McGill University

BORING BY MACRO-ORGANISMS IN THE CORAL
MONTASTREA ANNULARIS ON BARBADOS REEFS

by

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ABSTRACT

The fauna boring into Montastrea annularis includes sponges, bivalves, sipunculid and polychaete worms and barnacles. Sponges and spionid polychaetes are most important in hard tissue destruction and account for more than 90% of the total boring in most heads. Bivalves and barnacles are locally important. Sipunculids and sabellids account for less than 4% of the total boring.

The volume removed from coral samples by boring ranged from 3 - 60% and samples from a deeper bank reef were more highly bored than fringing reef samples. An average of 20% of the volume of bank reef corals, and 5% of the volume of fringing reef corals, was removed by boring.

The distribution of individual borers is not a function of depth. The density and variety of borers and the extent of boring in coral heads is greater in older heads. The ratio of living coral surface to dead encrusted areas on colonies also influences borer density and the extent of boring.

RÉSUMÉ

Les organismes perforants de Montastrea annularis comprennent les éponges, les bivalves, Sipunculidae et polychètes et les balanes. Les éponges et les polychètes Spionidae sont les destructeurs les plus actifs de tissu résistant et produisent plus de 90% des perforations dans la plupart des madrépores. Les perforations causées par les bivalves et les balanes sont importantes localement. Les Sipunculidae et Sabellidae sont responsables pour moins de 4% des perforations.

Le volume de matériel extrait des échantillons de coraux par les organismes perforants varie entre 3 et 60%. Les échantillons provenant d'un banc récifal plus profond présentaient plus de perforations que les échantillons provenant d'un récif frangeant. En moyenne, on a trouvé que 20% du volume des coraux du banc récifal, et 5% du volume des coraux du récif frangeant avait été enlevé par les organismes perforants.

La distribution par individu des organismes perforants ne varie pas en fonction de la profondeur. La densité et la variété des organismes perforants et le degré de perforation atteint est plus élevé chez les madrépores les plus vieux. Le rapport entre les surfaces représentant des coraux vivants et les zones mortes couvertes d'incrustations pour une colonie donnée influence également la densité des organismes perforants et le degré atteint dans la perforation.

CONTENTS

	<u>Page</u>
LIST OF TABLES	iv
LIST OF FIGURES	v
LIST OF PLATES	vi
INTRODUCTION	1
Study site description	5
The coral <u>Montastrea annularis</u>	7
General outline of study	10
PART I: FIELD FAUNAL ANALYSIS	12
Materials and Methods	13
Results and Discussion	14
The boring fauna of <u>M. annularis</u>	14
Sponges	14
Bivalves	21
Sipunculids	23
Polychaetes	26
Barnacles	30
Statistical treatment of data	31
Factors controlling distribution of boring organisms	35
PART II: LABORATORY X-RAY ANALYSIS	40
Materials and Methods	41
Sample preparation	41
Method of estimating % boring	42
Treatment of clionid bored areas	43
Results and Discussion	46
DISCUSSION: The effect of boring organisms on <u>M. annularis</u>	52
SUMMARY	55
ACKNOWLEDGEMENTS	57
REFERENCES CITED	58
PLATES	64
APPENDIX A	74
APPENDIX B	80

LIST OF TABLES

Table		Page
1	List of boring organisms present in <u>Montastrea annularis</u>	15
2-6	Number of individuals of each borer/coral sample on transects 1-5 (Appendix A)	75-79
7	Results of correlation analysis of faunal data (Appendix B)	81
8	Results of chi-square and t-tests performed on faunal data (Appendix B)	82
9	Comparison of number of individuals of each type of borer in a large and small coral head from the same locality	37
10	Percentages of total bored volume removed by different borers	45
11	Percentage of the volume of coral samples removed by boring	47
12	Regression and correlation analyses of % boring data (Appendix B)	83

LIST OF FIGURES

Figure		Page
1.	Location of study areas on west coast of Barbados: transects numbered	6
2.	Diagrammatic depth profile of west coast of Barbados	8
3.	Boring sponge spicules	17
4.	Graph of % boring in corals against depth	48
5.	Graph of coral sample age against depth	50
6.	Graph of % boring in corals against age	51

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LIST OF PLATES

Plate		Page
1A	Aerial view of Bellairs fringing reef	64
1B	Typical benthic community on bank reef	64
1C	Author at work on bank reef transect	64
2A	Multiple lobed colony of <u>M. annularis</u> on fringing reef buttress	65
2B	Multiple lobed colony of <u>M. annularis</u> in marginal region of fringing reef	65
2C	Flattened colonies of <u>M. annularis</u> on the sloping side of the bank reef.	65
2D	'Bumpy' <u>M. annularis</u> colony on bank reef	65
2E	Large columnar <u>M. annularis</u> colony on bank reef	65
2F	Modification of the growth morphology of <u>M. annularis</u> by <u>Mycale laevis</u>	65
3A	<u>M. annularis</u> colony partly infested by <u>Cliona delitrix</u>	66
3B	<u>Montastrea annularis</u> colony infested by <u>Siphonodictyon cachacrouense</u>	66
3C	Papillae of the sponge, <u>Cliona</u>	66
3D	<u>Siphonodictyon cachacrouense</u> papilla	66
3E	Papillae of <u>Siphonodictyon brevitubulatum</u>	66
3F	Ectosomal part of a spirastrellid sponge	66
4A	Cross-section of a clionid/spirastrellid bored coral head	67
4B	Cross-section of a clionid/ <u>Siphonodictyon</u> bored coral head	67

Plate		Page
4C	<u>Siphonodictyon cachacrouense</u> cavity	67
4D	Scanning Electron Microscope photograph of sponge bored coral substrate	67
4E	Scanning Electron Microscope photograph of sponge chips produced by boring	67
5A	The boring bivalve fauna of <u>M. annularis</u>	68
5B	<u>Lithophaga</u> borehole aperture	68
5C	<u>Gastrochaena</u> borehole aperture.	68
5D	<u>Gregariella</u> borehole aperture	68
5E	<u>Lithophaga nigra</u> borehole	68
5F	<u>Lithophaga bisulcata</u> borehole	68
5G	<u>Gastrochaena hians</u> borehole	68
5H	<u>Gregariella coralliophaga</u> borehole	68
6A	The sipunculid fauna of <u>M. annularis</u>	69
6B	<u>Phascolosoma dentigerum</u> borehole	69
6C	<u>Pherusa ?dubia</u> in hole	69
6D	'U'-shaped hole of <u>Polydora?</u>	69
6E	Double 'O' aperture of <u>Polydora?</u> hole	69
6F	<u>Lithotrya</u> in borehole	69
6G	Oval aperture of <u>Lithotrya</u> borehole	69
6H	Slit-shaped apertures of <u>Kochlorine</u> borings	69
7	X-radiograph of <u>M. annularis</u> sample from a depth of 15 m on bank reef	70
8	X-radiograph of <u>M. annularis</u> sample from a depth of 40 m on bank reef	71

9A	X-radiograph of <u>M. annularis</u> sample from a depth of 3 m on fringing reef	72
9B	X-radiograph of <u>M. annularis</u> sample from a depth of 4 m on fringing reef	72
10A	X-radiograph of <u>M. annularis</u> sample from 28 m showing marginal alteration by clionid sponge and spionid polychaetes and a sabellid hole.	73
10B	X-radiograph of clionid-bored margin of a <u>M. annularis</u> colony	73
10C	X-radiograph of <u>Cliona vermicifera</u> boring.	73
10D	X-radiograph of <u>Lithophaga</u> borehole	73
10E	X-radiograph of <u>Gastrochaena</u> borehole	73

INTRODUCTION

Construction of the primary framework of coral reefs is accompanied by continuous destruction by physical and biological processes. The rate of expansion of the reef depends upon the relative importance of these counteractive processes.

Biological agencies, in the form of boring and rasping organisms, play an important role in reef erosion. Fish and molluscs feeding on algal-coated substrate and coral tissue scrape calcareous material off the substrate surface while borers, principally sponges, bivalves, worms and barnacles, penetrate the substrate and remove material from its interior. The effect of these organisms can be seen in the numerous borings and abrasions within and upon the carbonate substrate of the reef. The term 'bioerosion' has been coined by Neumann (1966) to describe the destruction and removal of consolidated mineral or lithic substrate by the direct action of organisms.

Both types of activity are important in sediment production. Rasping and boring directly produce considerable quantities of fine calcareous detritus. Coarser debris is formed when substrate, weakened by boring, collapses. The material accumulates on and around the reef framework, the coarse in sheltered depressions on the reef surface or in rubble zones, and the fine in deeper water off the reef front.

Rasping organisms have no significant effect on the structural stability of the reef since they affect only the external surface. Boring organisms have a significant effect since they remove material from the interior. Their action results in modification of the shape of the frame since protruding parts, which are highly bored, are most liable to be broken off. Coral colonies, on the reef surface, are particularly prone to this damage. Since boring is localized in their dead basal regions, their attachment area is gradually weakened and they are easily detached during storms or, if they grow on a sloping surface, under their own weight. The present study is concerned with boring in the coral Montastrea annularis on the Barbados reefs.

The importance of boring organisms in effecting reef destruction was noted in 1903 by Gardiner in his work on the coral reefs of the Maldives and in 1904 by Finckh on the reefs of Funafuti atoll. Appreciation of the real significance of these organisms followed the work of Otter on the Low Isles of the Great Barrier Reef (1937). His detailed study revealed the importance of molluscs, sponges, sipunculid and polychaete worms and barnacles as reef-destroying agents. Since that time several workers have recognized the destructive effects of such organisms in reef environments. Robertson (1963) made a detailed study of the boring fauna of the coast of south-east Florida. Goreau and Hartman (1963) stressed the importance of boring sponges as erosive agents in corals on the Jamaican fore-reef. The role of boring organisms on the reefs of the Bermuda platform was discussed by James (1970). Scoffin (1972), in a preliminary report on the fossilization of patch reefs in Bermuda's North Lagoon

described the destructive effect of successive generations of borers on the preserved framework. Zankl and Schroeder (1972) discussed modification of the growth framework of the reefs of North Eleuthera, in the Bahamas, by repeated boring. The same effect was described in more detail by Ginsburg and Schroeder (1973) on Bermudan algal cup reefs. Hein and Risk (in press) studied bioerosion in coral heads in the inner patch reefs of the Florida reef tract.

In spite of the widespread occurrence of boring organisms in reef environments and their general acceptance as important erosive agents and sediment producers, little precise quantitative information on their importance in these roles is available. Quantitative work on bioerosion is restricted to the intertidal zone of carbonate coastlines where the effectiveness of grazing organisms in removing carbonate substrate has been investigated (Emery, 1946; North, 1954; McLean, 1967).

A few studies provide quantitative data on rates of substrate disintegration by borers. Jehu (1918) recognized the importance of boring organisms in coastal erosion in the British Isles and quoted estimates made by C. Reid, of 1 to 2 cm per year, for rates of erosion of the chalky sea floor, off the Norfolk coast, by boring bivalves. Erosion of submerged calcareous clastic rocks, by bivalves and sipunculids, has been studied by Warne and Marshall (1969). Erosion rates of 2 to 10 mm per year were obtained from the depth of penetration of borers and their estimated life span. The significance of the boring sponge Cliona in coastal erosion and sediment production in Bermuda has been noted by Neumann (1966). Measurements made on the erosion rate of the sponge

showed it to be capable of removing 22 to 26 kg of material from 1 square metre of carbonate substrate in one year.

The only quantitative study of boring in coral heads is that of Hein and Risk in which X-ray radiography was used to calculate the percentage of boring in corals from the Florida reef tract. The application of X-ray radiography to analysis of coral structure provides a means of obtaining quantitative data on coral growth and destruction. Using this technique the percentage of coral skeleton removed by boring organisms from a coral head can be estimated and the relative importance of different groups of borers ascertained.

Hein and Risk found that an average of 28% of the primary skeletal matrix of coral heads was biogenically reworked. Examination of the role of the more important boring organisms showed clionid sponges and spionid polychaetes to be quantitatively most significant. Mytilids were locally important. Total volumes reworked by sponges, polychaetes and mytilids ranged from 7% to 69%.

Quantitative studies of this type are essential if we are to gain an understanding of the budget of coral reefs and of the relative importance of bioerosion compared to purely physical and chemical processes of erosion. The main purpose of the present study was to obtain quantitative data on boring by sponges, bivalves, worms and barnacles in the coral Montastrea annularis on the Barbados reefs. The activity of these organisms was examined in two different reef environments, one deep, the other shallow, and the extent of their boring in the two environments compared.

Study site description

The fieldwork for the study was conducted during the summer of 1973 at the Bellairs Research Institute, $\frac{1}{2}$ mile north of Hometown, on the west coast of Barbados. The two areas selected for study and the location of line transects in each area are shown in fig. 1. Transects 1 and 2 are situated on a fringing reef, the Bellairs reef, which lies immediately offshore from Bellairs' laboratory. An aerial view of the reef is shown in plate 1A. This reef is typical of the fringing reefs of Barbados which have been described by Lewis (1960). Prominent zones, each characterized by distinctive faunal elements and/or physiographic features, are developed across the reef. These are the reef flat and Diploria-Palythoa zone of the back-reef environment, the central reef crest zone and the seaward slope and reef front of the fore-reef environment. Coral growth is most prolific in the reef crest and seaward slope zones; the principal corals present are Montastrea annularis, Porites porites, Porites astreoides, Siderastrea siderea and Agaricia agaricites. These zones are characterized by typical spur and groove development.

Along most of the coast, except in the Bellairs region, a prominent trough separates the fringing reef from an outer bank reef (fig. 2). Transects 3, 4 and 5 are located on a section of this reef. The bank reef forms a ridge of varying width which roughly parallels the west coast of the island over most of its length at a distance of 600 to 800 metres offshore. In the area studied the bank is approximately 800 metres from shore and its crest lies at a depth of 15 metres. The form and development of the bank reef have been described by Macintyre (1967).

FIG. I. LOCATION OF STUDY AREAS ON WEST COAST OF BARBADOS: TRANSECTS NUMBERED.

He suggested it is a submerged barrier reef which grew on an erosional terrace formed during a stillstand in sea-level between 12,500 and 11,500 years B.P. Reef growth probably began around 10,000 years B.P. and kept pace with rising sea level.

The benthic communities of the bank reef have been described by Ott (in prep.). Plates 1B and 1C show the type of community which occurs on the bank top (the bank top is arbitrarily defined as the region between the 20 metre depth limit on each side of the bank). The coral community on the bank is similar to that found in the reef front environment of the fringing reef. All of the corals present on the fringing reef, except Acropora palmata and Siderastrea radians, occur on the bank reef. Large vase-sponges (Xestospongia muta) and soft corals (Pseudopterogorgia sp.) are common in some areas (plate 1B). Coral coverage changes with depth across the bank and is consistently greater on the inner slope than on the outer (Ott, 1975).

The coral *Montastrea annularis*

Montastrea annularis, the most important reef-builder on both the fringing reef (Lewis, 1960) and bank reef (Ott, 1975), was the only coral studied. It exhibits a wide variety of growth forms (plate 2), all of which are readily recognizable. This and its widespread occurrence throughout the entire depth range of coral growth made location of samples easy.

On the fringing reef several growth forms occur. Small rounded heads are common on the reef crest. Large multiple lobed colonies are best developed on the buttress sides (plate 2A) but are

FIG. 2. DIAGRAMMATIC PROFILE OF THE WEST COAST OF BARBADOS.

also present in marginal areas of the reef (plate 2B). A wide range of different morphologies is found on the bank reef. Colonies growing out from the sloping sides develop a characteristic horizontally flattened growth habit (plate 2C). Goreau (1963) attributes the flattening effect to the decrease in light intensity with increasing depth. Light intensity on the bank reef drops from 30% of surface levels on the top to 7% at the lower limits of coral growth on the sides (Ott, 1975). On the bank top multiple lobed colonies with mushroom and columnar-shaped lobes are common. The mushroom shape is produced by peripheral growth of the colony. Single colonies of similar shape also occur (plate 2E). The surface of many colonies has a distinctive 'bumpy' appearance. 'Bumps' apparently develop when a single polyp or group of polyps grows above the level of the rest of the polypary surface and attains a greater degree of freedom of division (Barnes, 1974). A typical colony of this type is shown in plate 2D.

Colony development on the bank top is often affected by the sponge Mycale laevis (Carter). The sponge encrusts the undersides of Montastrea colonies and appears as a bright orange rim around the periphery of the colony. Oscules are present at intervals on this rim and a marked infolding of the margins of the coral colony occurs in their vicinity (plate 2F). The effect has been described by Goreau and Hartman (1966) who suggest it is a response to the exhalent currents of water expelled through the

oscles.

The mechanism(s) controlling the growth form of Montastrea annularis is not known. However, since overlapping of the various growth forms occurs throughout the depth range studied it cannot be purely environmental. Barnes (1974), in his description of the growth morphology of Montastrea annularis on the reefs in front of Discovery Bay, Jamaica, points out that the most obvious differences in morphology exist between colonies which have different colored tissue. Brown, green and purple colonies, similar to those he describes, were observed in this study. These may well be different genotypes.

Variation in the susceptibility to biological attack and mechanical breakdown of different colony types will be discussed later.

General outline of study

The study consisted of two parts:

The first was conducted in the field area and involved systematic analysis of the boring fauna of freshly collected coral heads. This provided information on the nature and habits of the boring fauna and on the types and characteristics of the boreholes produced. The relative abundance and pattern of distribution of the different boring organisms present, in the two study areas, were determined from the data obtained. The second part was carried out later in the laboratory. Coral heads collected during the fieldwork were analysed using X-ray radiography. This study was useful in several ways. The morphology of boreholes, boring strategy of different borers and the distribution and spatial relationships of borings within coralla were examined. Its most

important use was in obtaining quantitative data on the extent of boring within individual coral heads and in distinguishing the relative importance of different types of borer.

The following report is divided into two sections. In the first the fieldwork phase of the study is described and in the second the laboratory work is described.

Note: The term 'boring' is used in this report to describe the penetration of hard substrate. 'Nestling' refers to those organisms which occupy vacated boreholes.

Boring algae and fungi were present but their bioerosive effects were not examined.

PART I: FIELD
FAUNAL ANALYSIS

MATERIALS AND METHODS

Sampling procedure

Samples for splitting and X-ray work were collected at regular intervals along a nylon rope marked off in metre intervals. The colony lying closest to a 25 or 10 metre mark on the line was sampled. Coral heads were detached from the substrate using a hammer and chisel. A representative part of large aggregate colonies was taken. Both schnorkel-diving and S.C.U.B.A. were used during sampling.

To eliminate any bias which may arise due to sample size variation, a conscious effort was made to collect coral heads of similar size.

Faunal analysis

The boring fauna of each of the coral samples collected on the transect lines was carefully analysed. Each head was broken down into small fragments (less than 1 square cm) with a hammer, chisel and pounding block. During this process all the borers encountered were removed and sorted into phylum or class groups. Observations were made on both borer and borehole characteristics.

When the breakdown of the coral was completed the organisms were identified and the number of individuals per species counted. The boring sponges were identified from spicule mounts prepared from tissue samples.

RESULTS AND DISCUSSION

The boring fauna of Montastrea annularis

A variety of boring sponges, bivalves, polychaete and sipunculid worms and barnacles are active in colonies of Montastrea annularis on the Barbados reefs. Table 1 lists the species encountered during the splitting survey. In the following section each of the groups of borers is considered in terms of their occurrence, morphology and habits, substrate preferences, borehole characteristics and boring strategies. Their modes of penetration, sediment-producing and reef-destroying capabilities are briefly mentioned.

Sponges

The general morphology and physiology of clionid sponges has been described by Goreau and Hartman (1963). Further terminology is given by Rützler (1974). The main part of the sponge body, called the choanosome, contains choanocyte chambers and lies inside the substrate. The peripheral ectosomal layer of sponge tissue lacks choanocyte chambers and parts of it protrude from the substrate as papillae which bear ostia and an osculum (openings of incurrent and excurrent canals). Boring sponges all secrete a siliceous skeleton, consisting of spicules, which are embedded in sponge tissue. The three main types of spicules, tylostyles, oxeas and spirasters differ in size, shape and abundance in different sponge species. Sponge classification is based mainly on spicule morphology and to some extent upon the characteristics of the borings formed.

TABLE 1: FAUNAL LIST

PORIFERA

- Family CLIONIDAE: Cliona aprica Pang, 1971
Cliona caribbaea Carter, 1882
Cliona delitrix Pang, 1971
Cliona langae Pang, 1971
Cliona peponaca Pang, 1971
Cliona schmidtii (Ridley), 1881
Cliona vermifera Hancock, 1867
ADOCIIDAE: Siphonodictyon brevitubulatum Pang, 1971
Siphonodictyon cachacrouense Rützler, 1971
Siphonodictyon coralliphagum forma obruta Rützler, 1971
SPIRASTRELLIDAE: Spheciospongia sp. (?)

MOLLUSCA

- Class BIVALVIA: Lithophaga nigra (d'Orbigny), 1842
Lithophaga bisulcata (d'Orbigny), 1842
Gastrochaena hians (Gmelin), 1791
Gregariella coralliophaga (Gmelin), 1791
Petricola lapicida (Gmelin), 1791

SIPUNCULA

- Phascolosoma antillarum Grube & Oersted, 1859
Phascolosoma dentigerum (Selenka & de Man), 1883
Phascolosoma varians Keferstein, 1865
Paraspidosiphon speciosus Gerould, 1913
Paraspidosiphon fischeri Ten Broeke, 1925
Paraspidosiphon steenstrupi Diesing, 1859
Lithacrosiphon alticonum Ten Broeke, 1925

POLYCHAETA

- Family EUNICIDAE: Eunice schemacephala Schmarda, 1861
Eunice mutilata Webster, 1884
Eunice kinbergi (Webster), 1884
SPIONIDAE: Polydora sp. (?)
SABELLIDAE: Hypsicomus elegans (Webster), 1884
FLABELLIGERIDAE: Pherusa ?dubia (Treadwell), 1929

CRUSTACEA

- Subcl. CIRRIPIEDIA: Lithotrya ?dorsalis Sowerby, 1822
Kochlorine sp. (?)

Tissue colour may also be important.

Sponges belonging to three different families were active in the two study areas. Clionids and spirastrellids can be readily distinguished since they produce markedly different excavations. They are difficult to differentiate on the basis of spicule morphology since they both possess tylostyles and spirasters. Typical clionid and spirastrellid spicules are shown in fig. 3. Large parts of the spirastrellids grow on the surface of the coral substrate (Rützler, 1974).

Three Siphonodictyon species were present. S. cachacrouense and S. coralliphagum have been described by Rützler (1971) and S. brevitubulatum has been described by Pang (1973). The large cavities they excavate in coral skeletons are filled with pale brown, soft mucous-rich choanosomal tissue. Siphonodictyon coralliphagum possesses four distinct morphological forms which are believed to be different growth stages or ecophenotypes. One of these was recorded in the present study. All Siphonodictyon species possess distinctive bent oxeas (fig. 3).

Boring sponges are ubiquitous in the two study areas and every coral sampled was bored to some extent by species from one or more of the three families shown in the table. Clionids are the most abundant and diverse group and different clionid species were commonly found in the same coral head. Siphonodictyon and spirastrellid species were never present in the same head.

FIG. 3: BORING SPONGE SPICULES

Cliona langae spicules:

A. Tylostyle (scale=35 μ m)

B. Spiraster (scale=5 μ m)

Spirastrellid spicules:

A. Tylostyle (scale=35 μ m)

B. Spiraster (scale=4 μ m)

Siphonodictyon coralliphagum

oxeas (scale=20 μ m)

Boring activity is mainly localized in dead basal parts of coral colonies. During early stages of penetration only marginal layers of colonies are affected. As infestation proceeds, sponges spread farther into coralla forming networks of cavities which may eventually ramify throughout the entire colony. In extensively infested coralla the coral substrate is completely broken down and taken over. This state is referred to as gamma-stage infestation (Vosmaer, 1933).

The majority of these sponges are cryptic and live entirely within the cavities which they excavate. Because of their cryptic habit they are not conspicuous members of the reef community. They maintain communication with the external environment through tunnels which lead from the internal cavities to the surface of the corallum. The papillae which protrude from these tunnels are often the only indication of a sponge's presence within the coral.

Papillae of the three sponge families are distinctive. Clionid papillae are small, roughly circular in outline and protrude only slightly above the substrate surface (plate 3C). They are scattered randomly over the substrate. Siphonodictyon papillae are larger and more prominent. They range in form from tubes, a few millimetres in diameter and up to 1 cm in length (plate 3E), to conical mounds a few centimetres in diameter and height (plate 3D). The ectosomal part of the spirastrellid sponge consists of a dark greyish-brown perforated membrane which protrudes from tunnels in the substrate (plate 3F). In certain clionid species papillary fusion leads eventually to complete

encrustation of the substrate by a thin layer of sponge tissue. This is particularly common in Cliona delitrix and a Montastrea colony infested by this sponge is shown in plate 9A. The bright reddish-orange colour of this species makes it conspicuous. Its surface is often covered by numerous individuals of the small, white, symbiotic zoanthid, Parazoanthus parasiticus (Duchassaing and Michelotti).

Since boring is mainly confined to the dead basal parts of coral colonies the papillae are usually found in this region. They appear on the dead surface of corals or penetrate encrustations on the coral. Only Siphonodictyon is capable of establishing papillae on the living coral surface (plate 3B).

The boring patterns of each of the three families differ considerably. The clionids form a network of interconnecting galleries which give the substrate a distinctive honeycombed appearance (plates 4A, B). Each of the individual chambers is filled with choanosomal tissue and separated by thin remnants of coral skeleton. The excavated chambers, produced by a particular clionid species, are all a typical size and shape for that species. Many clionids exhibit a preference, during boring, for the central axial region of corallites (plate 10B). This phenomenon has been observed in substrate bored by Cliona vermifera (Ward and Risk, in press). The alignment of adjacent galleries in rows, due to concentration of the lobes of the sponge in the corallites, produces a distinctive 'string of beads' appearance (plate 10C). Cliona delitrix also occupies the central part of corallites. It penetrates coral skeletons by excavating the tabular endothecal

dissepiments (Pang, 1973).

Cavities inhabited by members of the other two sponge families are simpler. Siphonodictyon species form spherical to ovoid cavities which are linked to the substrate surface by tunnels. Different sized cavities are produced by the different species. Those formed by Siphonodictyon coralliphagum forma obruta are spherical (5-10 mm) in early stages and become ovoid (10 - 25 mm) in later stages of development. The long axis of ovoid cavities is always parallel to the substrate surface (Rützler, 1971). Tunnels leading to the coral surface are up to 3 mm in diameter. Cavities produced by Siphonodictyon brevitubulatum are similar in shape but larger. Siphonodictyon cachacrouense chambers encountered in this study reached 3 cm in diameter with tunnels up to 4 mm wide (plate 4C). Larger cavities have been recorded by Rützler (1971). Spirastrellid excavations take the form of tunnels which are circular (5-10 mm diameter) or elliptical (up to 28 x 10 mm) and ragged in outline (plate 4A). They may penetrate 10 to 12 cm into the corallium and are commonly branching.

Literature on the boring mechanism of clionid sponges (1849-1958) has been reviewed by Goreau and Hartman (1963). More recent studies, done by Cobb (1969), and Rützler and Rieger (1973) using scanning electron microscopy, indicate that the mode of penetration is mainly chemical. Small, roughly hemispherical chips are freed from the substrate by cellular etching and leave a characteristic pitted surface (plate 4D). Sediment particles produced are in the 40-60 micron size range (Rützler and Rieger, 1973). Their characteristic faceted appearance (plate 4E) makes them readily identifiable in calcareous sediments. Sponge chips are an

important component of the silt fraction of sediments on the Bellairs reef and account for 10-20% of that size fraction (I. Hunter, personal communication). The importance of sponges in sediment production in the Persian Gulf, northern Adriatic Sea and Fanning Islands of the Pacific is described by Fütterer (1974).

Bivalves

Five different bivalve species were found boring in Montastrea annularis (table 1). The shells of each of these are shown in plate 5A. The two Lithophaga species and the gastrochaenid occur most frequently; the other two are rare.

Their boring activity is confined to dead encrusted substrate in the basal parts of coral colonies. Larval settlement, it seems, can only occur successfully in these regions. The distinctive borehole apertures of the different genera aid greatly in their field identification.

Mature individuals of the genus Lithophaga form a bilobate aperture which has a characteristic 'figure of eight' shape (plate 5B). The inhalent and exhalent siphons protrude from the two openings. The entrance to gastrochaenid boreholes consists of two cylindrical tubes of aragonite which project above the substrate surface (plate 5C). These tubes are secreted by the siphons and form an extension of the borehole lining. Petricola apertures are oval and those of Gregariella, roughly triangular (plate 5D).

The boreholes of the two Lithophaga species are shown in plates 5E, F. They are circular in cross-section and roughly $1 \frac{1}{2}$ times the length of the occupant. When the substrate bored is soft and friable the

walls in the anterior part of the borehole are smooth and lined with aragonite. Linings are common in clionid bored substrate. Gastrochaena boreholes are more globose in shape (plate 5G) and are always lined with aragonite in their upper regions. The boreholes of Petricola and Gregariella are unlined. The snug fit of Petricola and Gregariella shells in the boreholes suggests that the occupant enlarges its living space as it grows. The cast of the Gregariella borehole interior is an almost perfect replica of the shell of the inhabitant.

There is no evidence of a preferred orientation in borings of any of these genera. They enter the substrate surface at angles of around 90 degrees. Borehole size increases towards the base of coral colonies.

The mode of penetration of calcareous substrates differs in the different bivalve species. Boring by Lithophaga is achieved by combined mechanical and chemical means (Yonge, 1955; Turner and Boss, 1962; Soliman, 1969). An acidic secretion, released by gland cells on the margins of the mantle, softens the substrate, making it amenable to mechanical abrasion by the rotary movement of the valves. The boring mechanism of Petricola is mainly mechanical by means of the rocking action of the valves (Otter, 1937; Yonge, 1963; Ansell and Nair, 1969). The nature of the boring activity of Gastrochaena is uncertain. Otter (1937) and Yonge (1963) believe it is mainly mechanical whereas Kuhnelt (1930) thinks the borehole is periodically enlarged by chemical dissolution of the calcareous lining and surrounding substrate.

Although sediment production by boring bivalves has received little attention, the common occurrence of calcareous granular deposits

of sand and silt in Lithophaga boreholes (Soliman, 1969; Hein and Risk, in press) suggests these organisms may be important sediment producers. McLean (1964) in his work on the erosion of calcareous beach rock in Six Men's Bay, Barbados points out that the boring activity of Lithophaga is significant as a source of fine sediment. James (1970) mentions that Lithophaga nigra, on account of its prolific occurrence and preference for the undersides of corals, is likely to be a major contributor of fine sediment on the Bermudan reefs. His calculations on sediment production by Lithophaga boring, in 40 colonies of the coral Diploria, yielded an estimate of 0.5 kg. If an extrapolation is made from this figure over the whole reef surface some idea of the sediment producing capabilities of this genus in this area can be obtained.

Since their boring occurs mainly in the basal regions of coral colonies, bivalves are important structural weakening agents. Their undermining action has been noted by Robertson (1963) and James (1970). The amount of break-off of corals in the Al-Ghardaga region of the Red Sea coast, by bivalves, was estimated to be around 20% (Bertram, 1936).

Sipunculid worms

The species of sipunculid worms found in Montastrea annularis are indicated in table 1. All of these, except Phascolosoma varians, are believed to be active borers. The species most commonly occurring are Phascolosoma dentigerum and Lithacrosiphon alticonum. Paraspidosiphon spp. and Phascolosoma antillarum are less abundant and Phascolosoma varians is rare.

Each of these worms has distinctive morphological attributes which are useful in their identification. Some of these features are evident in plate 6A. P. dentigerum and P. varians, both of which have slender bodies with a long introvert, can be distinguished on the basis of body colour and distribution of papillae. The purplish-pink colour of P. dentigerum contrasts strongly with the yellow-brown of P. varians. In P. varians the papillae are distributed over the entire trunk and introvert whereas in P. dentigerum they are grouped anteriorly and posteriorly on the trunk. P. antillarum is a fatter, more robust worm with numerous papillae on the anterior and posterior ends of the trunk and a large tentacular crown on the end of the introvert. The genus Paraspidosiphon is characterized by a distinct horny shield-like structure at each end of the trunk. Lithacrosiphon possesses a hard calcareous cone-shaped structure at the anterior end of the body. This is overlain by a thick cuticular sheath which is often overgrown by an algal tuft. Rows of minute hooks are present near the end of the introvert of all species except P. antillarum. All species bear tentacular crowns on the introvert. The significance of many of these structures in boring is discussed by Rice (1969).

Boreholes, like those of bivalves, are confined to areas of dead substrate. The small circular apertures are usually inconspicuous. Boreholes formed by different species, although of similar plan, display sufficient morphological variation to allow distinction between them. All are circular in cross-section but their diameters depend on the species forming them. In longitudinal section they may be long or short

(up to 4 cm) and straight or sinuous. The length and degree of sinuosity are also distinctive of species. They commonly taper towards the aperture and base. The posterior end differs in shape in different species; in P. antillarum it is blunt and cup-shaped whereas in P. dentigerum it is pointed. A borehole of P. dentigerum is shown in plate 6B. The walls are smooth and are commonly coated, in the main section of the hole, with a brownish mucous secretion. A white powdery deposit was commonly detected in the basal region. This may be produced by abrasion.

Boreholes, in general, have no preferred orientation. They penetrate the substrate at various angles. Some however are directed down individual corallites into the colony. The trend of these holes is being influenced by the coral structure. Sipunculids prefer to bore in areas already weakened by boring sponges.

P. varians was found in vacated bivalve boreholes and serpulid tubes or beneath encrustations on the substrate surface. Its occurrence in such areas suggests it is a nestling form.

Attachment and incipient borehole development in sipunculids occur in juvenile stages (Rice, 1969). The adult form is relatively immobile and remains in a single borehole throughout its lifetime, enlarging it as it grows (Cutler, 1968). The boring activity apparently involves a combination of both chemical and mechanical action. Chemical secretions from the epidermal glands weaken the substrate and facilitate removal by the scraping action of the papillae or shield-like structures. Areas which are partially denuded of papillae are frequently observed on the trunk (Rice, 1969). This may result from the abrasive action.

No data are available on sediment production by sipunculids. The fine calcareous deposits observed in their boreholes suggest that abrasion is involved in their boring and that fine detritus is produced. If this is the case they must contribute to the sediment supply on the reef. The amount of sediment they produce will depend upon their abundance on the reef. Since their borings are small and do not penetrate far into coralla, sipunculids cannot be regarded as significant weakening agents of coral skeletons.

The boring activities of sipunculids (and the barnacle Lithotrya) cause up to 20% porosity in the intertidal zone at Raroia (Newell, 1956). Phascolosoma antillarum is extremely abundant in coral rubble in the back-reef environment of the Bellairs reef and undoubtedly plays a major role in the breakdown of this rubble to sediment. Sipunculid boring in coral rubble on the Barbados reefs has been described by Rice and Macintyre (1972).

Polychaete worms

Representatives of several different polychaete families were found in Montastrea colonies (table 1). Whether these worms bore or nestle in the holes they occupy is difficult to ascertain. Some of the specimens encountered have previously been described as borers.

a) Eunicids

The eunicids Eunice schemacephala, Eunice mutilata and Eunice kinbergi were found inhabiting holes in the basal parts of colonies. Individual holes are of variable diameter (0.5 - 2 mm) and may extend

up to 10 cm into the interior of the corallum. The walls of the holes are usually coated with a brown secretion.

The boring mechanism of eunicids is believed to be mainly mechanical with the worm using its strong mandibles to dig its way through the substrate (Hartman, 1954). Particulate calcareous material, ranging in size from sand to mud, has been observed in the gut and boreholes of eunicids (Crossland, in Gardiner 1903; Ebbs, 1966; James, 1970) and it is generally accepted that this sediment is directly produced by their boring activity. The role of eunicids in the destruction of corals is discussed by Ebbs (1966). Gardiner (1903) stressed the importance of polychaetes in reef destruction.

b) Spionids

Spionid polychaetes of the genus Polydora? were found in 'U'-shaped holes (plate 6D) with a distinctive double 'O' aperture (plate 6E). The holes had a calcareous lining and a uniform diameter of around 1 mm.

Unlined spiral shaped holes (1 mm or less in diameter) were present in regions of intense clionid infestation. These are attributed also to spionid activity (Hein and Risk, in press). Anastomosing tunnel systems of a similar diameter, probably also formed by spionids, may extend into the interior of the corallum. Examples of these are shown in plate 8.

The coincidence of many polychaete borings with endolithic algal bands suggests that the worms may be using the algae as a food source.

Spionid boring is believed to be mainly chemical with

perhaps a minor amount of abrasion by the setae (Haigler, 1969). Calcareous substrate is dissolved by an acid product of metabolism. Observations of boring activity on test substrates showed the worms were capable of rapid rates of boring; conchiolin layers of visible thickness (in oyster shells) were penetrated within a month. These worms are not important sediment producers since substrate penetration is achieved by chemical dissolution. No particulate products were found in Haigler's boring experiments. Since polychaete borings of this type are so numerous in coral skeletons they probably play an important part in weakening coralla.

c) Sabellids

Sabellid polychaetes are also common in Montastrea colonies. Their apertures are usually located on the living surface of the corallium. Holes occupied by sabellids extend into the central parts of coralla and may be straight or winding. They are uniform in diameter (1 - 4 mm) and taper gradually towards the base. The walls are smooth and lined with a brown leathery sheath underlain by a white calcareous deposit.

No direct evidence has yet been obtained which shows that sabellids are capable of penetrating carbonate substrates. Like serpulid polychaetes, they are believed to establish on the coral surface and grow upward, keeping pace with the coral growth. The observations made during this study suggest that sabellids do bore. Disturbance of the coral growth structure in the vicinity of sabellid holes would be expected if the worm and coral were growing synchronously. No such

disturbances have been observed. Cross-cutting relationships which exist between sabellid holes and corallites (plate 10A) provide strong evidence for boring.

The presence of the sabellid, Sabella saxicava, in what appear to be boreholes in limestones, on the south coast of England, has been noted by Jehu (1918). Hypsicomus elegans has been extracted from holes in corals on Barbados reefs by Marsden (1960). She also believes this species may be capable of boring (personal communication).

Large aggregations of sabellids, believed to be due to gregarious settlement of larvae, were frequently observed in corals. Gregarious settlement of sabellarid polychaetes has been described by Wilson (1968) who shows it is induced by a chemical substance secreted by previously settled worms.

Sabellids, like spionids, probably produce very little sediment since their boring is likely to be mainly chemical. They are most abundant in the upper parts of coralla and are not significant weakening agents.

d) Flabelligerids

The flabelligerid polychaete, Pherusa ?dubia, was found in holes in Montastrea colonies on the fringing reef (plate 6C). The worm body is 15 - 25 mm long and tapers from the anterior end (1 - 2 mm diam.) to a point at the posterior end. The dimensions of the holes occupied are similar and all are directed down individual corallites.

This polychaete has not previously been described as a boring form. However, in all the samples observed, the "snug" fit of the worm body in the hole suggests it is not occupying a pre-existing borehole but

actually boring the hole it inhabits.

Barnacles

The barnacle, Lithotrya ?dorsalis, was commonly found boring into algal-encrusted basal parts of Montastrea colonies on the fringing reef.

The shape of the borehole conforms to that of its occupant. The aperture (plate 6G) and borehole cross-section are oval-shaped and the hole tapers gradually and curves inward slightly towards the base (plate 6F). The maximum cross-sectional diameters of oval apertures were 7 x 5 mm and borings reached 3 cm in length. Borings are commonly inclined at an angle to the horizontal (plate 6F) so that the animal hangs downward.

The morphology and boring mechanism of Lithotrya has been described by Ahr and Stanton (1972). They are important agents of bio-erosion and sediment production in the intertidal zone. The sediment they produce is bimodal; fine material is produced directly by their boring and coarse detritus forms when substrate weakened by intensive boring disintegrates.

Aggregations, similar to those found in sabellid populations, were noted in barnacle populations. Gregarious settlement of barnacle cyprids has been studied by Knight-Jones (1953) and Crisp and Meadows (1962).

Borings of another barnacle, tentatively identified as Kochlorina sp., were occasionally found. These borings have a characteristic slit-shaped aperture (plate 6H) and are usually less than 4 mm in depth. The borings and boring action of these barnacles have been described by

Tomlinson (1969).

Statistical treatment of data from faunal analysis

The results of the faunal analysis are presented in tables 2-6 (Appendix A). The numbers of individuals of different types of borer in coral samples from the fringing and bank reef transects are listed. Sample locations and depths are indicated.

The data obtained was statistically analysed to determine:

- a) if any significant variation exists within or between the fringing and bank reef populations.
- b) what factors are controlling the distribution patterns.

Correlation and regression coefficients, chi-squared and t-values, obtained in the tests described in the following section, are given in table 7 and 8 (Appendix B).

a) Fringing reef

The distribution of sipunculid worms was tested against both depth and distance offshore across the fringing reef using correlation analysis and a chi-squared test. The chi-squared and correlation coefficient values obtained showed there was no valid association at the .05 level of confidence between the variables in either depth or distance. A similar result was obtained when the distribution of individual sipunculid species was correlated against depth. Correlations, of a similar type, performed on bivalve and barnacle distributions also failed to show any relationship between their distribution and depth.

The lack of significant correlation in these tests indicates that the distribution of boring organisms on the fringing reef is not related to depth or distance offshore. This might be expected since the entire depth range across the fringing reef is only a few metres and the depth variation between sample locations is commonly less than 1 metre.

b) Bank reef

On the bank reef, where the total depth variation is much greater, similar tests yielded somewhat different results. A chi-squared test showed that a positive relationship exists at the .05 level of confidence between sipunculid distribution and distance over the reef. This distribution is clearly a function of depth and becomes more evident when samples from the inside and outside edges of the reef are correlated separately against depth. A chi-squared test applied to the sipunculid communities on either side reveals that a clear positive correlation exists between their abundance and depth. The association is valid at the .01 level on the inside edge and the .05 level on the outside edge.

The relationship expresses the variation in borer density between samples from the bank sides and bank top. Since corals on the bank top in general contain more individuals of each boring species than those on its sides, the number of individuals per species decreases away from the bank crest on either side. This trend is believed to be produced by differences in the growth morphology of Montastrea colonies between the bank top and its sloping sides, to be discussed later. The correlation coefficients obtained for the abundance of individual sipunculid species against depth on the bank, although higher, than those found on the fringing

reef, are not significant at the .05 level. The tests suggest that although the distribution of individual sipunculid species is not related to depth, the distribution of the whole sipunculid community is. When sipunculid species are taken individually the sample may not be large enough to show a strong association. Alternatively, individual species may be mutually exclusive; the occurrence of one inhibiting the settlement of larvae of the other. This would account for the random distribution of individual species with depth despite the systematic relationship between depth and the whole community.

c) Comparison of the fringing and bank reef environments

The fringing and bank reef environments are between 600 and 800 metres apart and are separated over most of the coast by a trough which is approximately 50 metres at the deepest. The distance between the two environments is not such as to form a barrier to the dispersal of the larvae of boring organisms in the coastal region. Although most of the boring organisms encountered during the course of the study do occur in each environment, several discontinuities in distribution are evident.

The most obvious of these is the complete absence of Phascolosoma antillarum and Pherusa ?dubia from the bank reef. P. antillarum rarely occurs in coral samples from the fringing reef although independent observation showed it to be quantitatively important in coral rubble in the shallow back-reef environment. Pherusa ?dubia occurred in just over half of the corals sampled on the fringing reef but does not contribute significantly to hard tissue destruction. The barnacle Lithotrya

?dorsalis is virtually absent from the bank reef although it occurs abundantly in some samples on the fringing reef. These large aggregations may result from its ability to secrete hormones which attract its larvae. The bivalve Gregariella coralliophaga does not occur on the fringing reef and was rarely found on the bank reef.

Apart from these obvious differences there is no apparent variation in the distribution of any of the other boring species. They all occur throughout the two environments. The sipunculid worms Phascolosoma dentigerum, Lithacrosiphon alticonum and Paraspidosiphon spp. (listed in order of abundance) are common in both environments. P. dentigerum is the most abundant boring species in Florida also (Robertson, 1963). Eunicid, spionid and sabellid polychaetes are also present in both environments. Lithophaga nigra, the most abundant of the bivalve species, is distributed throughout both environments. Lithophaga bisulcata, though slightly less abundant, shows a similar pattern of distribution. Gastrochaena hians is more abundant on the bank reef. Petricola lapicida rarely occurs in either environment.

The mean values of species density in samples from the fringing and bank reef were compared by means of t-tests to determine whether the populations in the two environments differ significantly. The t-value obtained by comparing the sipunculid worm communities of each area is not significant at the .05 level of confidence. When the distributions of individual sipunculid species in the two areas were compared, no significant differences emerged. Although no significant difference exists between the Lithophaga populations of

the two regions, the total bivalve communities were found to be significantly different at the .10 level of confidence. This is due, no doubt, to the uneven distribution of Gastrochaena hians and Petricola lapicida in the two areas. Comparison of the sabellid worm populations yielded a significant difference at the .05 level of confidence.

Finally, samples from both environments were grouped and the distribution of the important bivalve and worm species correlated with depth over the entire depth range. The low correlation coefficients obtained indicate that the abundance of individual boring species is not a function of depth.

Factors controlling the distribution of boring organisms

The co-occurrence of most boring species on the fringing and bank reefs probably results from their larval dispersal mechanism. The larval stages of all of the boring species are meroplanktonic and are carried some distance by currents before they find a suitable substrate and settle. In the case of Lithotrya and P. antillarum, which are confined to the inshore zone, rapid larval settlement may restrict distribution. Lithotrya is a known intertidal form and has been described as such in Florida (Robertson, 1963), Raroia (Newell, 1956) and Jamaica (Colman, 1940). Little is known about the larval behaviour of P. antillarum, but the predominance of the species in the near-shore region suggests it may, like Lithotrya, be mainly intertidal.

The lack of significant correlation between the distribution of individual boring organisms and depth is not surprising since they are not limited by the same factors as other benthic invertebrates.

Their endolithic habit makes them independent of light. They are dependent only upon the presence of an area of calcareous substrate into which they can bore. Coral substrates, in general, must be bare of living tissue since most borers are unable to establish upon the tissue covered surface of the corallum. For this reason boring activity usually occurs in the dead basal region of the coral colony.

The variation in species density which occurs in coral samples in both environments does not appear to be a function of depth. Two interrelated factors, which are probably responsible for controlling density variations, are sample size and availability of suitable substrate. Comparison of the boring fauna from different sized coral heads, collected from the same area, reveals that larger heads in general contain a greater number of borers (table 9). Since the larger heads are older this variation is clearly a function of the age of the colony. This relationship only holds for heads which have proportionately similar amounts of substrate exposed since the amount of exposed substrate strongly influences borer density in a particular head. Similar sized heads with different amounts of dead substrate contain different numbers of borers. The ratio of surface covered with living tissue to dead encrusted area on coral heads therefore significantly influences borer density. This ratio differs considerably in different growth morphologies of M. annularis and accounts for much of the variation in borer density which occurs across the bank reef.

Encrusting organisms present on the base of Montastrea colonies

TABLE 9

COMPARISON OF NUMBER OF INDIVIDUALS OF EACH TYPE OF BORER
IN A LARGE AND SMALL CORAL HEAD FROM THE SAME LOCALITY

ORGANISM	NUMBER OF INDIVIDUALS	
	Small head 1250 cc	Large head 2240 cc
<u>Cliona</u> spp.	2	3
<u>Siphonodictyon</u> spp.	1	1
<u>Spirastrellid</u>	0	0
<u>L. nigra</u>	2	4
<u>L. bisulcata</u>	1	3
<u>G. hians</u>	3	2
<u>G. coralliophaga</u>	0	0
<u>P. lapicida</u>	0	0
<u>P. dentigerum</u>	6	42
<u>Lithacrosiphon</u> sp.	7	10
<u>Paraspidosiphon</u> spp.	3	4
Eunicids	4	6
Spionids	P	P
Sabellids	2	8

P=PRESENT

can also affect the number of borers present. Their growth may block off the apertures of previously established boreholes or may prevent larval settlement. The type of encruster and the extent of its encrustation are important. Organisms like corals, sponges, hydrozoans, foraminifera and bryozoans protect the underlying coral skeleton since there is usually no evidence of boring activity beneath them. Calcareous algae apparently have no effect on borers since borings are always found beneath them.

The general downslope decrease, in numbers of borers present in coral samples on the inside of the bank, is mainly due to changes in the growth morphology of Montastrea. Colonies on the inner slope grow to a characteristic platey form in response to the lower light intensity (Goreau and Hartman, 1963). The dark undersides of the flattened colonies provide a favourable habitat for a variety of encrusting sponges, bryozoans, foraminifera and algae. These (except algae apparently) protect the substrate from borers and account for the low numbers of borers present.

It is unlikely that the same process operates on the gentler outer slope since flattening is less pronounced there and the levels of encrustation lower. The reason for the low numbers of borers in corals in this environment is not known. Coral growth is not as prolific here as on the top or inner edge of the bank. This may be due to higher sedimentation rates, caused by stronger current activity, in this region (Ott, personal communication). Boring sponges, especially clionids, are predominant in Montastrea colonies here and the high levels

of boring they cause will be discussed in the next section.

PART II: LABORATORY

X-RAY ANALYSIS

MATERIALS AND METHODS

Sample preparation

Coral samples collected for radiography were treated in the following manner. Their volume was initially measured by water displacement. To obtain the total volume of the sample (coral skeleton, internal voids caused in construction and bore-hole volume) it was placed in a polythene bag and evacuated before immersion. Each head was then serially sectioned into vertical slices 7 mm thick. Care was taken during sectioning to ensure that the slices cut were of uniform thickness over the entire area. X-ray exposures of the slices were made using Kodak Industrex AA film. An exposure time of 10 seconds at 45 kv produced good quality results.

The X-ray negatives produced clearly reveal the skeletal structure of the coral and the pattern of attack on the structure by boring organisms. Plates 7 and 9 show positive prints of two negatives. In each of the coral slices a well-defined concentric growth banding is apparent. This is due to cyclic variations in skeletal density and has been shown to be annual in nature (Buddemeier et al., 1974). Dark areas correspond to areas of high skeletal density and light areas to low skeletal density.

The effect of boring organisms on the coral structure is evident in the areas indicated on the prints. These represent the excavations of various borers. Each type of borer has a particular boring strategy and produces a characteristic type of borehole which facilitates their identification on the radiograph. Several

representative types are indicated on plates 7 - 10.

Although some borers may penetrate the central region of the corallum most of the boring activity is confined to the peripheral regions of the base of the coral colony. These areas are often so intensely bored by clionids and spionid polychaetes that separation of individual borings in them is impossible. For this reason no attempt was made to differentiate between clionid cavities and spionid borings in these areas.

Method of estimating % boring

The percentage of the volume of each coral sample which had been bored was estimated from the radiographs. The method used is similar to that described by Hein and Risk (in press) except in areas of clionid activity.

Each radiograph was overlain by an acetate sheet and placed on a light table. Individual borings (of Siphonodictyon and spirastrellid sponges, bivalves, sipunculids, sabellids and barnacles) and clionid-bored areas on each slice were traced around with black ink.

The dimensions of thin tubular worm borings were measured and their volumes calculated by multiplying cross-sectional area by length. The total volume of these borings in a sample was found by summing the individual borehole volumes. The proportion between this and the total volume of the sample gives the percentage removed by these organisms.

The volume of larger boreholes of sponges, bivalves and barnacles was more easily estimated. The cross-sectional areas of each slice affected by sponges, bivalves and barnacles were measured using either a planimeter

(areas greater than about 2 square cm) or a millimetre square grid underlay (smaller areas) then, since the slice thickness was known, the areas were converted to volumes. The total volume removed from the sample by these organisms was found by summing the volume removed from individual slices.

Small spionid polychaete borings (less than 1 mm diameter) were abundant in some samples. Since they commonly occur in areas of clionid activity they were treated along with clionids. Part of the estimate of percentage boring by clionids is therefore attributable to polychaetes. It was not possible to determine the relative importance of the two since their borings were difficult to differentiate.

Treatment of clionid bored areas

Extensive areas of clionid boring, which were common on many slices, were treated in a different manner. Since outlining of each individual bored cavity was impractical a method was devised for estimating the percentage of coral skeleton removed per unit volume of slice in such areas. This was done using a simple photo-cell circuit, of battery, ammeter and photo-cell, to measure the average amount of light transmitted through the bored area. The amount of non-transmission can be used as an index of boring.

A series of current readings was taken on areas of fresh unbored skeleton and on areas bored by a particular clionid species. The proportion between the average readings on the unbored and bored parts gives the percentage of coral skeleton removed. The actual volume removed by clionid sponge(s) in each slice is found by multiplying

the volume of the slice affected by clionid activity by the percentage figure obtained.

The total bored volume of the entire coral sample is obtained by summing the volumes removed by each different borer present. The proportion between this amount and the volume of the sample gives the total percentage boring in the sample:

$$\% \text{ boring} = \frac{\text{sum of individual bored volumes}}{\text{total volume of coral sample}} \times 100$$

The relative importance of different groups of borers in samples can be assessed by identifying their traces on the radiographs. The percentage boring was initially estimated in several samples containing large numbers of sabellid and sipunculid worms. The results obtained (table 10) showed these organisms did not account for much more than 2-3% of the total boring in any sample. (Bivalves were not abundant in these samples). Because sipunculids and sabellids were not volumetrically important, and since estimation of the volume they remove is tedious, only sponges, bivalves and barnacles were treated in the remainder of the samples.

TABLE 10

PERCENTAGES OF TOTAL BORED VOLUME REMOVED BY DIFFERENT BORERS
(Total borehole volume of each borer bracketed)

BORER	CORAL SAMPLE								
	T5:120	T5:100	T5:20	T4:100	T3:40	T3:30	T1:125	T2:125	T2:175
<u>Cliona</u> (+Spionids)	86.1 (425cc)	95.9 (144.8cc)	94.4 (65.7cc)	96.1 (183cc)	91.8 (114.3cc)	89.6 (138.4cc)	93.3 (59.4cc)	87.2 (59.3cc)	95.6 (94cc)
Spirastrellid	13.2 (65.2cc)	2.6 (3.9cc)	—	0.8 (1.6cc)	5.1 (6.2cc)	9.2 (14.5cc)	—	—	—
Bivalves	—	—	1.9 (1.3cc)	—	0.8 (1.1cc)	0.2 (0.3cc)	—	—	—
Barnacles	—	—	—	—	—	—	4.7 (3cc)	11.3 (7.6cc)	3.7 (3.6cc)
Sipunculids	0.2 (1cc)	0.8 (1.2cc)	0.9 (0.6cc)	1.2 (2.5cc)	0.9 (1.2cc)	1.0 (1.5cc)	2.0 (1.3cc)	1.5 (1cc)	0.7 (0.7cc)
Sabellids	0.5 (2.6cc)	0.7 (1cc)	2.8 (2cc)	1.9 (3.7cc)	1.4 (1.3cc)	—	—	—	—

T=TRANSECT; Sample location in metres offshore
on T1 and T2 and in metres across reef on T3, T4 and T5.

RESULTS AND DISCUSSION

The percentage of the volume of a coral removed by boring organisms ('percentage boring') was calculated for each of the samples collected in the fringing and bank reef environments. The results are presented in table 11 along with age estimates of the samples from radiographs and depths from which the samples were collected. It is evident from the data that the bank reef corals are both older and more highly bored than those on the fringing reef. The data was tested statistically to determine the significance of these trends. The values of coefficients obtained are given in table 12 (Appendix B).

The 'percentage boring' in coral samples from the two environments was tested against depth using correlation and regression analyses. The correlation and regression coefficients obtained show there is a significant correlation at the .05 level of confidence and that a direct linear relationship exists between the variables. The graph of 'percentage boring' against depth (fig. 4) shows there is a general increase in the extent of boring in coral heads with depth and samples from the bank reef environment are more highly bored than those on the fringing reef. Fringing reef samples are clustered and display a fairly uniform low level of boring. 'Percentage boring' and depth on the fringing reef show no significant correlation. On the bank reef 'percentage boring' is correlated with depth. When the inside and outside edges of the bank reef are treated separately a positive correlation is evident only on the outside.

TABLE 11

PERCENTAGE OF THE VOLUME OF CORAL SAMPLES REMOVED BY BORING

Sample location	% Bored	Age (yr)	Depth (m)
T1:50	3.0	10	1.8
75	6.5	16	2.7
100	3.5	13	3.4
125	5.0	15	4.0
175	8.0	14	7.3
T2:125	6.0	15	1.5
150	3.0	8	1.8
175	7.5	14	3.0
200	3.0	17	3.7
225	6.0	13	5.5
250	5.5	14	6.4
T3:10	22.0	37	29.0
20	25.5	15	20.7
30	14.0	28	15.9
40	16.5	31	14.0
60	19.5	24	16.8
80	55.0	46	21.3
100	59.5	48	36.6
T4:20	6.0	26	22.9
30	15.5	40	18.3
40	14.0	35	13.4
60	16.5	25	14.0
70	16.0	27	17.1
80	17.0	33	18.3
90	20.0	29	26.0
100	19.0	34	29.0
110	36.0	34	33.5
T5:0	15.0	34	32.0
10	5.0	31	27.4
20	7.0	39	22.9
50	17.0	24	12.5
80	16.0	21	17.7
100	24.0	28	25.9
110	10.5	23	30.5
115	17.5	15	35.1
120	47.0	32	36.6

T=Transect; Sample location in metres offshore on T1 and T2 and across reef on T3, T4 and T5.

FIG.4. GRAPH OF %BORED v. DEPTH

Analysis of the growth banding, which is apparent on X-rays of samples, reveals that the average annual growth increment for bank reef corals is 4.5 mm and that of fringing reef corals, 12.8 mm. Since similar sized heads were collected from both environments bank reef samples are likely to be two or three times older than fringing reef samples. This is confirmed by a plot of the age distribution of coral samples against depth (fig. 5) which shows a general increase in age from the fringing reef to the bank reef environment. The 'r' value obtained indicates the association is strongly positive.

The positive association between the level of boring and depth may be a function of the age distribution of corals sampled. A regression analysis performed on 'percentage boring' and colony age reveals that a direct linear relationship exists between them. Although wider scatter occurs in the plot of 'percentage boring' against age (fig. 6), a correlation analysis shows that these variables are strongly correlated. The greatest departures from the general trend are due to samples on the inside and outside edges of the bank reef with lowest percentages in corals from the inside edge and highest values in corals from the outside edge. The variation can be explained by examining the growth of corals in these two areas.

The low levels of boring on the inner slope always occur in flattened colonies which are highly encrusted on their undersurfaces. The effect of encrusters on borer density in these colonies, which was described earlier, results in these low levels of boring. The high levels of boring in colonies from the outer edge of the bank are mainly due to

FIG.5. GRAPH OF AGE v. DEPTH

FIG. 6. GRAPH OF %BORED v. AGE

the growth rate of Montastrea colonies there. Colonies are stunted and unhealthy in this region and their average annual growth increment is lower than on the top or inside edge of the bank reef. Boring sponges, particularly clionids, are very important in this environment and the high levels of boring are due mainly to their activity. Their rate of spreading into the corallum is apparently as fast as the rate of growth of the coral colony. Since the coral is not able to keep ahead of the sponge growth, levels of infestation such as those shown in plate 4B occur.

The effect of boring organisms on Montastrea annularis

Boring organisms have an important effect on the structural stability of Montastrea annularis since they preferentially infest the holdfast regions of colonies. Different growth forms of Montastrea annularis differ in their susceptibility to biological attack and subsequent break-off since the strength of their holdfast areas differs. The most obvious differences exist between shallow and deep water colonies.

In shallower regions of the reefs, where calcification rates are higher, the attachment area is mostly covered with polyps and grows in proportion to the bulk of the corallum forming a stable support for the colony (Goreau and Hartman, 1963). Since boring activity is confined to the peripheral regions of the base of these colonies their stability is not greatly affected and break-off mainly results from storm-wave action. The continuous erosion of the outer parts of such colonies by borers and grazers gradually decreases the effective diameter of the base

and reduces their ability to withstand strong wave action. This effect has been discussed by Hein and Risk (in press) who compare coral colonies to cylinders:

"Resistance of a cylindrical structure to an applied couple is a function of the effective radius of the structure, and a small decrease in this radius results in significant weakening of the structure."

They believe this effect may be partly responsible for placing an upper limit on the size of massive coral heads.

Colonies on the bank top, of comparable size to those on the fringing reef, are always more highly bored. Their presence in growth position suggests they are not subject to physical forces as strong as those encountered by their counterparts on the fringing reef. During periods of severe swells wave surge can be felt on the bank to depths of over 50 m (Ott, 1975) but is probably not strong enough to detach weak colonies from the reef surface. Break-off of colonies in this region, in my opinion, is primarily the result of bioerosion. Many of the Montastrea colonies examined on the bank reef broke off easily when pushed. All the basal parts of these colonies were highly bored.

Flattened colonies which grow on the slopes of the bank reef are inherently unstable. Since only the upper surface of these colonies is actively growing the holdfast does not develop in proportion to the rest of the colony (Goreau and Hartman, 1963). Most are supported by a thin holdfast which is weakened by borers to the point where it can no longer support the weight of the colony. Encrusting organisms which

attach to the undersides and bases of these colonies increase their weight and hasten break-off (Goreau and Hartman, 1963). Collapsed colonies, some of which had slumped downslope, were commonly observed on the sides of the bank.

Since Montastrea annularis is quantitatively the most important coral species on the bank reef (average live coverage 5%) and on the fringing reef (average live coverage 4%) its breakdown must contribute significant amounts of sediment to the reefs, especially the bank reef, where the highest levels of boring were recorded. Some idea of the contribution made to the reef sediments by different groups of boring organisms can be obtained by assessing their relative importance in removal of hard tissue from corals on the reefs. The results of the present study show that sponges are most important in this respect and bivalves and barnacles locally important. Sipunculid and polychaete worms, although abundant in some coral heads, are not volumetrically important. Since spionid polychaetes bore mainly by chemical means they do not produce sediment.

The contribution made by boring sponges to the reef sediment can be directly estimated since they produce distinctive chips which can be recognized using scanning electron microscopy. This cannot be done in other groups of borers as none of them have yet been shown to produce distinctive chips. Determination of the role of these organisms in sediment production awaits investigation.

SUMMARY

1. A variety of organisms bore into the coral Montastrea annularis on Barbados reefs. These include sponges of the genera Cliona and Siphonodictyon and one member of the family Spirastrellidae; bivalves of the genera Lithophaga, Gastrochaena, Gregariella and Petricola; sipunculid worms of the genera Phascolosoma, Lithacrosiphon and Paraspidosiphon; members of the polychaete families Eunicidae, Spionidae, Sabellidae and Flabelligeridae and barnacles of the genera Lithotrya and Kochlorina.
2. Most of the borers occur in both the fringing and bank reef environments. Notable exceptions are Phascolosoma antillarum and Pherusa ?dubia which occur only on the fringing reef and Gregariella coralliphaga which occurs only on the bank reef.
3. Sponges (especially clionids) and spionid polychaetes, are the most important borers in both environments and account for more than 90% of the total boring in most samples. Bivalves and barnacles are locally important. Sipunculids and sabellids are abundant but do not remove large amounts of hard tissue.
4. The percentage of the volume of coral samples removed by boring ranges from 3-60% and corals on the bank reef display higher levels of boring than those on the fringing reef. An average of 20% of the

volume of bank reef corals, compared to 5% of fringing reef corals, was removed.

5. The distribution of individual borers is not a function of depth.

The number and variety of borers and the extent of boring in a coral colony is dependent on the age of the colony. Older colonies are more highly bored. The ratio of surface covered with live tissue to dead encrusted area on coral heads significantly influences borer density. This ratio differs in different growth morphologies of Montastrea and gives rise to much of the variation in borer density in corals on the reefs. Encrusting organisms on the base of colonies impede borers by preventing establishment of larvae or by blocking off previously formed boreholes. The type of encruster and extent of its encrustation are important.

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REFERENCES CITED

- Ahr, W.M., and Stanton, R.J., Jr., 1973. The sedimentologic and paleoecologic significance of Lithotrya, a rock boring barnacle. J. Sed. Pet., 43: 20-23.
- Ansell, A.D., and Nair, N.B., 1969. A comparative study of bivalves which bore mainly by mechanical means. Amer. Zoologist, 9: 857-868.
- Barnes, D.J., 1973. Growth in colonial scleractinians. Bull. Mar. Sci., 23 (2):280-298.
- Bertram, G.C.L., 1936. Some aspects of the breakdown of coral at Ghardaqa. Proc. Zool. Soc. London, 106: 1011-1026.
- Buddemeier, R.W., Maragos, J.E., and Knutson, D.W., 1974. Radiographic studies of reef coral exoskeletons: rates and patterns of coral growth. J. exp. mar. Biol. Ecol., 14: 179-200.
- Cobb, W.R., 1969. Penetration of calcium carbonate substrates by the boring sponge, Cliona. Amer. Zoologist, 9: 783-790.
- Colman, J., 1940. Geography of the Jamaican shoreline. Geogr. J., 46: 323-327.
- Crisp, D.J., and Meadows, P.S., 1962. The chemical basis of gregariousness in cirripedes. Proc. Roy. Soc. B., 156: 500-520.
- Cutler, E.B., 1968. A review of coral inhabiting Sipuncula (abstr.) Amer. Zoologist, 8: 796.
- Ebbs, N.K., 1966. The coral-inhabiting polychaetes of the northern Florida reef tract. Bull. Mar. Sci., 16: 485-555.

- Emery, K.O., 1946. Marine solution basins. J. Geol., 54: 209-228.
- Finckh, A.E., 1904. Biology of reef-forming organisms at Funafuti Atoll. In: The Atoll of Funafuti. Royal Society London: 125-150.
- Fütterer, D.K., 1974. Significance of the boring sponge Cliona for the origin of fine grained material of carbonate sediments. J. Sed. Pet., 44(1): 79-84.
- Gardiner, J.S., 1903. The origin of coral reefs as shown by the Maldives. Amer. J. Sci., 16: 203-213.
- Ginsburg, R.N., and Schroeder, J.H., 1973. Growth and submarine fossilization of algal cup reefs, Bermuda. Sedimentology, 20: 575-614.
- Goreau, T.F., 1963. Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. Ann. N.Y. Acad. Sci., 109: 127-167.
- Goreau, T.F., and Hartman, W.D., 1963. Boring sponges as controlling factors in the formation and maintenance of coral reefs. In: Mechanisms of Hard Tissue Destruction. Amer. Assoc. Adv. Sci., Publ. 75: 25-54.
- Goreau, T.F., and Hartman, W.D., 1966. Sponge: Effect on the form of reef corals. Sci., 151(3708): 343-344.
- Haigler, S.A., 1969. Boring mechanism of Polydora websteri inhabiting Crassostrea virginica. Amer. Zoologist, 9: 821-828.
- Hartman, O., 1954. Marine annelids from the northern Marshall Islands. Prof. Pap. U.S. Geol. Surv., 260Q: 615-644.
- Hein, F.J., and Risk, M.J., 1975. Bioerosion of coral heads: inner patch reefs, Florida reef tract. Bull. Mar. Sci., 25(1): 133-138.

- James, N.P., 1970. Role of boring organisms in the coral reefs of the Bermuda platform. In: Reports of research seminar on organism-sediment interrelationships. Bermuda Biol. Sta. Spec. Publ. 6: 19-29.
- Jehu, T.J., 1918. Rock-boring organisms as agents in coast erosion. Scottish Geogr. Mag., 34: 1-10.
- Knight-Jones, E.W., 1955. The gregarious settling reaction of barnacles as a measure of systematic affinity. Nature, Lond., 174: 266.
- Kühnelt, W., 1930. Bohrmuschelstudien I., Palaeobiologica, 3: 53-91.
- Lewis, J.B., 1960. The coral reefs and coral communities of Barbados, W.I. Can. J. Zool., 38: 1133-1145.
- Macintyre, I.G., 1967. Submerged coral reefs, west coast of Barbados, West Indies. Can. J. Earth Sci. 4: 461-474.
- Marsden, J.R., 1960. Polychaetous annelids from the shallow waters around Barbados and other islands of the West Indies, with notes on larval forms. Can. J. Zool., 38: 989-1020.
- McLean, R.F., 1964. Mechanical and biological erosion of beachrock in Barbados, W.I. Ph.D. Thesis, 266 p. McGill Univ., Montreal.
- McLean, R.F., 1967. Measurement of beachrock erosion by some tropical marine gastropods. Bull. Mar. Sci. Gulf Caribbean, 17: 551-561.
- North, W.J., 1954. Size distribution, erosive activities and gross metabolic efficiency of the marine intertidal snails, Littorina planaxis and L. scutulata. Biol. Bull., 106: 185-197.

- Neumann, A.C., 1966. Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, Cliona lampa. Limnol. and Oceanogr., 11: 92-108.
- Newell, N.D., 1956. Geological reconnaissance of the Raroia (Kon Tiki) Atoll, Tuamotu Archipelago. Bull. Amer. Mus. Nat. Hist., 109: 315-372.
- Ott, B.S., 1975. Quantitative analysis of community pattern and structure on a coral reef bank in Barbados, West Indies. Ph. D. Thesis, 185 p., McGill Univ., Montreal.
- Ott, B.S., 1975. A description of the bank reef and deep water reefs of Barbados, West Indies, with an extended and revised species list. (in prep.)
- Otter, G.W., 1937. Rock-destroying organisms in relation to coral reefs. British Mus. (Nat. Hist.) Great Barrier Reef Expdn. 1928-1929., 1(12):323-352.
- Pang, R.K., 1973. The systematics of some Jamaican excavating sponges (Porifera). Postilla, Peabody Mus. Nat. Hist., Yale Univ., 161: 75p.
- Rice, M.E., 1969. Possible boring structures of sipunculids. Amer. Zoologist, 9: 803-812.
- Rice, M.E., and Macintyre, I.G., 1972. A preliminary study of sipunculan burrows in rock thin sections. Carib. J. Sci. 12(1-2): 41-44.
- Robertson, P.B., 1963. A survey of the marine rock-boring fauna of south-east Florida. M.Sc. Thesis, Univ. of Miami.

- Rützler, K., 1971. Bredin-Archbold-Smithsonian biological survey of
Dominica: Burrowing sponges, genus Siphonodictyon (Bergquist),
from the Caribbean. Smithson. Contr. Zool., 77: 1-37.
- Rützler, K., and Rieger, G., 1973. Sponge burrowing: Fine structure of
Cliona lampa penetrating calcareous substrata. Mar. Biol., 21:
144-162.
- Rützler, K., 1974. The burrowing sponges of Bermuda. Smithson. Contr.
Zool., 165: 32p.
- Scoffin, T.P., 1972. Fossilization of Bermudan patch reefs. Science,
178: 1280-1282.
- Soliman, G.N., 1969. Ecological aspects of some coral-boring
gastropods and bivalves of the northwestern Red Sea.
Amer. Zoologist, 9: 887-894.
- Tomlinson, J.T., 1969. Shell-burrowing barnacles. Amer. Zoologist,
9: 837-840.
- Turner, R.D., and Boss, K.J., 1962. The genus Lithophaga in the
western Atlantic. Johnsonia, 4(41): 81-116.
- Vosmaer, G.C.J., 1933-35. The sponges of the Bay of Naples. Porifera
Incalcareae. With analyses of genera and studies in the
variations of species. Martinus Nijhoff, The Hague.
- Ward, P., and Risk, M.J., Strategy of a boring sponge: Cliona
vermifera in M. annularis. (ms. submitted to J. Paleo.)
- Warne, J.E., and Marshall, N.F., 1969. Marine borers in calcareous
terrigenous rocks of the Pacific coast. Amer. Zoologist,
9: 765-774.

Wilson, D.P., 1968. The settlement behaviour of the larvae of

Sabellaria alveolata . J. Mar. Biol. Ass. U.K., 48: 387-435.

Yonge, C.M., 1955. Adaptation to rock-boring in Botula and Lithophaga

(Lamellibranchia, Mytilidae) with a discussion of this habit.

Quat. J. Microscop. Sci. 96: 383-410.

Yonge, C.M., 1963. Rock-boring organisms. In: Mechanisms of Hard Tissue

Destruction. Amer. Assoc. Adv. Sci., Publ. 75:1-24

Zankl, H., and Schroeder, J.H., 1972. Interaction of genetic processes

in Holocene reefs off North Eleuthera Island, Bahamas.

Geol. Rundschau, 61 (2): 520-541.

PLATE 1

- A. Aerial view of Bellairs fringing reef.
- B. Typical mixed coral-sponge community on the bank reef crest:
the large sponge (a) is Xestospongia muta and the large
gorgonian, (b) Pseudopterogorgia sp.
- C. Author at work on a bank reef transect.

PLATE 2

- A. Multiple lobed colony of M. annularis on fringing reef buttress (depth = 5 m).
- B. Multiple lobed colony of M. annularis in marginal region of fringing reef (depth = 4 m).
- C. Flattened colonies of M. annularis on sloping side of bank reef (inside edge 35 m depth).
- D. Typical 'bumpy' M. annularis colony on the bank top (15 m depth)
- E. Large columnar M. annularis colony on bank reef (16 m depth)
- F. Modification of the growth morphology of M. annularis by the encrusting sponge Mycale laevis (depth = 18 m).

Scale in all above photographs 0.5 m: each division 5 cm.

PLATE 3

- A. Columnar-lobed colony of M. annularis partly infested by Cliona delitrix: lobes in foreground completely taken over by sponge (note large oscules), those in background not affected. (scale = 0.5 m)
- B. Montastrea annularis colony infested by Siphonodictyon cachacrouense. Note large circular papillae on living surface of corallum. (scale = 0.5 m)
- C. Papillae of clionid sponge on dead base of M. annularis colony (bar = 5 mm).
- D. S. cachacrouense oscular papilla (mm scale).
- E. S. brevitubulatum oscular (a) and ostial (b) papillae (actual size).
- F. Ectosomal portion of a spirastrellid (actual size).

PLATE 4

- A. Cross-section of a Montastrea colony which has been intensely bored by Cliona (honeycombed area) and a spirastrellid (circular and elliptical holes). Sample from 40 m depth.
- B. Cross-section of a Montastrea colony which has been intensely bored by Cliona. The large cavity in the right side of colony is a Siphonodictyon borehole. Scale is in cm. (Depth = 40 m)
- C. Spherical cavity of Siphonodictyon cachacrouense. Note tunnel leading from cavity to live surface of corallum. (Bar = 5 mm).
- D. Scanning Electron Microscope photograph of pitted surface of coral substrate bored by sponge.
- E. Scanning Electron Microscope photograph of chips produced by boring sponge: note characteristic faceted appearance (bar = 50 μ m.)

PLATE 5

- A. The boring bivalve fauna of M. annularis: (from left to right) Lithophaga bisulcata, Lithophaga nigra, Gastrochaena hians, Petricola lapicida, Gregariella coralliophaga (actual size).
- B. Characteristic 'figure of eight' shaped aperture of Lithophaga spp. (scale in cm).
- C. Double cylindrical tube aperture of Gastrochaena hians borehole (scale in cm).
- D. Triangular aperture of Gregariella coralliophaga borehole (scale in mm).
- E. Lithophaga nigra borehole (scale in cm).
- F. Lithophaga bisulcata borehole (scale in cm).
- G. Borehole of Gastrochaena hians (scale in mm).
- H. Borehole of Gregariella coralliophaga (scale in mm).

PLATE 6

- A. The sipunculid fauna of M. annularis: (from left to right) Phascolosoma varians, Phascolosoma dentigerum, Phascolosoma antillarum, Paraspidosiphon speciosus, Paraspidosiphon fischeri and Lithacrosiphon alticonum (actual size).
- B. P. dentigerum borehole (cm scale): note dark coloured secretion on walls.
- C. Pherusa ?dubia in hole (bar = 1 cm).
- D. 'U'-shaped Polydora? hole (mm scale): note smooth calcareous lining.
- E. Double 'O' aperture of Polydora? hole (mm scale).
- F. Lithotrya borehole (cm scale).
- G. Oval apertures of Lithotrya boreholes (bar = 5 mm).
- H. Slit-shaped apertures of Kochlorine borings (scale in mm).

PLATE 7

X-radiograph of M. annularis colony from a depth of 15 m on bank reef top. Note eccentric growth banding. Areas (a), connected to dead surface of coral by tunnels, are Siphonodictyon cavities. Areas (b), in marginal parts of sample, are Cliona galleries (actual size).

PLATE 8

X-radiograph of two consecutive slabs from a Montastrea annularis colony from a depth of 40 m on outside edge of bank reef. (Higher skeletal density than previous sample). Circular and elliptical areas (a) represent cross-sections of spirastrellid borings. Honeycombed areas (b) are clionid bored. Fine traces (c) are probably spionid polychaete borings (actual size).

①

PLATE 9

- A. X-radiograph of Montastrea annularis colony from a depth of 3 m on fringing reef. Barnacle boreholes indicated. Small holes in marginal parts of colony are produced by the sponge Cliona.
- B. X-radiograph of Montastrea annularis colony from a depth of 4 m on fringing reef. Sipunculid borehole (a) and cross-section of Lithophaga borehole (b) indicated. Note Cliona boring in marginal parts of base of colony.

PLATE 10

- A. X-radiograph of M. annularis slice (actual size) showing marginal alteration by clionid sponge and spionid polychaetes. Note long curved sabellid hole extending into centre of corallum.
- B. X-radiograph of clionid-bored margin of a Montastrea colony. Note localization of sponge galleries in central parts of corallites (bar = 1 cm).
- C. X-radiograph of Cliona vermifera bored coral skeleton. Note 'string of beads' appearance due to concentration of sponge lobes in corallites (bar = 1 cm).
- D. X-radiograph of Lithophaga boring (bar = 1 cm).
- E. X-radiograph of Gastrochaena boring (bar = 1 cm).

APPENDIX A

RESULTS OF FAUNAL ANALYSIS

TABLE 2: NUMBER OF INDIVIDUALS OF EACH BORER/CORAL SAMPLE ON TRANSECT 1

BORER	SAMPLE LOCATION (metres offshore)/DEPTH (m)															
	30	40	50	60	70	80	90	100	110	120	130	140	150	160	180	300
	1.2	0.9	1.8	2.7	3.1	3.2	3.4	3.4	4.0	3.7	4.6	4.3	5.5	6.0	7.3	12
<u>Cliona</u> sp.	1	1	2	2	1	1	1	1	1	2	1	2	3	2	3	2
<u>Siphonodictyon</u> spp.	0	0	0	1	0	0	1	0	0	0	1	1	0	0	1	0
<u>Spirastrellid</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>L. nigra</u>	0	0	0	0	1	2	2	3	0	3	1	3	1	3	6	2
<u>L. bisulcata</u>	1	0	0	0	0	0	0	4	2	0	0	3	3	0	7	1
<u>G. hians</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>P. lapicida</u>	0	0	0	0	0	0	0	0	0	0	1	4	0	0	1	0
<u>G. coralliphaga</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>P. dentigerum</u>	1	0	3	3	1	4	8	8	0	12	6	7	14	21	8	1
<u>Lithacrosiphon</u> sp.	0	0	1	1	0	0	7	2	1	7	3	13	4	6	10	10
<u>Paraspidosion</u> spp.	1	0	1	2	4	4	6	4	3	6	0	4	1	10	2	4
<u>P. antillarum</u>	1	0	0	1	0	1	2	0	0	2	0	2	0	0	0	0
<u>Eunice</u> spp.	0	0	1	1	0	0	0	0	0	2	2	1	1	0	1	1
Spionids	NP	NP	P	P	NP	NP	P	NP	NP	P	P	P	NP	P	P	P
Sabellids	1	7	3	5	2	2	5	17	7	9	3	1	0	1	2	7
<u>Pherusa</u> ? <u>dubia</u>	1	2	0	9	0	3	5	0	0	7	2	0	0	1	1	0
<u>Lithotrypa</u> sp.	5	0	5	0	1	2	22	0	2	1	1	0	0	0	19	2

TABLE 3: NUMBER OF INDIVIDUALS OF EACH BORER/CORAL SAMPLE ON TRANSECT 2

BORER	SAMPLE LOCATION (metres offshore)/DEPTH (m)											
	120	130	140	150	160	170	180	190	200	210	220	230
	2.0	1.8	2.1	2.3	2.0	1.8	2.4	2.9	3.4	3.7	4.0	4.3
<u>Cliona</u> spp.	2	1	1	1	2	2	1	2	1	3	2	2
<u>Siphonodictyon</u> spp.	0	0	0	1	0	0	1	1	0	0	1	0
<u>Spirastrelli</u>	0	0	0	0	0	0	0	0	0	0	0	0
<u>L. nigra</u>	0	0	1	1	2	2	0	0	0	1	2	2
<u>L. bisulcata</u>	0	0	0	0	3	0	0	0	0	1	1	1
<u>G. hians</u>	0	0	0	0	0	0	0	0	0	0	0	0
<u>P. laticida</u>	0	0	0	0	0	0	0	0	0	0	0	0
<u>G. coralliophaga</u>	0	0	0	0	0	0	0	0	0	0	0	0
<u>P. dentigerum</u>	5	9	4	23	15	49	0	2	0	2	22	10
<u>Lithacrosiphon</u> sp.	2	3	6	7	7	11	1	0	1	2	11	2
<u>Paraspidosiphon</u> spp.	3	2	4	2	7	8	0	0	2	0	6	5
<u>P. antillarum</u>	1	0	0	0	0	0	0	0	0	0	1	0
<u>Eunice</u> spp.	0	0	2	1	0	0	9	0	1	2	0	1
Spionids	NP	NP	NP	NP	P	P	P	P	NP	P	P	P
Sabellids	7	1	4	8	6	0	0	1	0	0	0	5
<u>Pherusa</u> ? <u>dubia</u>	0	0	0	2	1	0	2	0	1	3	1	0
<u>Lithotrya</u> sp.	10	7	1	9	4	30	0	6	0	4	13	4

TABLE 4

TRANSECT 3: NUMBER OF INDIVIDUALS OF EACH BORER/CORAL SAMPLE

BORER	SAMPLE LOCATION (m across reef)/DEPTH (m)					
	5	30	40	50	60	75
	32.3	15.9	14.0	13.7	15.2	19.8
<u>Cliona</u> sp.	3	2	3	1	3	2
<u>Siphonodictyon</u> spp.	2	1	1	1	1	0
<u>Spirastrellid</u>	0	0	0	1	0	0
<u>L. nigra</u>	6	3	0	3	1	0
<u>L. bisulcata</u>	0	1	0	1	3	0
<u>G. hians</u>	1	0	2	0	2	0
<u>P. lapicida</u>	2	0	0	0	0	0
<u>G. coralliophaga</u>	2	0	0	0	0	0
<u>P. dentigerum</u>	3	3	15	4	44	0
<u>Lithacrosiphon</u> sp.	7	4	1	2	2	2
<u>Paraspidosiphon</u> spp.	4	0	4	1	0	1
<u>P. antillarum</u>	0	0	0	0	0	0
<u>Eunice</u> spp.	2	2	0	1	3	1
Spionids	P	P	P	P	P	P
Sabellids	5	8	9	2	5	0
<u>Pherusa</u> ? <u>dubia</u>	0	0	0	0	0	0
<u>Lithotrya</u> sp.	0	0	0	0	0	0

TABLE 5

TRANSECT 4: NUMBER OF INDIVIDUALS OF EACH BORER/CORAL SAMPLE

BORER	SAMPLE LOCATION (m across reef)/DEPTH (m)					
	30	35	40	50	60	70
	17.1	14.9	14.0	13.4	13.7	15.2
<u>Cliona</u> spp.	2	3	1	1	2	2
<u>Siphonodictyon</u> spp.	1	0	1	0	1	1
<u>Spirastrellid</u>	0	0	0	0	1	0
<u>L. nigra</u>	2	3	0	1	2	1
<u>L. bisulcata</u>	0	2	0	0	0	0
<u>G. hians</u>	0	0	4	3	0	1
<u>P. lapicida</u>	0	0	0	0	0	0
<u>G. coralliophaga</u>	0	0	0	0	0	0
<u>P. dentigerum</u>	4	0	17	0	12	3
<u>Lithacrosiphon</u> sp.	4	9	5	2	12	1
<u>Paraspidosiphon</u> spp.	4	1	3	0	6	2
<u>P. antillarum</u>	0	0	0	0	0	0
<u>Eunice</u> spp.	2	0	0	5	0	1
<u>Spionids</u>	P	P	P	P	P	P
<u>Sabellids</u>	6	9	12	3	9	6
<u>Pherusa ?dubia</u>	0	0	0	0	0	0
<u>Lithotrya</u> sp.	0	0	2	0	0	0

TABLE 6

TRANSECT 5: NUMBER OF INDIVIDUALS OF EACH BORER/CORAL SAMPLE

BORER	SAMPLE LOCATION (m across reef)/DEPTH (m)						
	20	35	45	55	65	75	85
	22.9	15.2	13.1	12.8	13.1	14.6	17.7
<u>Cliona</u> spp.	1	2	3	3	2	3	3
<u>Siphonodictyon</u> spp.	1	1	1	0	1	0	0
<u>Spirastrellid</u>	1	0	0	0	0	1	1
<u>L. nigra</u>	1	1	2	4	1	1	2
<u>L. bisulcata</u>	1	2	1	0	0	2	0
<u>G. hians</u>	2	1	3	4	0	1	1
<u>P. lapicida</u>	0	0	0	0	0	0	0
<u>G. coralliophaga</u>	1	0	0	0	1	1	0
<u>P. dentigerum</u>	0	2	6	19	16	23	1
<u>Lithacrosiphon</u> sp.	5	1	7	4	4	3	5
<u>Paraspidosiphon</u> spp.	1	0	3	3	0	1	3
<u>P. antillarum</u>	0	0	0	0	0	0	0
<u>Eunice</u> spp.	0	0	0	4	3	4	0
<u>Spionids</u>	P	P	P	P	P	P	P
<u>Sabellids</u>	10	2	2	0	18	48	9
<u>Pherusa ?dubia</u>	0	0	0	0	0	0	0
<u>Lithotrya</u> sp.	0	0	0	0	0	0	0

APPENDIX B

RESULTS OF STATISTICAL ANALYSIS

TABLE 7

CORRELATION ANALYSES

Locality	Variables	r	df
FR	Sipunculids with depth	0.25	10
	<u>P. dentigerum</u> with depth	0.24	10
	<u>Lithacrosiphon</u> with depth	0.18	10
	Bivalves with depth	0.24	10
	Barnacles with depth	0.23	10
BR	<u>P. dentigerum</u> with depth	0.63	5
	<u>Lithacrosiphon</u> with depth	0.20	5
FR+BR	<u>P. dentigerum</u> with depth	0.19	29
	<u>Lithacrosiphon</u> with depth	0.03	29
	<u>Lithophaga</u> with depth	0.28	29

FR=Fringing reef

BR=Bank reef

r=correlation coefficient obtained

df=degrees of freedom

TABLE 8

CHI-SQUARE TESTS

Locality	Variables	$\chi^2_{\text{comp.}}$	$\chi^2_{\text{tab.}}$ $\alpha=95$	df
FR	Sipunculids with distance offshore	20.54	21.03	10
BR	Sipunculids with distance across reef	52.98	23.60	9
	Sipunculids with depth (inside edge)	13.05	9.49	4
	Sipunculids with depth (outside edge)	10.31	9.49	4

T-TESTS

The hypothesis that the mean value of species density of fringing reef samples does not differ significantly from the mean value of species density of bank reef samples was tested.

Population	$t_{\text{comp.}}$	$t_{\text{tab.}}$ $\alpha=95$	df
Sipunculids	1.03	2.04	33
<u>P. dentigerum</u>	0.61	2.04	33
<u>Lithacrosiphon</u>	0.39	2.02	45
Bivalves	2.00	2.02	45
<u>Lithophaga</u>	0.20	2.02	45
Sabellids	1.92	2.02	45

FR=Fringing reef; BR=Bank reef

comp.=computed value; tab.=value from tables.

α =level of confidence.

TABLE 12

REGRESSION AND CORRELATION ANALYSES OF %BORING DATA

Locality	Variables	a	b	r	df
FR	%Boring with depth	-	-	0.47	9
BR	%Boring with depth	-	-	0.42	23
BR(inside)	%Boring with depth	-	-	0.05	6
BR(outside)	%Boring with depth	-	-	0.52	15
FR+BR	%Boring with depth	2.56	0.24	0.64	34
FR+BR	%Boring with age	3.51	0.80	0.63	34
FR+BR	Age with depth	14.86	0.17	0.60	34

a = intercept

b = regression coefficient

r = correlation coefficient

df= degrees of freedom