribution of this foraminiferan.

Morphological and anatomical studies of encrusting foraminiferans and bryozoans undertaken in the present study reveal a correlation between skeletal morphology and the degree of hydrodynamic exposure, those forms characteristic of high energy environments having a heavily calcified skeleton, while those of low energy environments possess delicate skeletons which exhibit adaptations to life in this type of environment.

While the overall distribution of encrusters is brought about by variations in physical environmental factors, their local distribution and final form is determined by random biotic factors such as predation and also by competition for space from neighbouring encrusters and/or the underlying substrate. The effects of predation are greatest on exposed external surfaces of the reef frame where grazers such as the sea urchin Diadema antillarum and parrot fishes are primarily responsible for controlling the local distribution of crustose corallines and exposed foraminiferans (Monotrema rubrum - encrusting form) and bryozoans (Tretatooecia sp. and Heptacladumella sp.). While competition for space exists in both exposed and cryptic environments, it is most active in cryptic habitats where the controlling influence of the larger grazing organisms is minimal. However, this absence of any grazing control in cryptic environments is probably compensated by the slower growth rates of many sciaphilic organisms here.

The study of experimental substrates reveals that, providing the environment of growth remains constant, there is a simple succession in
terms of encruster colonisation from initial primary colonisers (all of which are common encrusters) through to secondary and, in general, less common encrusters.

Growth rates of encrusting organisms were also measured from experimental substrates. While these substrates provided the expected result that organisms exposed to direct incident light have higher growth rates (1.5-3.0mm/month for Porolithon and Leogoniolithon in shallow, well lit and lighted situations), they also indicated that certain sciaphilic bryozoans (Stylopora informata, Parasmittina ophidiana and Rhynchozoan grandicella) possess growth rates (1.5-6.0mm/month) which were frequently equal to and occasionally exceeded those of photophilic crustose corallines. In general, however, growth rates of sciaphilic encrusters were low (for example, 0.2-1.0mm/month).

A summary of the information obtained from analyses of the distribution of individual encruster species in various environments on both natural and artificial substrates provides a model of Recent encruster ecology. This model is based on a large number of individual species representing various animal and plant groups of diverse but specific ecological requirements. As such, it provides a method of palaeoecological analysis which is more accurate than one based on a single species or on a particular group of organisms.

Interpretations of the conditions of growth of the Pleistocene reefs of Barbados were previously based on morphological and faunal comparisons made with similar reefs in Florida and Jamaica. In applying the model of Recent encruster distribution to the Pleistocene reefs of Barbados, an alternative, and in some aspects, a more accurate palaeoecological interpretation can be made. Encrusters can not only indicate the environmental conditions prevailing at the time of growth of the reef, they can, by continued growth, even after the death of the primary framework, document the entire history of the death and breakup of the reef, right up to the time of burial.
Because encrusters appear late in the process of reef formation, their potential for preservation is high. The Mg-calcite skeleton of many encrusters further improves this potential since skeletal structures do not undergo the void stage associated with diagenetic alteration of aragonite skeletons.

While the absence of pre-Pleistocene reefs on Barbados prevented the extrapolation of the Recent encruster model further into the fossil record, the principles adopted in this study could be applied to the interpretation of much older fossil assemblages, either by direct comparison of living organisms and their fossil counterparts or, in some cases, by indirect comparison of unrelated groups using analogous morphological and anatomical features.


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ADDENDUM

Additional References


DESCRIPTIVE KEY TO THE GENERA OF CRUSTOSE CORALLINE ALGAE FOUND BY THE
PRESENT STUDY OFF THE WEST COAST OF BARBADOS

1) Sporangia in horizontal rows of oval sori. Simple, curved hypothallus, overlain by perithallus of vertical rows of cells with sori. Occurs as thin, pink-brown crusts with a smooth glossy surface. Concealed shaded situations.

.... ARCHAEO lithothamnium

1) Multipored, asexual conceptacles present.

2) Plants generally a single layered hypothallium composed of isodiametric cells (>25μ in width) with single heterocysts. Individual thin thalli overlap to form thick leafy crusts with waxy dark green surfaces. Just lighted situations.

.... POSLIELLA

2) Plants with well developed perithallium

3) Hypothallus coaxial on radial sections. Non-radial sections show structureless granular hypothallus and perithallus of isodiametric cells. Green, cream or pink crusts, tangentially ridged with a glossy surface, the growing edge often raised into a colourless, rounded lip. Knobby centre to older crusts in just lighted situations. Normally cryptic, shaded situations.

.... L SESOPHYLLUM

3) Hypothallus non-coaxial.
4) Large, isodiametric-celled hypothallus visible in vertical section, overlain by perithallus of small (>10μ) pigmented cells. Forms thin (>1mm) brightly coloured crusts which are loosely attached to the substrate and often drape surface irregularities. Just lighted situations.

**NEOPOLYPOROLITHON**

4) Simple hypothallus of rounded cells, overlain by perithallus of vertical columns of small, pigmented cells. Forms thin, closely adherent grey-brown crusts with matt, cratered surface. Dim, cryptic situations.

**LITHOTHANNIUM**

1) No multipored asexual conceptacles or sori

5) Individual crusts thin, primarily hypothallus. Thicker crusts developed by overlapping.

6) Large (>15x30μ) vertically elongated hypothallial cells.

No perithallus. Mottled pink-white crusts develop as plumose overgrowths. Lighted situations.

**TENIAREA**

6) Isodiametric hypothallial cells.

**FOSILIELLA**

5) Thicker crusts developing perithallus

7) Heterocysts present

8) Heterocysts in horizontal clusters. Coaxial hypothallus overlain by thick dense perithallus with heterocysts and reniform conceptacles. Crusts have light coloured, chalky surface with finger-print patterning. Well lit situations.

**POROLITHON**
8) Heterocysts either single or in vertical rows.

9) Hypothallus coaxial or multilayered on vertical sections overlain by a perithallus with vertical rows of heterocysts. Forms mottled pink and white mammilated crusts with lighter growing edge. Lighted situations.

   NEOGONIOLITHON

9) Hypothallium not coaxial. Thin if multilayered.

10) Perithallus and hypothallus granular in section Single heterocysts. Conceptacles large and often numerous in perithallus. Purple, pink or cream pustulose crusts. Just lighted situations.

   HYDROLITHON

10) Perithallus non-granular

   NEOGONIOLITHON

7) Heterocysts absent

11) Surface glossy, pink or brown.

   ARCHAEOLEITHOTHALITHUM

11) Surface dull

12) Hypothallus coaxial on radial fracture. Dense perithallus.

   NEOSPHYLLUM

12) Hypothallus non-coaxial

13) Large-celled sunken meristem (= region of active cell division) and hypothallus visible in vertical section.

   NEOPOLYPOROLITHON
13) Meristematic and hypothallus cells small (10\mu diam.)

14) Secondary pits present between cells

15) Vertically elongate hypothallus cells in vertical section.

...... TENAREA

15) Isodiametric cells. Simple curved hypothallus overlain by thick, dense perithallus. Purple and green glossy crusts develop into knobby growths on upper surfaces in exposed situations. Lighted habitats.

...... LITHOPHYLLUM

14) Secondary pits absent.

...... LITHOTHAMNION

For illustrations of anatomical features described, see Appendix plates 1 - 10.
APPENDIX PLATE 1

Thin section of Porolithon sp. The tangential section shows simple curved hypothallus (H) overlain by dense perithallus (P) of isodiametric cells, with larger horizontal clusters of heterocysts (T).

Scale bar: 0.2mm

APPENDIX PLATE 2

Thin section of Neogoniolithon sp. The radial section shows coaxial hypothallus (H) overlain by dense perithallus (P) with vertical columns of heterocysts (T).

Large oval conceptacles (C) included within the perithallus are visible near to the surface. Darker, pigmented cells are clearly visible in the outer epithallus.

Scale bar: 0.2mm
APPENDIX PLATE 3

Thin section of *Lithophyllum* sp overgrowing crust of *Porolithon*. Simple hypothallus (II) of curved rows of cells is overlain by a perithallus of large isodiametric cells, often connected by secondary pits (not visible).

Scale bar: 0.2mm

APPENDIX PLATE 4

Thin section of multiple crusts of *Tenarea* sp overgrowing the foraminiferan *Gypsina plana* and overgrown by the bryozoan *Schizoporella* sp.

Individual laminae of *Tenarea* are 1 cell thick and are composed of inclined rectangular cells, 15μ x 30μ in size. Overgrowth of successive laminae results in crusts of considerable thickness.

Scale bar: 0.2mm
APPENDIX PLATE 5

Thin section of crust of *Hydrolithon* sp overgrowing dead skeletal substrate. No obvious distinction can be seen hypo- and perithallus. Cells of the thallus are irregular in form, giving the thallus a granular appearance in cross-section.

Large conceptacles (C) produce a pustulose external surface.

Scale bar: 0.5mm

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APPENDIX PLATE 6

Thin section of loosely attached crust of *Neopolyporolithon* sp showing large hypothallial cells (H) overlain by smaller, heavily pigmented cells of the perithallus (P).

Scale bar: 0.1mm
Thin section of multiple crusts of *Fosliella* sp overgrowing *Gypsina plana*. Individual laminae consist of a hypothallus (H) of isodiametric cells only.

Scale bar: 0.2mm

Thin section of crust of *Archaeolithothamnium* sp (A). No distinction can be seen between hypothallus and perithallus, cells of both being small, isodiametric and heavily pigmented. *Archaeolithothamnium* is characterised by extensive horizontal rows of large oval sori (S).

Scale bar: 0.2mm
Thin section of three crusts of *Mesophyllum* sp (labelled 1, 2 and 3). Depending on the orientation of the section, the hypothallus may be simple (S) or coaxial (P), consisting of large isodiametric cells. These are overlain by a dense perithallus of smaller cells whose outline is often obscured (as here) by micritisation (M). Conceptacles (C) are large and oval and are often seen to contain reproductive structures.

Scale bar: 0.2mm

Thin section of crust of *Lithothamnium* sp overlying heavily micritised crust of *Mesophyllum*. The simple hypothallus (H) of *Lithothamnium* consists of large rounded cells overlain by a perithallus (P) of vertical rows of small, heavily pigmented cells.

Scale bar: 0.1mm
CARPENTERIA UTRICULARIS - conical form (Appendix plate 11)

Adult tests

4-5 mm in basal diameter, grey-green in colour and conical in shape. Calcified chambers radiate from the central apical aperture region, which consists of one or more aperture necks. Juvenile test walls thin and perforated by numerous canals (Appendix plate 11b) which open as fine pores on the granular exterior (Appendix plate 11a). Secondary calcification of the adult test produces a honeycombed surface texture.

CARPENTERIA UTRICULARIS - globose form (Appendix plate 12)

Mature individuals are small (1-2 mm basal diameter) and grey-white in colour, with a characteristic reticulate secondary calcification of the chamber walls. Juveniles of conical and globose forms are similar but in the globose form, environmental and/or physiological controls restrict lateral growth, so that chambers are added on top of aperture necks, producing tall globose tests (Appendix plate 12).

CARPENTERIA HASSELI (Appendix plate 13)

Large conical tests are brown in colour with a basal diameter of 10-15 mm. Chambers are closely adherent to the substrate and often spread laterally by root-like outgrowths from the distal margin. Chambers are thin walled, often pustulose, with a single apical aperture.
Surface (upper plate) and thin section (lower plate) views of the conical form of *Carpenteria utricularis* on a dead coral substrate. Small, initial chambers can be seen to be overgrown by younger, much larger chambers which radiate out from the central aperture.

Canals can be seen passing perpendicularly through the chamber walls which show no secondary calcification.

Scale bar: 1mm
Scanning electron micrograph of the surface (upper plate) and thin section view (lower plate) of the globose form of *Carpenteria utricularis*.

Surface view shows two mature individuals exhibiting reticulate secondary calcification of the external surface. That on the left is older and shows terminal development of additional chambers.

Scale bar: 1mm

Thin section illustrates depressed globose form from a relatively high energy environment. Additional globose chambers are added radially to the test, rather than vertically. Coral substrate (C) exhibits colonisation by the crustose coralline *Lithothamnium* (L) prior to encrustation by *C. utricularis*.

Scale bar: 0.5mm
Surface views of two forms of *Carpenteria hassleri*. The upper plate illustrates the root-like outgrowths from the outer chambers at the point of attachment to the dead coral substrate. *C. hassleri* in the lower plate (labelled C) illustrates the pustulose ornamentation of the chambers.

The fragile nature of the test is shown by the broken chambers (arrowed) at the lower left.

Competition for space with bryozoans (B) on this dead skeletal substrate is intense.

Scale bar: 2mm
HOMOTREMA RUBRUM

All three forms of H. rubrum are pale pink - bright red in colour with a reticular areolate outer surface, surrounded by imperforate chamber walls.

HOMOTREMA RUBRUM - branching form (Appendix plate 14)

Tests 2mm in basal diameter and 1-3mm in height. Morphology depends on degree of hydrodynamic exposure and varies from a depressed conical test (Appendix plate 14b) in exposed habitats, to a tall delicate branched test (App. plate 14a) in protected habitats.

HOMOTREMA RUBRUM - encrusting form (Appendix plate 15)

Tests occur as thin encrusting sheets, 2-3mm in diameter from which arise truncated conical projections.

HOMOTREMA RUBRUM - globose form (Appendix plate 16)

Tests globose, dull red in colour with an average basal diameter of 3mm and a height of 4mm.

GYPSINA PLANA (Appendix plate 17)

Large sheet-like pale green, cream or brown tests range from 10 to 3,500mm² in areal coverage and from 0.1 to 2.0mm in thickness. Tests are characterised by an external surface of raised perforated polygonal chambers (App. plate 17) which overlie ordered columns of earlier-formed chambers.

BOHELLODINA sp. (Text plate 18)

Grey-green agglutinated tests occur in spiral or elongate growth forms, 10mm or more in diameter and less than 1mm thick.
Scanning electron micrograph of the surface (upper plate) and thin section views (lower plate) of the branching form of *Homotrema rubrum*.

The surface view illustrates the delicate nature of the 'branches'.

The thin section illustrates two tests from a relatively high energy environment in which branches have failed to develop or have been eroded off. Both are attached directly to the dead skeletal substrate and to serpulid worm tubes (extreme left and right).

*Scale bar: 0.2mm*
Scanning electron micrograph of the surface (upper plate) and thin section view (lower plate) of the encrusting form of *Hematremes rubrum*.

Surface view illustrates three truncated conical projections of the test, which is overgrowing the bryozoan *Labioporella* sp.

The thin section illustrates an extensive test overgrowing coral and serpulid worm substrates (S).

Two truncated conical projections are visible at (C).

Scale bar: 0.2mm
Surface (upper plate) and thin section (lower plate) views of the globose form of *Homotrema rubrum* attached to dead coral and bryozoan substrates.

Scale bar: 1mm
Scanning electron micrographs of the surface (upper and lower plates) and interior (lower plate) of *Gypsina plana*. Upper plate illustrates the irregular nature of the skeletal surface which is composed of castellated plates. In the lower plate, these plates can be seen to correspond to the upper surface of underlying columns of isodiametric chambers.

Scale bar: 0.1mm
Thin section of a crust of *Cyprina plana* overgrowing a dead coral substrate. The irregular chambers of the basal layer (B) are overlain by regular columns of isodiametric cells.

Scale bar: 1 mm

---

Scanning electron micrograph of the surface of the chambered foraminiferan *Planorbulina ?mediterranensis* on dead skeletal and filamentous algal substrates.

Scale bar: 0.1 mm
BIARRITZINa sp

A depressed, dark red conical test consisting of finely perforate chambers radiating from a central aperture.

PIANORBULINA MEDITERRANEENSIS (Appendix plate 18)

Tests are 1-2mm in diameter and consist of numerous coarsely perforate chambers which are closely attached to the substrate.
MORPHOLOGICAL AND ANATOMICAL DESCRIPTIONS OF ENCRUSTING SERPULIDS

FOUND OFF THE WEST COAST OF BARBADOS

PSEUDOVERMILIA MULTISPINOSA (Appendix plate 19)

Tubes heavily perforate, white or cream in colour with a number of longitudinally flattened, tooth-like keels spaced regularly along a median ridge. Tubes coiled or sinuous in form, 10 mm long, 3 mm wide and 0.5 - 1.5 mm thick. Usually attached to the substrate along the whole of the tube by extensive lateral outgrowths or flanges.

PSEUDOVERMILIA FUSCOSTRIATA (Appendix plate 20)

Tubes smaller than those of P. multispinosa with finer perforations of the tube and a smaller median keel. Tubes are characterised by their mottled brown cream colouration and by small lateral toothed keels flanking the median keel.

PSEUDOVERMILIA OCCIDENTALIS

Tubes thick-walled and imperforate, white in colour with a single median longitudinal keel, giving the tube a triangular cross-section. Most of tube is ornamented with fine vertical ribbing. Anterior smooth and cylindrical and often raised above the substrate.

VERMILIOPSIS ANNULATA (Appendix plate 21)

Tubes thin walled (less than 1 mm), pale-green, purple or white in colour
Surface view of *Pseudovermilia multispinosa* on dead skeletal substrate.

Surface view of *Pseudovermilia fuscostriata* (F) on dead skeletal substrate.

Surface view of *Vermiliopsis* sp. (V) with flared peristomes, associated with *Hydroides* sp (H), *P. multispinosa* (P), *Filocrana* sp (F), *Serpula* sp. and the bryozoan *Labicorella* sp. (L).

*Serpula Lobiancoi* associated with partially embedded *Sclerostyla ctenactis* (C) and other encrusters on a dead skeletal substrate.

Scale bars on plates: 2mm
with three median longitudinal ridges and two lateral flanges. Tubes are square in cross-section. They are initially coiled but become more sinuous during growth as the diameter increases. Development of flared collars or peristomes at irregular intervals along the length of the tube appears to be related to environmental influence (see text). Length varies from 5-35mm.

**SERPULA Lobiaconoi** (Appendix plate 22)

Thin (less than 1mm) tubes are characterised by their salmon-pink colour and smooth external surface. Although initially tightly coiled, tubes assume a more sinuous form during later stages of growth when they may reach 10-20mm long. Tubes have a circular cross-section of constant diameter and are usually attached to the substrate along their entire length.

**SclerostyIa CTENACTIS** (Text plates 27b and 29a)

Tubes are thick (2mm) walled, green or white in colour and are irregularly perforate with three indistinct longitudinal ridges. However, surface ornament is often obscured by the embedded mode of growth (Plate 29a). Tubes circular in cross-section with an average length of 25mm.

**Hydroides sp** (Text plate 21)

Tubes thin walled (less than 1mm), white imperforate with a single median longitudinal keel and two lateral keels. Generally 20mm long and 2mm wide.
FILOGRANA sp (Text plate 23)

Small, sinuous thin-walled tubes, 0.2 mm in diameter and 5 mm in length, are normally smooth with a vague concentric ornament and raised anterior margin. Usually found in dense aggregations.

SPIROBRANCHUS GIGANTEUS (Text plate 20)

Usually embedded within living coral tissue. Tubes are thick-walled (1-2 mm), pale purple or pink in colour with a prominent median ridge forming a tooth above the orifice. Length varies considerably - maximum observed size: 40 mm long and 5 mm in external diameter.
CRUSTOSE CORALLINE ALGAE

Introduction

Of the 10 genera of crustose coralline algae found on the Bellairs reefs (Chapter 2, section 2.21), only 5 were found colonising experimental blocks. All were types which were extremely common on the reefs themselves.

Porolithon (Appendix table 2)

Porolithon was only found colonising upward-facing substrates of blocks in shallow (less than 3m), well lit environments. This compares closely with the distribution of Porolithon on the reefs themselves (Fig 12, chapter 2, section 2.212). Crusts of Porolithon were generally much thicker (1mm) than those of neighbouring crustose corallines, but were otherwise of limited lateral extent. Maximum radial growth rates of 1.5mm/month occurred on roughened glass substrates of short period of immersion. Since the area of glass available for colonisation was extremely limited, the rates listed in appendix table 2 may be considerably lower than those of Porolithon in the natural environment. Slower growth rates were found on substrates of longer periods of immersion (although these slower rates need not necessarily represent growth during the full period of immersion).

Neogoniolithon (Appendix table 3)

Neogoniolithon is the most common crustose coralline on exposed blocks in depths of 1.5-33m. Crusts
**MAXIMUM COLONY SIZE**  
**MAX. DENSITY OF COLONISATION**  
**HIGHEST RADIAL GROWTH RATE**

**SMALLEST COLONY SIZE**  
**LOWEST DENSITY OF COLONISATION**  
**SLOWEST RADIAL GROWTH RATE**

---

### Appendix Table 1  Distribution of Crustose Coralline Algae in Relation to the Character and Orientation of Experimental Glass Substrates.

<table>
<thead>
<tr>
<th>Mean Radial Growth Incrt (mm/mth)</th>
<th>Max. Radial Area (mm²)</th>
<th>Av. Area of Samples</th>
<th>No. of Periods of Immersion</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.531</td>
<td>150</td>
<td>84.5</td>
<td>4</td>
<td>C</td>
<td>Glass, Horiz - Rough, top</td>
<td>1.5m Well-Lit/Lit, Exposed</td>
</tr>
<tr>
<td>1.225</td>
<td>96</td>
<td>29.0</td>
<td>25</td>
<td>C</td>
<td>Glass, Vert. - Rough</td>
<td>1.5m Well-Lit/Lit, Exposed</td>
</tr>
<tr>
<td>0.625</td>
<td>25</td>
<td>25</td>
<td>1</td>
<td>C</td>
<td>Glass, Horiz - Rough, U/side</td>
<td>1.5m Well-Lit/Lit</td>
</tr>
<tr>
<td>0.610</td>
<td>150</td>
<td>60</td>
<td>30</td>
<td>K</td>
<td>Concrete</td>
<td>1.5m Well-Lit/Lit</td>
</tr>
<tr>
<td>0.474</td>
<td>90</td>
<td>25.3</td>
<td>17</td>
<td>K</td>
<td>Glass, Vert. - Rough</td>
<td>1.5m Well-Lit/Lit, Lit/Lit</td>
</tr>
</tbody>
</table>

---

### Table 2  Summary of the Growth and Distribution of *POROLITHON* sp. on Experimental Substrates
were found on both horizontal and vertical surfaces and achieved their highest growth rates and largest size on just-lighted and lighted artificial (glass and perspex) substrates in mid- and shallow depths, (Appendix table 3), a distribution similar to that found in nature (Fig 14 and Chapter 2, section 2.212). Neogoniolithon was also found colonising outward-facing substrates of block D in a shaded cavity at 1.5m depth. Maximum growth rates were found on short term experiments on those blocks which had been immersed for periods of 9 months or longer, Neogoniolithon had much slower growth rates*

Tenarea (Appendix table 4)

Tenarea was only found on exposed blocks immersed for periods longer than 10 months. Environments occupied ranged in depth from 1.5m to 33m in exposed, just-lighted and lighted locations. Maximum growth rates were found on the just-lighted coral substrate of block N, immersed at 33m depth for a period of 18 months. On the reef itself, Tenarea achieves its greatest abundance and largest crustal area at depths of 5-8m in lighted and just-lighted habitats (Appendix table 4). Its complete absence from blocks immersed for 4-9 months in similar environments suggests that Tenarea is a late stage or secondary encruster (see Chapter 2, section 2.39). However, since all crusts were found attached directly to the substrate, it does not appear that preliminary colonisation by primary encrusters is necessary before colonisation by Tenarea can take place.

* On all blocks, the largest colony was assumed to be the oldest and to have grown during the entire period of immersion of the block - see Chapter 2, section 2.36.
<table>
<thead>
<tr>
<th>Mean Radial Growth Incr</th>
<th>Max. Radial Area mm²</th>
<th>Av. Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>I</td>
<td>Glass, Vert. 15m Just rough</td>
<td>Lighted</td>
</tr>
<tr>
<td>2.864</td>
<td>525</td>
<td>221</td>
<td>5</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.500</td>
<td>400</td>
<td>227</td>
<td>3</td>
<td>4</td>
<td>I</td>
<td>Glass, Horiz. 15m Just rough, top</td>
<td>Lighted</td>
</tr>
<tr>
<td>2.250</td>
<td>324</td>
<td>119</td>
<td>16</td>
<td>4</td>
<td>I</td>
<td>Perspex, vert. 15m Just Lighted</td>
<td></td>
</tr>
<tr>
<td>2.125</td>
<td>289</td>
<td>144</td>
<td>60</td>
<td>4</td>
<td>B</td>
<td>Perspex, vert. 6m Lighted</td>
<td></td>
</tr>
<tr>
<td>1.996</td>
<td>255</td>
<td>103</td>
<td>5</td>
<td>4</td>
<td>D</td>
<td>Glass, vert rough 1.5m Just Lighted</td>
<td></td>
</tr>
<tr>
<td>1.875</td>
<td>225</td>
<td>90</td>
<td>15</td>
<td>4</td>
<td>E</td>
<td>Perspex, vert. 6m Lighted</td>
<td></td>
</tr>
<tr>
<td>1.875</td>
<td>225</td>
<td>69.8</td>
<td>28</td>
<td>4</td>
<td>I</td>
<td>Brick, vert. 15m Just Lighted</td>
<td></td>
</tr>
<tr>
<td>1.858</td>
<td>221</td>
<td>54</td>
<td>12</td>
<td>4</td>
<td>C</td>
<td>Glass, vert. rough 1.5m Lighted</td>
<td></td>
</tr>
<tr>
<td>1.768</td>
<td>200</td>
<td>100</td>
<td>75</td>
<td>4</td>
<td>D</td>
<td>Perspex, vert. 1.5m J.Lighted /Shaded</td>
<td></td>
</tr>
<tr>
<td>1.763</td>
<td>199</td>
<td>63.4</td>
<td>11</td>
<td>4</td>
<td>D</td>
<td>Glass, horiz. 1.5m J.Lighted rough, U/Side /Shaded</td>
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</tr>
<tr>
<td>1.673</td>
<td>1120</td>
<td>276</td>
<td>11</td>
<td>10</td>
<td>K</td>
<td>Wood, vert. 1.5m Lighted</td>
<td></td>
</tr>
<tr>
<td>1.551</td>
<td>154</td>
<td>66</td>
<td>5</td>
<td>4</td>
<td>E</td>
<td>Glass, horiz. 6m Lighted rough, top</td>
<td></td>
</tr>
<tr>
<td>1.531</td>
<td>150</td>
<td>64</td>
<td>150</td>
<td>4</td>
<td>D</td>
<td>Brick, vert. 1.5m J.Lighted /Shaded</td>
<td></td>
</tr>
<tr>
<td>1.500</td>
<td>144</td>
<td>40</td>
<td>35</td>
<td>4</td>
<td>B</td>
<td>Coral, vert. 6m Lighted</td>
<td></td>
</tr>
<tr>
<td>1.500</td>
<td>144</td>
<td>30.2</td>
<td>22</td>
<td>4</td>
<td>E</td>
<td>Brick, vert. 6m Lighted</td>
<td></td>
</tr>
<tr>
<td>1.479</td>
<td>140</td>
<td>44.5</td>
<td>11</td>
<td>4</td>
<td>E</td>
<td>Glass, horiz. 6m Lighted rough, U/Side</td>
<td></td>
</tr>
<tr>
<td>0.760</td>
<td>750</td>
<td>208</td>
<td>8</td>
<td>18</td>
<td>N</td>
<td>Perspex vert. 33m Just Lighted</td>
<td></td>
</tr>
</tbody>
</table>

Table 3  Summary of the Growth and Distribution of *NEOGONIOLITHON* sp on Experimental Substrates.
<table>
<thead>
<tr>
<th>Mean Radial Growth Incrt</th>
<th>Max. Area mm²</th>
<th>Av. Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.833</td>
<td>900</td>
<td>900</td>
<td>1</td>
<td>18</td>
<td>N</td>
<td>Coral, vert.</td>
<td>33m Just L. /Shaded</td>
</tr>
<tr>
<td></td>
<td>900</td>
<td>500</td>
<td>2</td>
<td>18</td>
<td>N</td>
<td>Concrete 45°</td>
<td>33m Just Lighted</td>
</tr>
<tr>
<td>0.824</td>
<td>880</td>
<td>311</td>
<td>10</td>
<td>18</td>
<td>N</td>
<td>Concrete 45°</td>
<td>33m Just Lighted</td>
</tr>
<tr>
<td>0.713</td>
<td>660</td>
<td>300</td>
<td>7</td>
<td>18</td>
<td>N</td>
<td>Perspex vert.</td>
<td>33m Just Lighted</td>
</tr>
<tr>
<td>0.680</td>
<td>600</td>
<td>600</td>
<td>1</td>
<td>18</td>
<td>N</td>
<td>Coral horiz.</td>
<td>33m Lighted /J.Lighted</td>
</tr>
<tr>
<td>0.680</td>
<td>600</td>
<td>265</td>
<td>7</td>
<td>18</td>
<td>N</td>
<td>Perspex horiz.</td>
<td>33m Lighted /J.Lighted</td>
</tr>
<tr>
<td>0.645</td>
<td>540</td>
<td>320</td>
<td>3</td>
<td>18</td>
<td>N</td>
<td>Concrete 45°</td>
<td>33m Just Lighted</td>
</tr>
<tr>
<td>0.550</td>
<td>121</td>
<td>121</td>
<td>1</td>
<td>10</td>
<td>K</td>
<td>Coral vert.</td>
<td>1.5m Lighted</td>
</tr>
<tr>
<td>0.537</td>
<td>375</td>
<td>206</td>
<td>2</td>
<td>18</td>
<td>N</td>
<td>Perspex vert.</td>
<td>33m Just Lighted</td>
</tr>
<tr>
<td>0.500</td>
<td>100</td>
<td>100</td>
<td>1</td>
<td>10</td>
<td>K</td>
<td>Concrete 45°</td>
<td>1.5m Lighted</td>
</tr>
</tbody>
</table>

Table 4  Summary of the Growth and Distribution of TENAREA Sp on Experimental Substrates
Mesophyllum (Appendix table 5)

Mesophyllum was found at all depths sampled in just-lighted and shaded habitats, a distribution which corresponds closely with that found on the Bellairs reefs themselves (Fig 18. Chapter 2, section 2.212). Although maximum radial growth rates were found at 50m on exposed, just-lighted/shaded substrates, shaded substrates on blocks at shallower depth also supported crusts of high radial growth rates (=regional stenosis. See Appendix table 5).

There was very little difference in growth rate between those crusts of Mesophyllum growing on substrates immersed for a short period of time and those immersed for longer. This suggests that the growth rate of Mesophyllum is constant throughout growth, unlike the results obtained from other crustose corallines in which it is assumed that rates of growth are initially high, but decrease during later stages of growth.

Lithophyllum

Only 4 specimens of Lithophyllum were found on experimental substrates, all on block K at 1.5m. All were found occupying a lighted position. Although Lithophyllum is an extremely common encruster of shallow, exposed surfaces of the reef itself (Fig 13. Chapter 2, section 2.212), no examples were found on blocks of short periods of immersion in similar environments.

As all 4 examples were found overgrowing other algal crusts on a block which had been immersed for 10 months, it is assumed that Lithophyllum is a late-stage or secondary encruster which is only able to grow on surfaces previously colonised by other encrusters.

Other Crustose Coralline Algae

Only the above mentioned crustose
<table>
<thead>
<tr>
<th>Mean Radial Growth Incr mm/mth</th>
<th>Max. Radial Area mm²</th>
<th>Av. Radial Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.398</td>
<td>125</td>
<td>68</td>
<td>2</td>
<td>4</td>
<td>J</td>
<td>Glass, horiz. rough, top /Shaded</td>
<td></td>
</tr>
<tr>
<td>1.369</td>
<td>120</td>
<td>50</td>
<td>10</td>
<td>4</td>
<td>J</td>
<td>Perspex, horiz. /Shaded</td>
<td></td>
</tr>
<tr>
<td>1.250</td>
<td>100</td>
<td>43</td>
<td>5</td>
<td>4</td>
<td>J</td>
<td>Coral, horiz. /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.939</td>
<td>286</td>
<td>129</td>
<td>5</td>
<td>9</td>
<td>M</td>
<td>Concrete, vert. /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.726</td>
<td>255</td>
<td>-</td>
<td>-</td>
<td>11</td>
<td>L</td>
<td>Coral, vert. /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.724</td>
<td>170</td>
<td>170</td>
<td>1</td>
<td>9</td>
<td>M</td>
<td>Perspex, horiz,U/Side /Shaded</td>
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</tr>
<tr>
<td>0.660</td>
<td>144</td>
<td>144</td>
<td>1</td>
<td>9</td>
<td>M</td>
<td>Perspex, vert. /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.635</td>
<td>195</td>
<td>60.5</td>
<td>16</td>
<td>11</td>
<td>L</td>
<td>Brick, vert. /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.625</td>
<td>25</td>
<td>10</td>
<td>20</td>
<td>4</td>
<td>J</td>
<td>Brick, vert. /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.589</td>
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<td>202</td>
<td>3</td>
<td>18</td>
<td>N</td>
<td>Brick, vert. /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.500</td>
<td>325</td>
<td>130</td>
<td>7</td>
<td>18</td>
<td>N</td>
<td>Perspex, vert. /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.500</td>
<td>16</td>
<td>6.3</td>
<td>90</td>
<td>4</td>
<td>F</td>
<td>Brick, vert. /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.498</td>
<td>120</td>
<td>47</td>
<td>13</td>
<td>10</td>
<td>K</td>
<td>Concrete, 45°U/Side /Shaded</td>
<td></td>
</tr>
<tr>
<td>0.433</td>
<td>12</td>
<td>4</td>
<td>75</td>
<td>4</td>
<td>H</td>
<td>Perspex, vert. /Shaded</td>
<td></td>
</tr>
</tbody>
</table>

Table 5 Summary of the Growth and Distribution of *MENISOPHYLLUM* sp on Experimental Substrates
corallines were found colonising the various experimental substrates. Of the other crustose coralline algae found on the Bellairs reefs, *Hydrolithon, Neopolyporolithon and Lithothamnium* are locally quite abundant (Fig 20). Their absence, as well as that of the less common *Rosiliella* and *Archaeolithothamnium*, from the experimental substrates suggests that they may be secondary encrusters, which only occupy surfaces previously colonised by other, primary, encrusters.

**BRYOZOANS**

**Introduction**

Of the 33 species of bryozoans found on the Bellairs reefs (Chapter 2, section 2.22), only 15 species are represented on the experimental substrates. All 15 species were found to be primary encrusters, colonising short term blocks immersed for periods of 3-4 months. In the sections following, species are redescribed according to the classification given in Table 1.

**Cyclostomata**

*Lichenopora* sp (Appendix table 6)

*Lichenopora* was found predominantly on blocks in shallow shaded or shallow, dim environments. Maximum radial growth rates of 0.6-0.8 mm/month were found on concrete and coral substrates on blocks in shaded/dim cavities, 6-8 m deep. *Lichenopora* was most abundant on vertical faces of coral and brick substrates or on the under-sides of glass slides and of the concrete base itself. Its distribution, in terms of depth, light and orientation on the experimental substrates is similar to that on the reefs themselves (Compare Fig 23 and Appendix table 6).
<table>
<thead>
<tr>
<th>Mean Radial Growth Incr mm/mth</th>
<th>Max. Area mm²</th>
<th>Av. Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.875</td>
<td>49.0</td>
<td>16.0</td>
<td>7</td>
<td>4</td>
<td>F</td>
<td>Concrete, vert.</td>
<td>6.6m Shaded /Dim</td>
</tr>
<tr>
<td>0.791</td>
<td>48.0</td>
<td>20.0</td>
<td>2</td>
<td>4</td>
<td>F</td>
<td>Concrete, vert.</td>
<td>6.6m Shaded /Dim</td>
</tr>
<tr>
<td>0.750</td>
<td>30.0</td>
<td>3.6</td>
<td>25</td>
<td>4</td>
<td>A</td>
<td>Coral vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.740</td>
<td>35.0</td>
<td>35.0</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Coral vert.</td>
<td>6.6m Shaded</td>
</tr>
<tr>
<td>0.685</td>
<td>30.0</td>
<td>24.0</td>
<td>3</td>
<td>4</td>
<td>B</td>
<td>Concrete, vert.</td>
<td>6.6m Shaded /Dim</td>
</tr>
<tr>
<td>0.645</td>
<td>15.0</td>
<td>15.0</td>
<td>1</td>
<td>3</td>
<td>G</td>
<td>Glass, horiz. rough, U/Side</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>0.625</td>
<td>25.0</td>
<td>15.0</td>
<td>3</td>
<td>4</td>
<td>F</td>
<td>Brick, vert.</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>0.625</td>
<td>25.0</td>
<td>7.7</td>
<td>18</td>
<td>4</td>
<td>A</td>
<td>Concrete, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.625</td>
<td>25.0</td>
<td>15.0</td>
<td>3</td>
<td>4</td>
<td>F</td>
<td>Brick, vert.</td>
<td>6.6m Shaded</td>
</tr>
<tr>
<td>0.575</td>
<td>25.0</td>
<td>12.0</td>
<td>11</td>
<td>4</td>
<td>F</td>
<td>Perspex, vert.</td>
<td>6.6m Shaded /Dim</td>
</tr>
<tr>
<td>0.559</td>
<td>24.0</td>
<td>13.0</td>
<td>2</td>
<td>4</td>
<td>F</td>
<td>Coral, vert.</td>
<td>6.6m Shaded /Dim</td>
</tr>
<tr>
<td>0.500</td>
<td>16.0</td>
<td>6.7</td>
<td>12</td>
<td>4</td>
<td>A</td>
<td>Perspex, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.500</td>
<td>16.0</td>
<td>6.5</td>
<td>4</td>
<td>4</td>
<td>A</td>
<td>Glass, horiz. rough, U/Side</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>0.500</td>
<td>9.0</td>
<td>3.1</td>
<td>3</td>
<td>3</td>
<td>G</td>
<td>Glass, horiz. smooth, U/Side</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>0.442</td>
<td>12.5</td>
<td>11</td>
<td>3</td>
<td>4</td>
<td>F</td>
<td>Coral, horiz.</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>0.417</td>
<td>6.3</td>
<td>4.2</td>
<td>4</td>
<td>3</td>
<td>G</td>
<td>Glass, vert.</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>0.405</td>
<td>10.5</td>
<td>10</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Coral, vert.</td>
<td>6.6m Dim</td>
</tr>
</tbody>
</table>

Table 6 Summary of the Growth and Distribution of *Licheniopora* sp on Experimental Substrates.
Ana sca

Parellisina latirostris (Appendix table 7)

P. latirostris was only found on relatively protected areas of substrate blocks in shaded/dim localities. Unlike the predominately mid-depth distribution of P. latirostris on the reef itself (Fig 28), colonies on the experimental substrates were generally confined to blocks of shallow water (Appendix table 7). None were found at 15m, despite apparently suitable shaded/dim conditions on the underside. Similarly, only one small colony was found on the dim underside of block N at 33m.

Smittipora sp

The only recorded occurrence of Smittipora sp came from the vertical face of the coral substrate on block J at 50m. The single specimen, located in a shaded position, had a radial growth rate of 0.3 mm/month.

Cribrimorpha

Cribrilina radiata (Appendix table 8)

C. radiata was found on experimental substrates at all depths from 3-50m, on protected areas of substrate which ranged from shaded to dim in degree of illumination. Colonies with the highest growth rates, however, were found on concrete substrates at 15m and 50m in shaded/dim locations. Colonies of C. radiata on experimental substrates exhibited some degree of regional stenosis, in that colonies at depth were found in shaded or shaded/dim environments, whereas those from shallower waters were found in dim habitats only (Appendix table 8). A correlation was found between the distribution of colonies on the experimental substrates and those on the reef itself.
<table>
<thead>
<tr>
<th>Mean Radial Growth Incrt (mm²/mth)</th>
<th>Max. Area (mm²)</th>
<th>Av. Area (mm²)</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.000</td>
<td>64</td>
<td>64</td>
<td>1</td>
<td>4</td>
<td>A</td>
<td>Brick, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.601</td>
<td>175</td>
<td>175</td>
<td>1</td>
<td>11</td>
<td>L</td>
<td>Perspex, vert.</td>
<td>5m Shaded</td>
</tr>
<tr>
<td>0.559</td>
<td>20</td>
<td>11</td>
<td>4</td>
<td>4</td>
<td>H</td>
<td>Brick, vert.</td>
<td>3.3m Shaded/Dim</td>
</tr>
<tr>
<td>0.552</td>
<td>19</td>
<td>10</td>
<td>3</td>
<td>4</td>
<td>A</td>
<td>Concrete, horiz, U/Side</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.394</td>
<td>75</td>
<td>75</td>
<td>1</td>
<td>11</td>
<td>L</td>
<td>Perspex, vert.</td>
<td>5m Dim</td>
</tr>
<tr>
<td>0.375</td>
<td>9.0</td>
<td>9</td>
<td>1</td>
<td>4</td>
<td>H</td>
<td>Perspex, vert.</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>0.370</td>
<td>8.7</td>
<td>8.7</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Coral, horiz.</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>0.351</td>
<td>160</td>
<td>160</td>
<td>1</td>
<td>18</td>
<td>N</td>
<td>Concrete, vert.</td>
<td>33m Dim</td>
</tr>
<tr>
<td>0.306</td>
<td>6</td>
<td>6</td>
<td>1</td>
<td>4</td>
<td>H</td>
<td>Coral, vert.</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>0.250</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>4</td>
<td>A</td>
<td>Coral, vert.</td>
<td>8m Dim</td>
</tr>
</tbody>
</table>

Table 7 Summary of the Growth and Distribution of *Parellisina latirostris* on Experimental Substrates
<table>
<thead>
<tr>
<th>Mean Radial Growth Increment (mm/mth)</th>
<th>Max. Area mm²</th>
<th>Av. Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.405</td>
<td>10.5</td>
<td>6.1</td>
<td>5</td>
<td>4</td>
<td>J</td>
<td>Concrete, 50m Shaded/vert. Dim</td>
<td></td>
</tr>
<tr>
<td>0.354</td>
<td>8.0</td>
<td>8.0</td>
<td>1</td>
<td>4</td>
<td>I</td>
<td>Concrete, 15m Shaded vert.</td>
<td></td>
</tr>
<tr>
<td>0.342</td>
<td>7.5</td>
<td>2.6</td>
<td>7</td>
<td>4</td>
<td>A</td>
<td>Coral vert. 8m Dim</td>
<td></td>
</tr>
<tr>
<td>0.331</td>
<td>7.0</td>
<td>2.8</td>
<td>12</td>
<td>4</td>
<td>A</td>
<td>Concrete, 8m Dim horiz.</td>
<td></td>
</tr>
<tr>
<td>0.295</td>
<td>42.0</td>
<td>42.0</td>
<td>2</td>
<td>11</td>
<td>L</td>
<td>Brick, 5m Dim vert.</td>
<td></td>
</tr>
<tr>
<td>0.286</td>
<td>5.25</td>
<td>5.3</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Coral, 6.6m Dim vert.</td>
<td></td>
</tr>
<tr>
<td>0.223</td>
<td>24.0</td>
<td>24.0</td>
<td>1</td>
<td>11</td>
<td>L</td>
<td>Perspex, 5m Dim vert.</td>
<td></td>
</tr>
<tr>
<td>0.217</td>
<td>3.0</td>
<td>2.6</td>
<td>2</td>
<td>4</td>
<td>A</td>
<td>Brick, 8m Dim vert.</td>
<td></td>
</tr>
<tr>
<td>0.204</td>
<td>54.0</td>
<td>29.0</td>
<td>3</td>
<td>18</td>
<td>N</td>
<td>Concrete, 33m Shaded 45° U/Side Dim</td>
<td></td>
</tr>
<tr>
<td>0.140</td>
<td>27.0</td>
<td>7.6</td>
<td>13</td>
<td>18</td>
<td>N</td>
<td>Concrete, 33m Shaded 45° U/Side Dim</td>
<td></td>
</tr>
<tr>
<td>0.125</td>
<td>1.0</td>
<td>1.0</td>
<td>1</td>
<td>4</td>
<td>G</td>
<td>Coral, 3.3m Dim vert.</td>
<td></td>
</tr>
<tr>
<td>0.125</td>
<td>1.0</td>
<td>1.0</td>
<td>1</td>
<td>4</td>
<td>A</td>
<td>Glass, horiz. 8m Dim rough, U/Side</td>
<td></td>
</tr>
<tr>
<td>0.090</td>
<td>10.5</td>
<td>4.4</td>
<td>4</td>
<td>18</td>
<td>N</td>
<td>Concrete, 33m Shaded vert.</td>
<td></td>
</tr>
</tbody>
</table>

Table 8 Summary of the Growth and Distribution of CRICRILINA radiata on Experimental Substrates
Ascophora

Trypostega venusta (Appendix table 9)

Only 4 colonies of *T. venusta* were recorded from experimental substrates. All occurred on substrates in dimly illuminated habitats in the 7-8m depth range. The maximum growth rate of 0.375mm/month was found on a brick substrate at 6.6m depth in a shaded/dim location.

Stylopoma informata (Appendix table 10)

*S. informata* was found on blocks in depths of water ranging from 3 to 50m, in environments which ranged from shaded to dim in degree of illumination. Maximum growth rates were found at depths greater than 33m on shaded surfaces. A certain amount of regional stenosis was exhibited in the distribution of *S. informata* (see Appendix table 11). Correlation with the non-experimental distribution of *S. informata* (Fig 27) was good. 'Giant' colonies having the highest growth rate of any encruster on the experimental substrates were found on wood and concrete. Reasons for this are not immediately apparent, but may be related to the lack of competition for space from other encrusters which existed on these particular substrates.

Hippopodina irregularis

Only 2 examples of *H. irregularis* were recorded from artificial substrates. Both occurred on blocks from dimly illuminated environments at 5m and 8m depth.

Escharina pes anseris (Appendix table 11)

Specimens of *E. pes anseris* were only found on substrates in shaded and dim environments at depths greater than 30m. A similar, although wider trend was found on the reefs themselves (Fig 28).
<table>
<thead>
<tr>
<th>Mean Radial Growth</th>
<th>Max. Radial Area</th>
<th>Av. Radial Area</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>mm²/mth</td>
<td>mm²</td>
<td>mm²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.375</td>
<td>9.0</td>
<td>9.0</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Brick,</td>
<td>6.6m Shaded vert./Dim</td>
</tr>
<tr>
<td>0.153</td>
<td>1.5</td>
<td>1.5</td>
<td>1</td>
<td>4</td>
<td>A</td>
<td>Brick,</td>
<td>8m Dim vert.</td>
</tr>
<tr>
<td>0.125</td>
<td>1.0</td>
<td>1.0</td>
<td>1</td>
<td>4</td>
<td>A</td>
<td>Coral,</td>
<td>8m Dim vert.</td>
</tr>
<tr>
<td>0.125</td>
<td>1.0</td>
<td>1.0</td>
<td>1</td>
<td>4</td>
<td>A</td>
<td>Concrete,</td>
<td>8m Dim vert.</td>
</tr>
</tbody>
</table>

Table 9 Summary of the Growth and Distribution of *TRYPOSTEGA* venusta on Experimental Substrates

<table>
<thead>
<tr>
<th>Mean Radial Growth</th>
<th>Max. Radial Area</th>
<th>Av. Radial Area</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>mm²/mth</td>
<td>mm²</td>
<td>mm²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5.995</td>
<td>2300.0</td>
<td>170.0</td>
<td>3</td>
<td>4</td>
<td>J</td>
<td>Concrete,</td>
<td>50m Shaded vert./Dim</td>
</tr>
<tr>
<td>3.375</td>
<td>729.0</td>
<td>729.0</td>
<td>1</td>
<td>4</td>
<td>J</td>
<td>Brick,</td>
<td>50m Shaded vert.</td>
</tr>
<tr>
<td>1.380</td>
<td>2475.0</td>
<td>2475.0</td>
<td>1</td>
<td>18</td>
<td>N</td>
<td>Wood,</td>
<td>33m Shaded vert.</td>
</tr>
<tr>
<td>1.046</td>
<td>70.0</td>
<td>70.0</td>
<td>1</td>
<td>4</td>
<td>J</td>
<td>Coral,</td>
<td>50m Shaded vert.</td>
</tr>
<tr>
<td>0.849</td>
<td>935.0</td>
<td>935.0</td>
<td>1</td>
<td>18</td>
<td>N</td>
<td>Wood,</td>
<td>33m Shaded vert./Dim</td>
</tr>
<tr>
<td>0.250</td>
<td>4.0</td>
<td>4.0</td>
<td>1</td>
<td>4</td>
<td>A</td>
<td>Coral,</td>
<td>8m Dim vert.</td>
</tr>
<tr>
<td>0.236</td>
<td>2.0</td>
<td>2.0</td>
<td>1</td>
<td>3</td>
<td>G</td>
<td>Coral,</td>
<td>3.3m Dim vert.</td>
</tr>
</tbody>
</table>

Table 10 Summary of the Growth and Distribution of *STYLOPOMA* informata on Experimental Substrates
<table>
<thead>
<tr>
<th>Mean Radial Growth Incr (mm/mth)</th>
<th>Max. Av. No. of Period of Block Substrate Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radial Area Area Samples Immersion (months)</td>
<td></td>
</tr>
<tr>
<td>mm²</td>
<td>mm²</td>
</tr>
<tr>
<td>0.559</td>
<td>20.0</td>
</tr>
<tr>
<td>0.375</td>
<td>9.0</td>
</tr>
<tr>
<td>0.110</td>
<td>10.0</td>
</tr>
<tr>
<td>0.068</td>
<td>6.0</td>
</tr>
</tbody>
</table>

Table 11 Summary of the Growth and Distribution of *ESCHARINA pes anseris* on Experimental Substrates.

<table>
<thead>
<tr>
<th>Mean Radial Growth Incr (mm/mth)</th>
<th>Max. Av. No. of Period of Block Substrate Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radial Area Area Samples Immersion (months)</td>
<td></td>
</tr>
<tr>
<td>mm²</td>
<td>mm²</td>
</tr>
<tr>
<td>3.373</td>
<td>728.0</td>
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<tr>
<td>1.875</td>
<td>225.0</td>
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<tr>
<td>1.146</td>
<td>84.0</td>
</tr>
<tr>
<td>0.750</td>
<td>36.0</td>
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<tr>
<td>0.523</td>
<td>17.5</td>
</tr>
<tr>
<td>0.250</td>
<td>4.0</td>
</tr>
<tr>
<td>0.217</td>
<td>3.0</td>
</tr>
<tr>
<td>0.117</td>
<td>18.0</td>
</tr>
</tbody>
</table>

Table 12 Summary of the Growth and Distribution of *PARASMITTINA ophidiana* on Experimental Substrates.
Parasmittina ophidiana (Appendix table 12)

*P. ophidiana* was found at depths of 6m to 50m on surfaces which ranged from just lighted to dim in degree of illumination. Although the highest growth rates were found at 50m in shaded/dim environments, there appears to be little correlation between colony growth rate and depth of occurrence - both large and small colonies being found at all depths examined. A similar distribution of *P. ophidiana* was found on the Bellairs reefs (Fig 28). On both the experimental substrates and on the reefs themselves, *P. ophidiana* is confined to the protected sides and undersides of substrates which were shaded or dim in degree of illumination.

Crepidacantha longiseta (Appendix table 13)

Numerous colonies of *C. longiseta* were found on experimental substrates in depths ranging from 5 to 33m. In all cases, colonies occupied the sides and undersides of dimly lit substrates (Appendix table 14). Maximum growth rates were found on shallow (less than 8m), dimly-lit surfaces. The sizes and distribution of *C. longiseta* on the experimental blocks are similar to those of *C. longiseta* on the reefs themselves (compare Appendix table 13 with text fig 28).

Rhynchozoon rastratum (Appendix table 14)

*R. rastratum* was found on substrate blocks in depths ranging from 6 to 33m and in habitats which ranged from just lighted to dim in degree of illumination. Maximum growth rates were found at mid-depth in shaded habitats. Although the total number of colonies found on experimental substrates was small, there was a close correlation with the distribution of *R. rastratum* on the Bellairs reefs themselves (compare Appendix table 14 with Fig 27).
<table>
<thead>
<tr>
<th>Mean Radial Growth Incm/mth</th>
<th>Max. Area (mm²)</th>
<th>Av. Area (mm²)</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.992</td>
<td>63.0</td>
<td>63.0</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Coral, vert.</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>0.612</td>
<td>24.0</td>
<td>11.0</td>
<td>7</td>
<td>4</td>
<td>A</td>
<td>Perspex, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.515</td>
<td>17.0</td>
<td>12.0</td>
<td>2</td>
<td>4</td>
<td>F</td>
<td>Coral, vert.</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>0.500</td>
<td>16.0</td>
<td>12.5</td>
<td>2</td>
<td>4</td>
<td>F</td>
<td>Concrete, horiz.U/Side</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>0.433</td>
<td>12.0</td>
<td>12.0</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Glass, horiz, U/Side</td>
<td>6.6m Shaded</td>
</tr>
<tr>
<td>0.405</td>
<td>10.5</td>
<td>8.0</td>
<td>2</td>
<td>4</td>
<td>F</td>
<td>Coral, vert.</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>0.405</td>
<td>10.5</td>
<td>5.4</td>
<td>5</td>
<td>4</td>
<td>A</td>
<td>Concrete, horiz.U/Side</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.375</td>
<td>9.0</td>
<td>6.4</td>
<td>2</td>
<td>4</td>
<td>A</td>
<td>Brick, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.250</td>
<td>4.0</td>
<td>2.4</td>
<td>3</td>
<td>4</td>
<td>A</td>
<td>Perspex, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.250</td>
<td>4.0</td>
<td>4.0</td>
<td>1</td>
<td>4</td>
<td>I</td>
<td>Concrete, horiz.U/Side</td>
<td>15m Dim/dark</td>
</tr>
<tr>
<td>0.183</td>
<td>2.3</td>
<td>2.3</td>
<td>1</td>
<td>4</td>
<td>A</td>
<td>Perspex, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.176</td>
<td>15.0</td>
<td>15.0</td>
<td>1</td>
<td>11</td>
<td>L</td>
<td>Coral, vert.</td>
<td>5m Shaded Dim</td>
</tr>
<tr>
<td>0.136</td>
<td>24.0</td>
<td>24.0</td>
<td>1</td>
<td>18</td>
<td>N</td>
<td>Concrete, horiz.U/Side</td>
<td>33m Dim/Dark</td>
</tr>
<tr>
<td>0.127</td>
<td>21.0</td>
<td>7.0</td>
<td>3</td>
<td>18</td>
<td>N</td>
<td>Perspex, vert.</td>
<td>33m Shaded Dim</td>
</tr>
<tr>
<td>0.125</td>
<td>1.0</td>
<td>1.0</td>
<td>1</td>
<td>4</td>
<td>G</td>
<td>Coral, vert.</td>
<td>3.3m Dim</td>
</tr>
</tbody>
</table>

Table 13 Summary of the Growth and Distribution of CREPIDACANTHA longiseta on Experimental Substrates.
<table>
<thead>
<tr>
<th>Mean</th>
<th>Max.</th>
<th>Av.</th>
<th>No. of</th>
<th>Period of</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radial</td>
<td>Area</td>
<td>Area</td>
<td>Samples</td>
<td>Immersion</td>
<td>(months)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth</td>
<td>mm²</td>
<td>mm²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inclt</td>
<td>mm/mth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.925</td>
<td>56.0</td>
<td>32.8</td>
<td>4</td>
<td>4</td>
<td>B</td>
<td>Concrete,</td>
<td>.6m Shaded</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6m</td>
<td>vert.</td>
</tr>
<tr>
<td>0.925</td>
<td>56.0</td>
<td>56.0</td>
<td>1</td>
<td>4</td>
<td>I</td>
<td>Concrete,</td>
<td>15m Shaded/Dim</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>15m</td>
<td>vert.</td>
</tr>
<tr>
<td>0.190</td>
<td>50.0</td>
<td>50.0</td>
<td>1</td>
<td>18</td>
<td>N</td>
<td>Brick,</td>
<td>33m J.Lighted</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>vert.</td>
<td>/Shaded</td>
</tr>
<tr>
<td>0.09</td>
<td>12.5</td>
<td>12.5</td>
<td>1</td>
<td>18</td>
<td>N</td>
<td>Coral,</td>
<td>33m Shaded</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>vert.</td>
<td></td>
</tr>
</tbody>
</table>

Table 14 Summary of the Growth and Distribution of *Rhynchozoa* rastratum on Experimental Substrates.

<table>
<thead>
<tr>
<th>Mean</th>
<th>Max.</th>
<th>Av.</th>
<th>No. of</th>
<th>Period of</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radial</td>
<td>Area</td>
<td>Area</td>
<td>Samples</td>
<td>Immersion</td>
<td>(months)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth</td>
<td>mm²</td>
<td>mm²</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inclt</td>
<td>mm/mth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.19</td>
<td>90.0</td>
<td>90.0</td>
<td>1</td>
<td>4</td>
<td>I</td>
<td>Concrete,</td>
<td>15m Dim</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>vert.</td>
<td></td>
</tr>
<tr>
<td>0.036</td>
<td>8.7</td>
<td>8.7</td>
<td>1</td>
<td>4</td>
<td>J</td>
<td>Concrete,</td>
<td>50m Dim</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>vert.</td>
<td></td>
</tr>
<tr>
<td>0.120</td>
<td>7.0</td>
<td>7.0</td>
<td>1</td>
<td>11</td>
<td>L</td>
<td>Perspex,</td>
<td>5m Dim</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>vert.</td>
<td></td>
</tr>
</tbody>
</table>

Table 15 Summary of the growth and distribution of *Cleidochasma* vestita on Experimental Substrates
Rhynchozoon grandicella

The only specimen of *R. grandicella* to be recorded was found on the shaded/dim underside of the concrete base of block I at 15m depth and had a mean radial growth rate of 1.83mm/month.

Trematoecia turrita

Only 2 specimens of *T. turrita* were recorded on the substrate blocks. A single specimen on the shaded/dim face of a brick substrate at 8m had a mean radial growth rate of 0.125mm/month, while a smaller specimen of 0.06mm/month growth rate was recorded on a just-lighted vertical perspex substrate of block N at 33m.

Cleidochasma vestita (Appendix table 15)

Only 3 examples of *C. vestita* were recorded. The highest growth rate was found on the dimly-lit underside of the concrete base of block I at 15m. Two other colonies, from 50m and 5m, colonised similar, dimly-lit substrates.

Dryozoan AN (Appendix table 16)

Occurrences of this unknown species were restricted to dimly-lit substrates in depths of 5 to 15m. There appears to be very little correlation radial growth rate and the depth and degree of illumination of the habitat. The maximum growth rate of 0.737mm/month was found in a shaded/dim locality at 6.6m. A similar distribution of this species was found on the reefs themselves.

**FORAMINIFERANS**

**Introduction**

All of the more abundant attached foraminiferans found on
<table>
<thead>
<tr>
<th>Mean Radial Growth Incr mm/mth</th>
<th>Max. Area mm²</th>
<th>Av. Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.780</td>
<td>39.0</td>
<td>28.0</td>
<td>2</td>
<td>4</td>
<td>F</td>
<td>Coral, vert.</td>
<td>6.6m Shaded /Dim</td>
</tr>
<tr>
<td>0.560</td>
<td>20.3</td>
<td>20.3</td>
<td>1</td>
<td>4</td>
<td>I</td>
<td>Concrete, vert.</td>
<td>15m Shaded</td>
</tr>
<tr>
<td>0.520</td>
<td>17.5</td>
<td>17.5</td>
<td>2</td>
<td>4</td>
<td>A</td>
<td>Concrete, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.452</td>
<td>99.0</td>
<td>99.0</td>
<td>1</td>
<td>11</td>
<td>L</td>
<td>Brick, vert.</td>
<td>5m Dim</td>
</tr>
<tr>
<td>0.450</td>
<td>98.0</td>
<td>77.0</td>
<td>2</td>
<td>11</td>
<td>L</td>
<td>Brick, vert.</td>
<td>5m Shaded</td>
</tr>
<tr>
<td>0.399</td>
<td>77.0</td>
<td>77.0</td>
<td>1</td>
<td>11</td>
<td>L</td>
<td>Brick, vert.</td>
<td>5m Shaded</td>
</tr>
<tr>
<td>0.370</td>
<td>8.8</td>
<td>5.1</td>
<td>2</td>
<td>4</td>
<td>A</td>
<td>Coral, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.340</td>
<td>7.5</td>
<td>7.5</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Brick, vert.</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>0.340</td>
<td>7.5</td>
<td>5.3</td>
<td>2</td>
<td>4</td>
<td>F</td>
<td>Brick, vert.</td>
<td>6.6m Shaded</td>
</tr>
<tr>
<td>0.331</td>
<td>7.0</td>
<td>6.5</td>
<td>2</td>
<td>4</td>
<td>F</td>
<td>Brick, vert.</td>
<td>6.6m Shaded /Dim</td>
</tr>
<tr>
<td>0.273</td>
<td>36.0</td>
<td>36.0</td>
<td>1</td>
<td>11</td>
<td>L</td>
<td>Perspex, vert.</td>
<td>5m Dim</td>
</tr>
<tr>
<td>0.242</td>
<td>3.7</td>
<td>3.7</td>
<td>1</td>
<td>4</td>
<td>A</td>
<td>Brick, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>0.203</td>
<td>20.0</td>
<td>20.0</td>
<td>1</td>
<td>11</td>
<td>L</td>
<td>Glass, vert. smooth</td>
<td>5m Shaded /Dim</td>
</tr>
<tr>
<td>0.177</td>
<td>12.0</td>
<td>12.0</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Coral, vert.</td>
<td>6.6m Shaded /Dim</td>
</tr>
<tr>
<td>0.125</td>
<td>1.0</td>
<td>1.0</td>
<td>1</td>
<td>4</td>
<td>F</td>
<td>Glass, Horiz. smooth, U/Side</td>
<td>6.6m Shaded /Dim</td>
</tr>
</tbody>
</table>

Table 16  Summary of the Growth and Distribution of Bryozoan AN on Experimental Substrates.
the Bellairs reefs were found encrusting the experimental substrates. *Homotrema rubrum* and *Planorhulina* sp. were found attached to blocks of short periods of immersion (4 months), whereas *Gynaxa plana* and *Carpenteria utricularis* were only found on blocks which had been underwater for longer periods.

*Carpenteria utricularis* - conical form

Occurrences of the conical form of *C. utricularis* were restricted to dimly-lit, artificial substrates of block L located in a cavity at 5m depth. The conical form appears to be a late-stage, secondary encruster, as no examples were found on blocks immersed for short periods (3-4 months) in similar habitats. As all examples were attached directly to the artificial substrate, it does not appear that previous colonisation by other encrusters is necessary. Similar distributions of the conical form in shallow, shaded/dim environments were found on the Bellairs reefs (Text Figs 31 and 37).

*Carpenteria utricularis* - globose form

The globose form of *C. utricularis* was only found on blocks which had been immersed for periods of 11 months or more. Individuals were attached directly to the surface of dimly-lit brick, glass and concrete substrates of block L and N at 5m and 33m respectively. No examples were found on coral substrates. Growth rates were low, generally 0.1mm/month or less. Its absence from apparently suitable blocks immersed for short periods suggests that the globose form of *C. utricularis*, like the conical form, is a late-stage, secondary encruster.
**Homotrema rubrum** - branching form (Appendix table 17)

Most examples of the branching form of *H. rubrum* were found on blocks of short term immersion in shaded and dim cavities at shallow depth (Appendix table 17). Although no examples were found on blocks of short term immersion in depths greater than 7m, a sparse fauna of branching forms was found at 33m on shaded surfaces of block N immersed for a total period of 18 months. Since the branching form of *H. rubrum* is found at all depths on the Bellairs reefs, this distribution on artificial substrates suggests that colonisation of shaded and dim substrates occurs most rapidly at shallow depths.

Unlike the patterns of colonisation of most crustose coralline algae and foraminifers, individuals of the branching form with high radial growth rates were not always found on substrates with a high density of colonisation of *H. rubrum* (Appendix table 17). However, maximum density of colonisation and maximum radial growth rates did occur within similar, shallow, dimly-lit habitats.

**Homotrema rubrum** - encrusting form (Appendix table 18)

All examples of the encrusting form of *H. rubrum* were found on the exposed sides and edges of substrates in shallow, shaded or just-lighted environments. In each case, colonisation occurred on artificial (concrete or brick) substrates, rather than on natural coral. Specimens with the highest growth rates were usually found on or near to the edges of their respective substrates, an exposed distribution similar to that on the reefs themselves (Text Figs 34 and 37).

**Homotrema rubrum** - globose form

Only 3 specimens of the globose form
### Table 17: Summary of the Growth and Distribution of the Branching form of *NOVOCRINIA rubrum* on Experimental Substrates

<table>
<thead>
<tr>
<th>Density of Colonies no/m²/mth</th>
<th>Mean Radial Growth Incr. mm²/mth</th>
<th>Rank based on mean</th>
<th>Max. Area mm²</th>
<th>Av. Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>11.0</td>
<td>0.144</td>
<td>4</td>
<td>10.0</td>
<td>2.6</td>
<td>18</td>
<td>11</td>
<td>L</td>
<td>Glass, vert. rough</td>
<td>5m Shaded/Dim</td>
</tr>
<tr>
<td>5.2</td>
<td>0.091</td>
<td>14*</td>
<td>4.0</td>
<td>2.2</td>
<td>13</td>
<td>11</td>
<td>L</td>
<td>Perspex, vert.</td>
<td>5m Dim</td>
</tr>
<tr>
<td>4.8</td>
<td>0.130</td>
<td>12</td>
<td>1.0</td>
<td>1.0</td>
<td>15</td>
<td>4</td>
<td>H</td>
<td>Brick, vert.</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>4.5</td>
<td>0.170</td>
<td>2</td>
<td>1.0</td>
<td>1.0</td>
<td>1</td>
<td>3</td>
<td>G</td>
<td>Glass, vert. rough</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>4.4</td>
<td>0.136</td>
<td>5</td>
<td>9.0</td>
<td>6.0</td>
<td>20</td>
<td>11</td>
<td>L</td>
<td>Brick, vert.</td>
<td>5m Dim</td>
</tr>
<tr>
<td>4.4</td>
<td>0.136</td>
<td>6</td>
<td>9.0</td>
<td>4.0</td>
<td>20</td>
<td>11</td>
<td>L</td>
<td>Brick, vert.</td>
<td>5m Dim/Dark</td>
</tr>
<tr>
<td>3.0</td>
<td>0.079</td>
<td>3</td>
<td>3.0</td>
<td>1.5</td>
<td>16</td>
<td>11</td>
<td>L</td>
<td>Brick, vert.</td>
<td>5m Shaded</td>
</tr>
<tr>
<td>2.9</td>
<td>0.016</td>
<td>11</td>
<td>1.0</td>
<td>1.0</td>
<td>3</td>
<td>3</td>
<td>G</td>
<td>Coral, vert.</td>
<td>3.3m Shaded</td>
</tr>
<tr>
<td>2.8</td>
<td>0.091</td>
<td>14*</td>
<td>4.0</td>
<td>2.1</td>
<td>8</td>
<td>11</td>
<td>L</td>
<td>Glass, horiz. rough, U/Side</td>
<td>5m Dim</td>
</tr>
<tr>
<td>2.7</td>
<td>0.129</td>
<td>13</td>
<td>8.0</td>
<td>8.0</td>
<td>7</td>
<td>11</td>
<td>L</td>
<td>Perspex, vert.</td>
<td>5m Shaded</td>
</tr>
<tr>
<td>2.7</td>
<td>0.130</td>
<td>7</td>
<td>1.0</td>
<td>1.0</td>
<td>3</td>
<td>4</td>
<td>H</td>
<td>Coral, vert.</td>
<td>3.3m Shaded</td>
</tr>
<tr>
<td>1.9</td>
<td>0.085</td>
<td>10</td>
<td>3.5</td>
<td>2.0</td>
<td>3</td>
<td>11</td>
<td>L</td>
<td>Glass, horiz. smooth, U/Side</td>
<td>5m Dim</td>
</tr>
</tbody>
</table>

### Table 18: Summary of the Growth and Distribution of the En克拉sting form of *NOVOCRINIA rubrum* on Experimental Substrates

<table>
<thead>
<tr>
<th>Density of Colonies no/m²/mth</th>
<th>Mean Radial Growth Incr. mm²/mth</th>
<th>Max. Av. Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>-</td>
<td>0.375</td>
<td>9.0</td>
<td>9.0</td>
<td>3</td>
<td>4</td>
<td>H</td>
<td>Concrete, upper edge</td>
</tr>
<tr>
<td>0.6</td>
<td>0.375</td>
<td>9.0</td>
<td>6.5</td>
<td>2</td>
<td>4</td>
<td>H</td>
<td>Brick, vert.</td>
</tr>
<tr>
<td>0.8</td>
<td>0.182</td>
<td>16.0</td>
<td>9.0</td>
<td>3</td>
<td>11</td>
<td>L</td>
<td>Perspex, vert.</td>
</tr>
<tr>
<td>-</td>
<td>0.150</td>
<td>9.0</td>
<td>3.0</td>
<td>21</td>
<td>10</td>
<td>K</td>
<td>Concrete, horiz. U/Side</td>
</tr>
<tr>
<td>-</td>
<td>0.071</td>
<td>2.0</td>
<td>2.0</td>
<td>1</td>
<td>10</td>
<td>K</td>
<td>Concrete, horiz. top.</td>
</tr>
</tbody>
</table>

Table 17: Summary of the Growth and Distribution of the Branching form of *NOVOCRINIA rubrum* on Experimental Substrates.

Table 18: Summary of the Growth and Distribution of the Encrusting form of *NOVOCRINIA rubrum* on Experimental Substrates.
were recorded from the experimental substrate blocks. All were found on dimly-lit perspex and brick substrates of block L, located within a cavity at 5m depth for 11 months.

**Gypsina plana** (Appendix table 19)

Crusts of *G. plana* were only found on exposed, just-lighted surfaces of block N immersed for a period of 18 months at 33m. Despite a ubiquitous distribution on exposed surfaces of the reefs themselves (Text figs 36 and 37), none of the experimental blocks of short-term immersion in similar, exposed habitats were colonised by *G. plana*. Its restriction to algal-encrusted areas of block N suggests that *G. plana* is a late-stage, secondary encruster which requires surfaces to be encrusted before settlement and colonisation takes place. The evidence from the experimental substrates suggests that colonisation will only occur after a considerable time period (more than 11 months), during which initial colonisation of the substrate, by other encrusters has taken place. The growth rates for *G. plana*, presented in Appendix table 19 are based on the total period of immersion of the substrates. As such, they represent minimum estimates. If *G. plana* is a late-stage encruster, then growth rates will be considerably higher.

**Planorbulina sp.** (Appendix table 20)

Although of apparently limited occurrence on the Bellairs reefs themselves (Chapter 2, section 2.233), *Planorbulina* occurs abundantly on artificial substrates. Numerous colonies were found on exposed surfaces of blocks in lighted environments at depths of 3-15m. Maximum growth rates and density of colonisation were found on just-lighted surfaces of block I at 15m. Colonisation was generally restricted to artificial substrates, such as brick and perspex. Comparatively few examples of *Planorbulina* were found on the natural coral substrates of either the experimental blocks or of the reefs.
<table>
<thead>
<tr>
<th>Mean Radial Growth</th>
<th>Max. Area mm²</th>
<th>Av. Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inert mm/mth</td>
<td>1.734</td>
<td>3900</td>
<td>445</td>
<td>28</td>
<td>N</td>
<td>Concrete,</td>
<td>33m J.Lighted 45° Top</td>
</tr>
<tr>
<td></td>
<td>0.962</td>
<td>1200</td>
<td>331</td>
<td>15</td>
<td>N</td>
<td>Concrete,</td>
<td>33m J.Lighted top.</td>
</tr>
<tr>
<td></td>
<td>0.680</td>
<td>600</td>
<td>154</td>
<td>7</td>
<td>N</td>
<td>Coral,</td>
<td>33m J.Lighted 45° U/Side</td>
</tr>
<tr>
<td></td>
<td>0.550</td>
<td>400</td>
<td>227</td>
<td>4</td>
<td>N</td>
<td>Perspex,</td>
<td>33m J.Lighted 45° top</td>
</tr>
<tr>
<td></td>
<td>0.416</td>
<td>225</td>
<td>225</td>
<td>1</td>
<td>N</td>
<td>Wood,</td>
<td>33m J.Lighted vert.</td>
</tr>
<tr>
<td></td>
<td>0.392</td>
<td>200</td>
<td>79</td>
<td>11</td>
<td>N</td>
<td>Brick,</td>
<td>33m J.Lighted 45° top</td>
</tr>
<tr>
<td></td>
<td>0.304</td>
<td>120</td>
<td>120</td>
<td>1</td>
<td>N</td>
<td>Glass,</td>
<td>33m J.Lighted vert.rough</td>
</tr>
</tbody>
</table>

Table 19 Summary of the Growth and Distribution of *Gypsina plana* on Experimental Substrates.

<table>
<thead>
<tr>
<th>Mean Radial Growth</th>
<th>Max. Area mm²</th>
<th>Av. Area mm²</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inert mm/mth</td>
<td>0.500</td>
<td>16</td>
<td>9</td>
<td>500+</td>
<td>I</td>
<td>Brick,</td>
<td>15m Just Lighted vert.</td>
</tr>
<tr>
<td></td>
<td>0.243</td>
<td>9</td>
<td>4</td>
<td>200</td>
<td>I</td>
<td>Perspex,</td>
<td>15m Just Lighted vert.</td>
</tr>
<tr>
<td></td>
<td>0.243</td>
<td>9</td>
<td>4</td>
<td>13</td>
<td>I</td>
<td>Glass,Horiz.</td>
<td>15m Just Lighted rough,U/Side Lighted</td>
</tr>
<tr>
<td></td>
<td>0.243</td>
<td>9</td>
<td>4</td>
<td>250</td>
<td>B</td>
<td>Brick,</td>
<td>6m J.Lighted vert. /Shaded</td>
</tr>
<tr>
<td></td>
<td>0.160</td>
<td>9</td>
<td>1.5</td>
<td>100+</td>
<td>M</td>
<td>Brick,</td>
<td>3.3m Lighted vert.</td>
</tr>
</tbody>
</table>

Table 20 Summary of the Growth and Distribution of *Planorbulina* sp on Experimental Substrates.
themselves, suggesting that this type of surface may be unsuitable for settlement of Planorbulina. Since each chamber of Planorbulina is approximately 0.1mm in diameter, growth rates of 0.2-0.5mm/month represent a rate of expansion of 2-5 chambers per month.

Serpulid Worms

Introduction

In the following sections, encrusting serpulid worms found colonising experimental substrates are described in terms of both their growth rate and settlement rate/unit area. Unlike the crustose coralline algae and the bryozoans, serpulid worms are limited in terms of the maximum size which they can attain (as with H. rubrum and C. utricularia). As a result, success in a particular habitat has been based on both average size of individuals and on their density of colonisation. In most cases, both factors are similar in terms of the degree of success of colonisation which they indicate. In most cases, the less expansive glass substrates were avoided. Unless otherwise stated, all organisms are randomly distributed on their respective substrates.

Pseudovernilia multispinosa (Appendix table 21)

P. multispinosa was found on experimental substrates at all depths from 1.5-50m, and in environments which ranged from just-lighted to dim in degree of illumination. Some degree of regional stenosis was exhibited in their distribution - individuals at depth occupied semi-exposed, just-lighted and shaded environments, whereas those in shallower waters occupied more cryptic, shaded and dim habitats (Appendix table 21). Growth rate, which was assumed to be uniform, varied from 3.25mm/month to 0.7mm/month. Settlement rates varied from 20 worms/dm$^2$/month to less than 1 worm/dm$^2$/month.
<table>
<thead>
<tr>
<th>Density of Colonization (no/cm²/mth)</th>
<th>Mean Linear Growth (mm/mth)</th>
<th>Rank Based on mlgi</th>
<th>Max. Length (mm)</th>
<th>Av. Growth Length (mm)</th>
<th>No. of Samples</th>
<th>Period of Immersion (months)</th>
<th>Block</th>
<th>Substrate</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>20.8</td>
<td>2.5</td>
<td>3rd</td>
<td>10.0</td>
<td>7.0</td>
<td>30</td>
<td>4</td>
<td>I</td>
<td>Coral</td>
<td>15m J. Lighted /Shaded</td>
</tr>
<tr>
<td>13.0</td>
<td>2.5</td>
<td>3rd</td>
<td>10.0</td>
<td>6.0</td>
<td>12</td>
<td>4</td>
<td>H</td>
<td>Perspeck, vert.</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>6.5</td>
<td>3.0</td>
<td>2nd</td>
<td>12.0</td>
<td>5.0</td>
<td>20</td>
<td>4</td>
<td>H</td>
<td>Brick, vert.</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>6.5</td>
<td>2.5</td>
<td>3rd</td>
<td>10.0</td>
<td>6.0</td>
<td>7</td>
<td>4</td>
<td>J</td>
<td>Coral, vert.</td>
<td>50m Shaded</td>
</tr>
<tr>
<td>5.4</td>
<td>2.5</td>
<td>3rd</td>
<td>10.0</td>
<td>7.4</td>
<td>5</td>
<td>4</td>
<td>F</td>
<td>Perspeck, vert.</td>
<td>6.6m Shaded /Dim</td>
</tr>
<tr>
<td>4.6</td>
<td>1.7</td>
<td>10th</td>
<td>7.0</td>
<td>5.0</td>
<td>5</td>
<td>4</td>
<td>H</td>
<td>Coral, vert.</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>4.3</td>
<td>1.0</td>
<td>14th</td>
<td>10.0</td>
<td>5.0</td>
<td>20</td>
<td>11</td>
<td>L</td>
<td>Brick, vert.</td>
<td>5m Dim</td>
</tr>
<tr>
<td>4.2</td>
<td>1.3</td>
<td>12th</td>
<td>5.0</td>
<td>3.0</td>
<td>7</td>
<td>4</td>
<td>F</td>
<td>Brick, vert.</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>3.7</td>
<td>3.3</td>
<td>1st</td>
<td>13.0</td>
<td>6.0</td>
<td>4</td>
<td>4</td>
<td>H</td>
<td>Coral, vert.</td>
<td>3.3m Shaded /Dim</td>
</tr>
<tr>
<td>3.6</td>
<td>2.5</td>
<td>3rd</td>
<td>10.0</td>
<td>5.0</td>
<td>7</td>
<td>4</td>
<td>A</td>
<td>Coral, vert.</td>
<td>8m Dim</td>
</tr>
<tr>
<td>3.6</td>
<td>2.5</td>
<td>3rd</td>
<td>10.0</td>
<td>7.0</td>
<td>6</td>
<td>4</td>
<td>F</td>
<td>Coral, vert.</td>
<td>5m Dim</td>
</tr>
<tr>
<td>3.6</td>
<td>1.0</td>
<td>14th</td>
<td>10.0</td>
<td>7.0</td>
<td>6</td>
<td>11</td>
<td>L</td>
<td>Glass, horiz. rough, U/Side</td>
<td>3.3m Dim</td>
</tr>
<tr>
<td>3.0</td>
<td>2.5</td>
<td>3rd</td>
<td>7.5</td>
<td>5.0</td>
<td>3</td>
<td>3</td>
<td>G</td>
<td>Coral, vert.</td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>2.9</td>
<td>1.5</td>
<td>11th</td>
<td>6.0</td>
<td>4.0</td>
<td>5</td>
<td>4</td>
<td>F</td>
<td>Coral, vert.</td>
<td>5m Shaded</td>
</tr>
<tr>
<td>1.9</td>
<td>0.9</td>
<td>16th</td>
<td>9.0</td>
<td>5.0</td>
<td>5</td>
<td>11</td>
<td>L</td>
<td>Perspeck, vert.</td>
<td>5m Dim</td>
</tr>
<tr>
<td>1.9</td>
<td>1.3</td>
<td>12th</td>
<td>13.0</td>
<td>9.0</td>
<td>5</td>
<td>11</td>
<td>L</td>
<td>Perspeck, horiz. U/Side</td>
<td>3.3m Shaded /Dim</td>
</tr>
</tbody>
</table>

Table 21: Summary of the Growth and Distribution of *Pseudovermilia multispinosa* on Experimental Substrates.
Pseudovermilia fuscostriata

*P. fuscostriata* was only found growing on shaded and dim substrates on blocks at depths greater than 15m. Maximum growth rates and densities of colonisation occurred on the shaded sides of the brick substrate of block J at 50m. A similar, cryptic distribution of *P. fuscostriata* at depth was found on the Bellairs reefs. (Text fig 38). In all cases, settlement rate (that is, density of colonisation) was extremely low, less than 1 worm/dm²/month.

Vermiliopsis sp. (Appendix table 22).

*Vermiliopsis* sp. was restricted to shaded and dim substrates on blocks at depths of 5 to 50m. Maximum growth rates were found on dim substrates at shallow depth and on shaded substrates in deeper water (=regional stenosis).

Growth rates varied from 7.5mm/month to 1.1mm/month. Settlement rates ranged from 10 worms/dm²/month to less than 1 worm/dm²/month.

Hydroides sp. (Appendix table 23)

*Hydroides* sp. was only found on block L immersed for a period of 11 months. Maximum growth rates (2.2mm/mth) and maximum density of colonisation (3 individuals/dm²/month) occurred on dim faces of brick substrates at 5m depth. In general, only dimly-lit and shaded substrates were colonised by *Hydroides*.

Pilorana sp. (Appendix table 24)

*Pilorana* sp. was found colonising shaded and dimly-lit substrates of blocks at depths of 1.5 to 50m. Although maximum growth rates were found on just lighted/ shaded substrates of block J at 50m, similar, although slightly slower rates, were found on dimly lit substrates at shallow depth. No information was obtained on
### Table 22 Summary of the Growth and Distribution of *Viloculopsis* sp on Experimental Substrates.

<table>
<thead>
<tr>
<th>Density of Colonies</th>
<th>Mean Linear Growth Rate</th>
<th>Rank</th>
<th>Max. Av. Length</th>
<th>No. of Period of Immersion</th>
<th>Block Substrate Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>10.8</td>
<td>2.5</td>
<td>3</td>
<td>10.0 5.0</td>
<td>10 4</td>
<td>F Perspex, 6.6m Shaded vert.</td>
</tr>
<tr>
<td>9.7</td>
<td>7.5</td>
<td>1</td>
<td>30.0 19.8</td>
<td>9 4</td>
<td>J Perspex, 50m Shaded vert.</td>
</tr>
<tr>
<td>5.5</td>
<td>1.7</td>
<td>11</td>
<td>7.0 5.0</td>
<td>8 4</td>
<td>I Coral, 15m Shaded vert.</td>
</tr>
<tr>
<td>2.3</td>
<td>3.8</td>
<td>2</td>
<td>15.0 10.0</td>
<td>4 4</td>
<td>F Coral, 6.6m Shaded vert.</td>
</tr>
<tr>
<td>2.3</td>
<td>2.3</td>
<td>9</td>
<td>9.0 7.0</td>
<td>4 4</td>
<td>F Coral, 6.6m Shaded vert.</td>
</tr>
<tr>
<td>2.3</td>
<td>2.5</td>
<td>3</td>
<td>10.0 10.0</td>
<td>4 4</td>
<td>F Brick, 6.6m Shaded vert.</td>
</tr>
<tr>
<td>1.4</td>
<td>2.5</td>
<td>3</td>
<td>10.0 7.0</td>
<td>2 4</td>
<td>F Coral, 6.6m Shaded vert.</td>
</tr>
<tr>
<td>1.2</td>
<td>2.5</td>
<td>3</td>
<td>10.0 10.0</td>
<td>2 4</td>
<td>F Brick, 6.6m Shaded vert.</td>
</tr>
<tr>
<td>0.6</td>
<td>1.4</td>
<td>13</td>
<td>15.0 15.0</td>
<td>1 11</td>
<td>L Glass, 5m Shaded vert.</td>
</tr>
<tr>
<td>0.6</td>
<td>2.5</td>
<td>3</td>
<td>10.0 10.0</td>
<td>1 4</td>
<td>F Brick, 6.6m Shaded vert.</td>
</tr>
</tbody>
</table>

### Table 23 Summary of the Growth and Distribution of *Hydrocladus* sp on Experimental Substrates.

<table>
<thead>
<tr>
<th>Density of Colonies</th>
<th>Mean Linear Growth Rate</th>
<th>Rank</th>
<th>Max. Av. Length</th>
<th>No. of Period of Immersion</th>
<th>Block Substrate Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.2</td>
<td>2.77</td>
<td>1</td>
<td>25.0 18.0</td>
<td>15 11</td>
<td>L Brick, 5m Dim vert.</td>
</tr>
<tr>
<td>3.2</td>
<td>1.54</td>
<td>2</td>
<td>17.0 10.0</td>
<td>15 11</td>
<td>L Brick, 5m Dim vert.</td>
</tr>
<tr>
<td>2.4</td>
<td>1.36</td>
<td>4</td>
<td>15.0 12.0</td>
<td>6 11</td>
<td>L Perspex, 5m Shaded vert.</td>
</tr>
<tr>
<td>1.8</td>
<td>1.36</td>
<td>4</td>
<td>15.0 11.7</td>
<td>3 11</td>
<td>L Glass, 5m Dim rough U/Side</td>
</tr>
<tr>
<td>1.8</td>
<td>1.54</td>
<td>2</td>
<td>17.0 12.0</td>
<td>3 11</td>
<td>L Perspex, 5m Dim vert.</td>
</tr>
<tr>
<td>Density of Colonies no./dm²/mth</td>
<td>Mean Linear Growth Incr. mm/mth</td>
<td>Rank based on Av. Length of Samples</td>
<td>Av. Length mm</td>
<td>No. of Period of Immersion (months)</td>
<td>Block</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>---------------------------------</td>
<td>--------------------------------------</td>
<td>--------------</td>
<td>-----------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>1.0</td>
<td>0.3</td>
<td>8</td>
<td>10.0</td>
<td>5.0</td>
<td>J</td>
</tr>
<tr>
<td>0.7</td>
<td>-</td>
<td>-</td>
<td>7.0</td>
<td>5.0</td>
<td>L</td>
</tr>
<tr>
<td>0.6</td>
<td>-</td>
<td>-</td>
<td>6.0</td>
<td>4.0</td>
<td>L</td>
</tr>
<tr>
<td>1.3</td>
<td>1.6</td>
<td>2</td>
<td>5.0</td>
<td>5.0</td>
<td>J</td>
</tr>
<tr>
<td>1.3</td>
<td>-</td>
<td>-</td>
<td>5.0</td>
<td>5.0</td>
<td>L</td>
</tr>
<tr>
<td>1.3</td>
<td>1.6</td>
<td>2</td>
<td>5.0</td>
<td>5.0</td>
<td>G</td>
</tr>
<tr>
<td>1.67</td>
<td>4.1</td>
<td>1</td>
<td>5.0</td>
<td>4.0</td>
<td>G</td>
</tr>
<tr>
<td>1.0</td>
<td>0.3</td>
<td>8</td>
<td>10.0</td>
<td>5.0</td>
<td>F</td>
</tr>
<tr>
<td>0.7</td>
<td>-</td>
<td>-</td>
<td>7.0</td>
<td>5.0</td>
<td>F</td>
</tr>
<tr>
<td>0.6</td>
<td>-</td>
<td>-</td>
<td>6.0</td>
<td>4.0</td>
<td>F</td>
</tr>
<tr>
<td>2.5</td>
<td>-</td>
<td>-</td>
<td>10.0</td>
<td>5.0</td>
<td>A</td>
</tr>
<tr>
<td>2.5</td>
<td>-</td>
<td>-</td>
<td>10.0</td>
<td>7.0</td>
<td>H</td>
</tr>
<tr>
<td>2.5</td>
<td>0.9</td>
<td>5</td>
<td>10.0</td>
<td>6.0</td>
<td>H</td>
</tr>
<tr>
<td>2.1</td>
<td>0.5</td>
<td>7</td>
<td>20.0</td>
<td>15.0</td>
<td>L</td>
</tr>
<tr>
<td>1.75</td>
<td>-</td>
<td>-</td>
<td>7.0</td>
<td>5.0</td>
<td>H</td>
</tr>
<tr>
<td>1.67</td>
<td>4.1</td>
<td>1</td>
<td>5.0</td>
<td>4.0</td>
<td>G</td>
</tr>
<tr>
<td>1.6</td>
<td>1.6</td>
<td>2</td>
<td>5.0</td>
<td>5.0</td>
<td>G</td>
</tr>
<tr>
<td>1.0</td>
<td>0.3</td>
<td>8</td>
<td>10.0</td>
<td>5.0</td>
<td>F</td>
</tr>
<tr>
<td>1.0</td>
<td>0.3</td>
<td>8</td>
<td>10.0</td>
<td>5.0</td>
<td>F</td>
</tr>
<tr>
<td>0.7</td>
<td>-</td>
<td>-</td>
<td>7.0</td>
<td>5.0</td>
<td>L</td>
</tr>
<tr>
<td>0.6</td>
<td>1.0</td>
<td>4</td>
<td>6.0</td>
<td>5.0</td>
<td>K</td>
</tr>
<tr>
<td>0.6</td>
<td>-</td>
<td>-</td>
<td>6.0</td>
<td>4.0</td>
<td>L</td>
</tr>
</tbody>
</table>

Table 24 Summary of the Growth and Distribution of FILIGRANA sp on Experimental Substrates.
overall density of colonisation of a substrate, since Filograna occurs in dense, isolated clumps of tubes. The largest clusters were most commonly found on the sheltered and shaded inside and underside of perspex dishes.

Serpula sp.

This species was only found on block N at 33m depth, immersed for a period of 18 months. Although the substrates occupied ranged from just-lighted to dim in degree of illumination, maximum growth rates of 1mm/month were found on the dimly-lit vertical face of the brick substrate.
<table>
<thead>
<tr>
<th>LOCATION</th>
<th>VERY SHALLOW WATER - EXPOSED LOCATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>PERIOD OF IMMERSION</td>
<td>4 months</td>
</tr>
<tr>
<td>BLOCK</td>
<td>C</td>
</tr>
<tr>
<td>RANGE IN ENVIRONMENT</td>
<td>1.5m Well lit - Lighted</td>
</tr>
<tr>
<td>ENCRUSTER SPECIES PRESENT</td>
<td>Neogoniolithon</td>
</tr>
<tr>
<td></td>
<td>Porolithon</td>
</tr>
<tr>
<td></td>
<td>Lithophyllum</td>
</tr>
<tr>
<td></td>
<td>Parasmittina ophidiana</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 25  Enencruster Species Colonising Experimental Substrate Blocks in Very Shallow water, Exposed Environments after periods of 4months and 10months immersion.

<table>
<thead>
<tr>
<th>LOCATION</th>
<th>SHALLOW WATER (2-7m) - SEMI-EXPOSED LOCATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>PERIOD OF IMMERSION</td>
<td>4 months</td>
</tr>
<tr>
<td>BLOCK</td>
<td>E</td>
</tr>
<tr>
<td>RANGE IN ENVIRONMENT</td>
<td>6m Lighted - Shaded</td>
</tr>
<tr>
<td>ENCRUSTER SPECIES PRESENT</td>
<td>Neogoniolithon</td>
</tr>
<tr>
<td></td>
<td>Planorbilina sp</td>
</tr>
<tr>
<td></td>
<td>Lichenopora sp</td>
</tr>
<tr>
<td></td>
<td>Rhynchozoan rastratum</td>
</tr>
<tr>
<td></td>
<td>Parasmittina ophidiana</td>
</tr>
</tbody>
</table>

Table 26  Enencruster Species Colonising Experimental Substrate Blocks in Shallow water, Semi-Exposed Environments after periods of 4months and 9months immersion.
<table>
<thead>
<tr>
<th>LOCATION</th>
<th>SHALLOW WATER (2-8m) - CRYPTIC LOCATIONS</th>
</tr>
</thead>
<tbody>
<tr>
<td>PERIOD OF IMMERSSION</td>
<td>3 months</td>
</tr>
<tr>
<td>BLOCK</td>
<td>G</td>
</tr>
<tr>
<td>RANGE IN ENVIRONMENT</td>
<td>3.3m Dim/Dark</td>
</tr>
<tr>
<td>ENCRUSTERS PRESENT</td>
<td></td>
</tr>
<tr>
<td>Mesophyllum</td>
<td></td>
</tr>
<tr>
<td>Lichenopora sp</td>
<td></td>
</tr>
<tr>
<td>Crib. radiata</td>
<td></td>
</tr>
<tr>
<td>Crep. Longiseta</td>
<td></td>
</tr>
<tr>
<td>Bryozoan AN</td>
<td></td>
</tr>
<tr>
<td>P. latirostris</td>
<td></td>
</tr>
<tr>
<td>H. irregularis</td>
<td></td>
</tr>
<tr>
<td>E. pes anseris</td>
<td></td>
</tr>
<tr>
<td>Cl. vestita</td>
<td></td>
</tr>
<tr>
<td>S. informata</td>
<td></td>
</tr>
<tr>
<td>Trem. turrita</td>
<td></td>
</tr>
<tr>
<td>Tryp. venusta</td>
<td></td>
</tr>
<tr>
<td>P. ophidiana</td>
<td></td>
</tr>
<tr>
<td>H. rubrum-branching</td>
<td></td>
</tr>
<tr>
<td>H. rubrum-encrusting</td>
<td></td>
</tr>
<tr>
<td>H. rubrum-globose</td>
<td></td>
</tr>
<tr>
<td>C. utricularis-conic.</td>
<td></td>
</tr>
<tr>
<td>C. utricularis-glob.</td>
<td></td>
</tr>
<tr>
<td>P. multispinosa</td>
<td></td>
</tr>
<tr>
<td>Vermiliopsis sp</td>
<td></td>
</tr>
<tr>
<td>Hydroiides sp</td>
<td></td>
</tr>
<tr>
<td>Pilegrana sp</td>
<td></td>
</tr>
</tbody>
</table>

Table 27  Encruster Species Colonising Experimental Substrate Blocks in Shallow water, Concealed Locations after periods of 3, 4 and 11 months.
CRUSTOSE CORALLINE ALGAE
Porolithon
Neogoniolithon
Mesophyllum

BRYOZOANS
Lichenopora sp
Parellisina latirostris
Smittipora sp
Cribrilina radiata
Trypostega venusta
Hippopodina irregularis
Escharina pes anseris
Stylopoma informata
Parasmittina ophidiana
Rhyhchozoon rastratum
Rhyhchozoon grandicella
Crepidacantha longiseta
Trematooccia turrita
Cleidochasma vestita
Bryozoa AN

PORAMINIFERANS
Placopsilina sp
Planorbulina sp
Homotrema rubrum-branching
H. rubrum-encrusting

SERPULID WORMS
Pseudovermilia multispinosa
Pseudovermilia fuscostriata
Filograna sp
Vermiliopsis sp

HYDROCORAL
Millepora-encrusting form

Table 28 Initial or Primary Colonisers of Experimental Substrates (i.e. those species which were already established on blocks of 3 and 4 months immersion)

CRUSTOSE CORALLINE ALGAE
Tenarea
Lithophyllum

CORALS
Agaricia sp

FORAMINIFERANS
Carpenteria utricularis -conical & globose
Homotrema rubrum-globose

SERPULID WORM
Hydroides sp

Table 29 Late Stage or Secondary Encrusters of Experimental Substrates in Shallow Water (0-10m). (i.e. species which were only found on previously colonised substrates on blocks immersed for 4-11 months)
<table>
<thead>
<tr>
<th>CRUSTOSE CORALLINE ALGAE</th>
<th>FORAMINIFERANS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tenarea</td>
<td>Gypsina plana</td>
</tr>
<tr>
<td></td>
<td>Carpenteria utricularis</td>
</tr>
<tr>
<td>CORAL</td>
<td>SERPULID WORMS</td>
</tr>
<tr>
<td>Agaricia sp</td>
<td>Serpula sp</td>
</tr>
<tr>
<td></td>
<td>Hydroides sp</td>
</tr>
</tbody>
</table>

Table 30  Late Stage or Secondary Encrusters of Experimental Block N in Deep Water (33m). (Species listed were only found after a period of immersion of 18 months on substrates which had been previously colonised by other, primary, encrusters).

<table>
<thead>
<tr>
<th>CRUSTOSE CORALLINE ALGAE</th>
<th>BRYOZOAENS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neopolyanorolithon</td>
<td>Labioporella sp</td>
</tr>
<tr>
<td>Lithothamnium</td>
<td>Steganoporella magnilabris</td>
</tr>
<tr>
<td>Archaeolithothamnium</td>
<td>Reptadeonella violatia</td>
</tr>
<tr>
<td>Hydrolithon</td>
<td>(Escharina porosa)</td>
</tr>
<tr>
<td>Posiliella</td>
<td>Entalophora sp</td>
</tr>
<tr>
<td>Neogoniolithon (frondose)</td>
<td>(Retepora sp)</td>
</tr>
<tr>
<td></td>
<td>(Gemmelliporidra magniporosa)</td>
</tr>
<tr>
<td></td>
<td>Trematoocia magnifera</td>
</tr>
<tr>
<td>FORAMINIFERANS</td>
<td>Hippopodina feegeensis</td>
</tr>
<tr>
<td>Carpenteria hassleri</td>
<td>(Membraniporella aragoi)</td>
</tr>
<tr>
<td>(Biarritzina)</td>
<td>Chorizopora brogniartii</td>
</tr>
<tr>
<td></td>
<td>(Parasmittina californica)</td>
</tr>
<tr>
<td>SERPULID WORMS</td>
<td>(Parasmittina nitidissima)</td>
</tr>
<tr>
<td>Spirobranchus giganteus</td>
<td>Holoporella tubulosa</td>
</tr>
<tr>
<td>Sclerostyla ctenactis</td>
<td>Schizoporella sp</td>
</tr>
</tbody>
</table>

Table 31  Encrusters Known from the Bellairs Reefs but which are Absent from Experimental Substrates. Uncommon species on the Reef are enclosed in parentheses.
<table>
<thead>
<tr>
<th>ENCROUSTER TYPE &amp; SPECIES</th>
<th>ENCROUTERS ON EXPOSED, LIGHTED SUBSTRATES</th>
<th>ENCROUTERS ON SHADED AREAS OF LIGHTED SUBSTRATES</th>
<th>ENCROUTERS ON CRYPTIC SUBSTRATES</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRUSTOSE CORALLINE ALGAE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porolithon</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neogoniolithon</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lithophyllum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Icraea</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mesophyllum</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BRYOZOA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lichenopora sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Farelliesina latirostris</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Smittpora sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cribrilina radiata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trypostega venusta</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hippopodina irregularis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Escharina pes anseris</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stylopora informata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parasmitina ophidiana</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhynchozoaon rastratum</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhynchozoaon grandicella</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crepidacantha longiseta</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trematoecia turrita</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cleidochasma vestita</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Schizoporella sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FORAMINIFERANS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cypina plana</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Planorbulina sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H.rubrum-branching</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H.rubrum-encrusting</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H.rubrum-globose</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C.urticularis-conical</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C.urticularis-globose</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BECKWITHIACEAE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudovermilia multi.spinosa</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudovermilia fuscometriata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vermiliopsis sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydroides sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pilograna sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Serpula sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CORALS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agaricia sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Milipes</em> sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Stylaster roseus</em></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 32 Distribution of Encrousters according to Experimental Substrate Location.
<table>
<thead>
<tr>
<th>ENCROUSTERS TYPE &amp; SPECIES</th>
<th>DEPTH RANGE(m)</th>
<th>LIGHT RANGE</th>
<th>Environment in which max. growth rate occurs</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRUSTACE CORALLIIDS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porolithon</td>
<td></td>
<td></td>
<td>1.5m Well Lit</td>
</tr>
<tr>
<td>Lithophyllum</td>
<td></td>
<td></td>
<td>1.5m Lighted</td>
</tr>
<tr>
<td>Neogoniolithon</td>
<td></td>
<td></td>
<td>15m Just Lighted</td>
</tr>
<tr>
<td>Tenarea</td>
<td></td>
<td></td>
<td>33m Just Lighted</td>
</tr>
<tr>
<td>Neopophyllum</td>
<td></td>
<td></td>
<td>50m J. Lighted/ Shaded</td>
</tr>
<tr>
<td>ECTOZOAS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lichenepora sp.</td>
<td></td>
<td></td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>Parellisina latirostris</td>
<td></td>
<td></td>
<td>6m Dim</td>
</tr>
<tr>
<td>Smittipora sp.</td>
<td></td>
<td></td>
<td>50m Shaded</td>
</tr>
<tr>
<td>Cribrillina radiata</td>
<td></td>
<td></td>
<td>50m Shaded/Dim</td>
</tr>
<tr>
<td>Trypostega venusta</td>
<td></td>
<td></td>
<td>6.6m Shaded/Dim</td>
</tr>
<tr>
<td>Hippodendra irregularia</td>
<td></td>
<td></td>
<td>5m Dim</td>
</tr>
<tr>
<td>Escharina pes anseris</td>
<td></td>
<td></td>
<td>50m Shaded</td>
</tr>
<tr>
<td>Stylopora informata</td>
<td></td>
<td></td>
<td>50m Shaded/Dim</td>
</tr>
<tr>
<td>Paramattina ophidia</td>
<td></td>
<td></td>
<td>50m Shaded/Dim</td>
</tr>
<tr>
<td>Rhyhoscocon rastratum</td>
<td></td>
<td></td>
<td>6m Shaded</td>
</tr>
<tr>
<td>Rhyhoscocon grandicella</td>
<td></td>
<td></td>
<td>15m Shaded/Dim</td>
</tr>
<tr>
<td>Crepidicantha longicola</td>
<td></td>
<td></td>
<td>6.6m Dim</td>
</tr>
<tr>
<td>Trematoecia turrita</td>
<td></td>
<td></td>
<td>6.6m Shaded/Dim</td>
</tr>
<tr>
<td>Cleidochasma vestita</td>
<td></td>
<td></td>
<td>15m Dim</td>
</tr>
<tr>
<td>Schisoporella sp.</td>
<td></td>
<td></td>
<td>6.6m Shaded/Dim</td>
</tr>
<tr>
<td>FORAMINIFERANS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grypsia plana</td>
<td></td>
<td></td>
<td>33m Just Lighted</td>
</tr>
<tr>
<td>Planorbulina sp.</td>
<td></td>
<td></td>
<td>15m Just Lighted</td>
</tr>
<tr>
<td>H. Rubrum-branching</td>
<td></td>
<td></td>
<td>5m Dim</td>
</tr>
<tr>
<td>H. rubrum-encrusting</td>
<td></td>
<td></td>
<td>3.3m Shaded</td>
</tr>
<tr>
<td>H. rubrum-globose</td>
<td></td>
<td></td>
<td>5m Dim</td>
</tr>
<tr>
<td>C. utricularis-conical</td>
<td></td>
<td></td>
<td>5m Dim</td>
</tr>
<tr>
<td>C. utricularis-globose</td>
<td></td>
<td></td>
<td>5m Dim</td>
</tr>
<tr>
<td>SERPULIDES</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P. multispinosa</td>
<td></td>
<td></td>
<td>3.3m Shaded/Dim</td>
</tr>
<tr>
<td>P. fuscocriata</td>
<td></td>
<td></td>
<td>50m Shaded</td>
</tr>
<tr>
<td>Vermiliospi sp.</td>
<td></td>
<td></td>
<td>6.6m Shaded/Dim</td>
</tr>
<tr>
<td>Hydroids sp.</td>
<td></td>
<td></td>
<td>5m Dim</td>
</tr>
<tr>
<td>Piligrana sp.</td>
<td></td>
<td></td>
<td>50m Shaded</td>
</tr>
<tr>
<td>Serpula sp.</td>
<td></td>
<td></td>
<td>33m Dim</td>
</tr>
<tr>
<td>CORALS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agaricia sp.</td>
<td></td>
<td></td>
<td>1.543m Lighted</td>
</tr>
<tr>
<td>Millepora sp.</td>
<td></td>
<td></td>
<td>15m Just Lighted</td>
</tr>
<tr>
<td>Stylaster roseum</td>
<td></td>
<td></td>
<td>33m Shaded/Dim</td>
</tr>
</tbody>
</table>

Table 33 Summary of the Environmental Distribution of Encrusters on Experimental Substrates.
<table>
<thead>
<tr>
<th>ENCRUSTER TYPE &amp; SPECIES</th>
<th>MEAN RADIAL GROWTH RATE mm/month</th>
<th>ENCRUSTER TYPE &amp; SPECIES</th>
<th>MEAN(RADIAL) GROWTH RATE mm/month</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crustose Coralline Algae</td>
<td></td>
<td>Bryozoans(contd)</td>
<td></td>
</tr>
<tr>
<td>Neogoniolithon</td>
<td>2.864</td>
<td>H.irregularis</td>
<td>0.640</td>
</tr>
<tr>
<td>Porolithon</td>
<td>1.531</td>
<td>E.pes anseris</td>
<td>0.559</td>
</tr>
<tr>
<td>Mesophyllum</td>
<td>1.398</td>
<td>C.radiata</td>
<td>0.405</td>
</tr>
<tr>
<td>Tenarea</td>
<td>0.833</td>
<td>T.venusta</td>
<td>0.375</td>
</tr>
<tr>
<td>Lithophyllum</td>
<td>0.750</td>
<td>Smittipora sp.</td>
<td>0.306</td>
</tr>
<tr>
<td>Bryozoans</td>
<td></td>
<td>T.turrita</td>
<td>0.125</td>
</tr>
<tr>
<td>S.informata</td>
<td>5.995</td>
<td>Poraminiferans</td>
<td></td>
</tr>
<tr>
<td>P.ophidiana</td>
<td>3.373</td>
<td>Gypsina plana</td>
<td>1.734</td>
</tr>
<tr>
<td>R.grandicella</td>
<td>1.825</td>
<td>Planorbulina sp.</td>
<td>0.500</td>
</tr>
<tr>
<td>C.vestita</td>
<td>1.190</td>
<td>H.rubrum-encrusting</td>
<td>0.375</td>
</tr>
<tr>
<td>P.latirostris</td>
<td>1.00</td>
<td>H.rubrum-branching</td>
<td>0.19</td>
</tr>
<tr>
<td>C.longiseta</td>
<td>0.992</td>
<td>Serpulids</td>
<td></td>
</tr>
<tr>
<td>R.rastratum</td>
<td>0.925</td>
<td>Vermiliopsis sp.</td>
<td>7.50</td>
</tr>
<tr>
<td>Lichenopora sp.</td>
<td>0.875</td>
<td>P.multispinosa</td>
<td>3.250</td>
</tr>
<tr>
<td>Schizoporella sp.</td>
<td>0.780</td>
<td>Pilograna sp.</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hydroides sp.</td>
<td>2.273</td>
</tr>
</tbody>
</table>

Table 34 Comparison of the Maximum Growth Rates of Encrusters on Experimental Substrates. Species within each group of encrusters are ranked according to growth rate.
COLLECTION

Samples of crustose coralline algal crust attached to the underlying coral substrate were collected with hammer and chisel and placed in a labelled polythene bag. This bag was itself placed in a black, light-tight collecting bag underwater, which was then returned to the laboratory.

EXTRACTION

Under dim light in the laboratory, 1 gram of the top 1mm of algal crust was removed and accurately weighed in water. This 1.0 gram sample was then ground for 10 minutes in a mortar with 0.5 grams of silica sand and 7.5 ml of chilled phosphate buffer solution.

The suspension was then mechanically shaken for 10 minutes to extract the water soluble pigment completely and was then centrifuged at 4500 r.p.m. for 15 minutes. The resultant pink supernatant liquid was then carefully decanted and its volume made up to 7.5 ml with chilled phosphate buffer. This liquid was subsequently used for spectroscopic determination of phycobilins.

The sediment which remained after centrifuging was then re-suspended in 7.5 ml of 90% acetone. The resulting suspension was mechanically shaken for 15 minutes to extract acetone soluble pigments and was then centrifuged at 4500 r.p.m. for 10 minutes. The green supernatant liquid was decanted and its volume made up to 7.5 ml with 90% acetone. This liquid was then used for spectroscopic determination of chlorophylls.
The light absorption of both the phosphate buffer and acetone extracts from each sample was then determined in a spectrophotometer using fresh phosphate buffer and 90% acetone as blank controls for the respective extracts.

Pigment extracts were decanted into a 1cm glass cell which was then placed in the light beam of a Gilford 240 spectrophotometer. Determinations of absorption were made at 20 μm intervals in the visible light range from 340 to 700 μm. Whilst absolute concentrations of pigment were not obtained using this machine, relative values of absorbance of light for each sample enabled comparisons to be made, since known and constant quantities of both tissue and solutions had been used in all extractions. (see chapter 2, section 2.213)

The relative absorbances of each solution at different wavelengths were then plotted graphically for comparison (text figs 21-23).

NOTES

1) All preparations, pigment extractions and analyses were undertaken in reduced light (either behind drawn blinds or at night) in an air-conditioned room maintained at a temperature of 23.5°C (the coldest possible).

   Ideally, samples should be extracted and analysed in the dark at a temperature approaching 0°C. The above conditions represent the closest approach possible to ideal conditions in the field.

2) All samples were collected between the hours of 11am and 2pm on bright sunlight days during the last week of April, 1975.
3) 'Exposed' samples were taken from upward-facing horizontal surfaces while 'shaded' samples were collected from the undersides of ledges and overhangs where they usually faced downwards.

4) Immediately after extraction and before removal to a new environment (e.g. into direct sunlight and/or shallower depths), all samples were sealed in a light-tight, water-filled black plastic collecting bag. Samples remained in this bag until later examination in the laboratory.

5) All pigments were extracted and analysed within 6 hours of collection. In general, 5 hours proved to be the fastest time possible for the extraction and analysis of both water and acetone-soluble pigments from three individual samples (the maximum number of samples which the spectrophotometer was capable of analysing simultaneously).

6) Times given for grinding, agitation and centrifuging were found, by experiment, to be the minimum necessary for complete extraction of pigment.
In the following appendix, only those localities with corals or coral frameworks exhibiting extensive crust development are listed. For each locality, descriptions are given of the environmental facies, faunal content and the extent and distribution of organic encrustations.

Against the sample locality name and/or reference code (see Text Fig 40 and Mesolella 1968, James 1972) is its grid coordinates (taken from the 1:50,000 sheet of Barbados) and its approximate age (from Mesolella 1968 and James 1972).

In the following descriptions, localities are listed according to age.

83,000yr reef tract - North Point Shelf area

Animal Flower Bay (AP) 58400 74700

Sea cliff exposure, 20-30m in height exposing sections through the offshore barrier reef facies. East cliff sections expose massive but broken Acropora palmata plates, while North cliff sections expose a continuous vertical sequence from the massive coral head facies at the base, through the A. cervicornis zone to the A. palmata plate zone at the cliff top. Although cliffs are generally inaccessible, the barren cliff tops and loose boulders provide exposures of the A. palmata facies.

Crusts are generally thin (1 cm) and of the mixed type. Individual fronds are broken but still show a transition from a thick crust on the top to a thinner crust on the underside.

The Tides Bay (TT) 59550 73950

Eastward-facing sea cliff exposure with A. palmata at base and A. cervicornis at top. Although most of the A. palmata facies consists of broken and detached fronds, many colonies...
can be found complete and in situ (Text plate 31). A. palmata plates and A. cervicornis sticks in both facies are covered by thick (2 cm) crusts of mixed composition, much of which binds broken fragments.

**River Bay (RB) 60200 73300**

A complex exposure of the 83,000 yr reef tract composed of numerous inlets and cliffs.

**River Bay - North side 60200 73400**

Exposure of sea cliffs, 20-30m high. At base is rhodolith horizon, 1-2m thick, which is overlain by a P. porites/A. cervicornis facies (3-5m thick). The majority of the cliff is composed of much broken A. palmata plates lying above the P. porites/A. cervicornis facies. All corals exposed show thin encrustations (1 cm) of mixed composition.

**River Bay - South side, East cliff. 60250 73200**

Seaward face of spur, 5-7m high composed of A. palmata at top and underlain by A. cervicornis. Although one or two colonies of A. palmata are in situ, most are broken and fragmented. Crusts are very thin or absent.

**River Bay - South side, west cliff and gully 60250 73200**

Landward face of spur (see E. cliff above) and gully walls are 5m high and are composed of A. palmata and A. cervicornis. Coral heads at the N. end of spur are intermixed with A. P., A. c., and organ-pipe Montastrea annularis (Text Plate 35), all set in an extensive sandy matrix. Organic encrustations, which are thin, are of the mixed type on A. palmata but of constant composition on M. annularis.

**River Bay - South side, North cliff 60250 73250**

Mostly organ pipe colonies of M. annularis associated with A. cervicornis, P. porites
and *A. palmata* in a seaward cliff, 5m high. Organic encrustations on *M. annularis* are of constant composition and of mixed composition on *A. palmata* and other branching corals.

**River Bay - West side and river channel 60100 73300**

Complex section in river gully. 5m high cliffs consist of intermixed facies of *M. annularis*, *A. palmata* and *A. cervicornis*. Organic encrustations of both constant and mixed type are thin (less than 1 cm).

**125,000 yr reef tract - First High Cliff**

**Nullins 55800 65800**

Large road cut running E-W through the First High Cliff. At base, massive coral heads (*M. annularis*, *Diploria* sp. and *Siderastrea* sp.) with thin encrustations of constant composition pass up-cut into *A. cervicornis* facies. At top of cut, *A. cervicornis* grades into *A. palmata* facies via a zone of organ pipe *M. annularis* colonies. *A. palmata* possesses thick (1-2 cm) organic encrustations of mixed composition.

**Trents (TR) 56650 59000**

Sinuous road cutting through First High Cliff. Poorly developed coral head facies at base passes up through facies of broken *A. cervicornis* sticks into *A. palmata* facies, consisting of broken plates with thin (1 cm) encrustations of mixed composition.

**Gibbons (BJ) 68250 45100**

Disused quarry in South-facing terrace. Excellent exposure consists almost entirely of very large fronds of *A. palmata* with thick (5-8 cm) encrustations, all of mixed composition.
220,000 yr reef tract
Mount Standfast (MS) 56300 60700

Low road cut in first minor terrace above First High Cliff. Consists of A. palmata fronds with thick (1-2 cm) encrustations of constant composition, sparsely distributed in a sandy matrix.

275,000 yr reef tract
Locality DMQ 56700 62090

Large quarry in prominent (25m) reef terrace. Most of quarry face consists of A. cervicornis overlying massive coral heads of Montastrea sp., Diploria sp., and Siderastrea sp. at base. Loose blocks of massive corals provide examples of well-developed crusts, 3-4 cm thick, of both constant and mixed composition.

Brighton (SI) 67550 51550 (approx. 270,000yrs)

Long road cut. At lower, southern end, massive M. annularis heads support thick (2 cm) encrustations of constant composition. At upper end, massive heads of M. annularis and Diploria sp. grade up into A. palmata with thin (1 cm) encrustations.

310,000 yr reef tract
Locality CU 57210 64390

A low (2-3m) road cut on the South side of the road. At top of cut, broken fronds of A. palmata support well-developed crusts of both constant and mixed composition. Lower down cut, this grades into the M. annularis facies consisting of in-situ massive heads, also with well-developed crusts of both constant and mixed composition.
530,000 yr reef complex - Second High Cliff

Free Hill (FH) 59750 71750


Mile and a Quarter (MQ) 57850 67450

Road cut in Second High Cliff. Sand and A. cervicornis at lower end of cut grades up into low growth forms of Montastrea sp., with thick algal crusts of both constant and mixed composition. Also represented are massive heads of Siderastrea sp. and Neandrina sp. A. palmata poorly developed at top of cut with thin crusts of both constant and mixed composition.

Bakers (BR) 57450 64200

Road cut. At lower end, massive heads of H. annularis showing thick encrustations of constant composition grade up into well-developed A. palmata facies with thick crusts of mixed composition.

Salisbury (SH) 64950 53750

Large road cut. At base, low growth forms of H. annularis and H. cavernosa support thick (2 cm) encrustations of constant composition. At top of cut, broken fronds of A. palmata have undergone extensive alteration and now appear like laminated algal crusts.

Bascombe (WN) 73350 55970

Road cut at S.E. end of Second High Cliff. Cut consists chiefly of H. annularis heads and pipes with thick (2 cm) encrustations of constant composition on tops.