SEDIMENT PRODUCTION VIA BIOEROSION BY

CLIONA VIRIDIS

SEDIMENT PRODUCTION VIA BIOEROSION BY *CLIONA VIRIDIS* ON GRAND CAYMAN ISLAND, B.W.I.

By

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A Thesis Submitted
to the Faculty of Undergraduate
Studies in Partial Fulfillment of the
Requirements for the
Degree
Bachelor of Science

McMaster University
April, 1983

BACHELOR OF SCIENCE
(Geology)

McMaster University
Hamilton, Ontario

TITLE: Sediment Production Via Bioerosion by *Cliona viridis* on Grand Cayman Island, B.W.I.

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NUMBER OF PAGES: x, 82

ABSTRACT

The overgrowing, boring sponge Cliona viridis was studied on the Southwest coast of Grand Cayman Island, British West Indies. The surface area covered by the sponge was estimated using transect and quadrat surveys. Between 1 and 8 m depth, the average substrate coverage was 5%.

Smaller sponge colonies were usually subcircular and larger colonies more dendritic. This change in shape may aid in exploiting new substrate.

The sponge removes between 13.9% and 32.2% of the substrate as it expands laterally and produces an average erosional rate of 0.6 mm yr^{-1}. Average sediment production rate is 1 kg m^{-2} yr^{-1}.

The chips produced by the sponge comprised only 0.0122% to 1.250% of the bottom sediments. Presumably, the majority of the sponge-produced sediments were transported out by water currents.

ACKNOWLEDGEMENTS

In expressing my gratitude I realize that I could not possibly acknowledge all of the many people who contributed in various ways to this project.

My idebtedness to my supervisor, Dr. M.J. Risk, for his endless hours of optimism, enthusiasm, criticism and patience is gratefully acknowledged. Funding was provided by a grant to Dr. M.J. Risk.

I would also like to acknowledge Mr. J. Whorwood's excellent photographic skills, Kathy Bergman's contribution to various aspects of the study and Helen Kennelly for patiently deciphering my scrawl and typing the manuscript.

Finally, my thanks are extended to my family, Doug McIlveen and my class peers for their moral support and encouragement.

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CHAPTER I

INTRODUCTORY CONSIDERATIONS

1.1 Introduction and Objectives

Bioerosion of carbonate rocks or biogenic hard parts, especially corals, red algae and molluscs, by *Cliona* sp., is an abundant process on reefs. In addition to polychaetes, sipunculids, bivalves, bryozoa and other boring sponges, *Cliona* contributes to coastal erosion, porosity and permability in the substrate and sediment production.

Bioerosion involves the breakdown or weakening of the substrate as the sponge bores, excavates galleries and produces characteristic chips from the substrate. In an area densely populated by the sponge, the percentage of the sediment composed of sponge-produced chips may be very high.

In the geological column, it is difficult to attribute all the fine-grained calcareous sediment to physical erosion and chemical precipitation alone. Futterer (1974) found *Cliona* bored Cretaceous and Tertiary fossils, which he believed signified the production of the fine-grained sponge chips as far back as the upper Mesozoic Era. Bathurst (1971) suggested that *Cliona* chips play an important role in the formation of calci-lutites. This is particularly true in areas of low current velocity or

in lagoons where the sediment transport is almost nil so the grains accumulate (Smith et al, 1970 in Futterer, 1974).

Bioerosion by polychaetes, bivalves and fish also produces sediment. Because the morphology of the Cliona-produced sponge chips is significantly different from other biogenically-produced debris, and because the study organism is extremely abundant in the area, the chips may be attributed to Cliona sp.

In this study, an attempt was made to quantify the percentage of the sediment that was composed of sponge chips and to find some relationship between the degree of abundance of sponge boring and the amount of sediment produced.

1.2 Location

The study was undertaken May 6 - 13, 1982 on Grand Cayman Island, B.W.I., the largest of the three Cayman Islands. Grand Cayman (19°16' to 19°24' N and 81°05' to 81°25' W; Fig. 1.1) lies equidistant, between Cuba and Jamaica. The island measures approximately 35 km East-West by 6-15 km North-South (Plate 1.1).

The sponge was more abundant in the Sunset House area than in South Sound or Georgetown Harbour on the Western side of the island. This was also the main study area for Cortès (1981). Sunset House was chosen as the main study area due to logistic considerations, the abundance of Cliona and coral in the area and the direction of sediment transport (Fig. 1.2).

Maps, valuable information and the essential sample collecting permits were provided by the Department of Natural

Fig. 1.1 Location map showing study area: Grand Cayman Island, B.W.I.

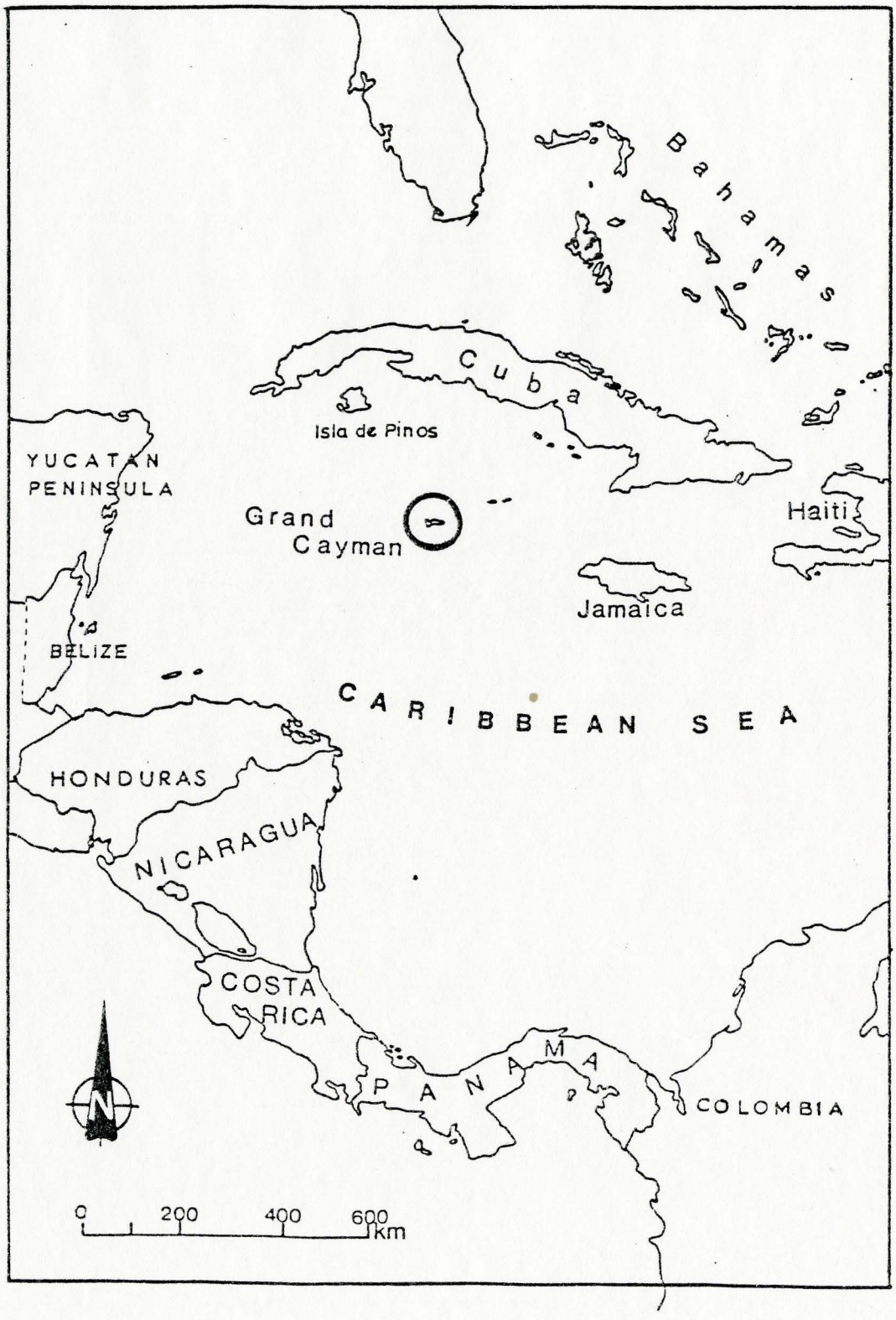
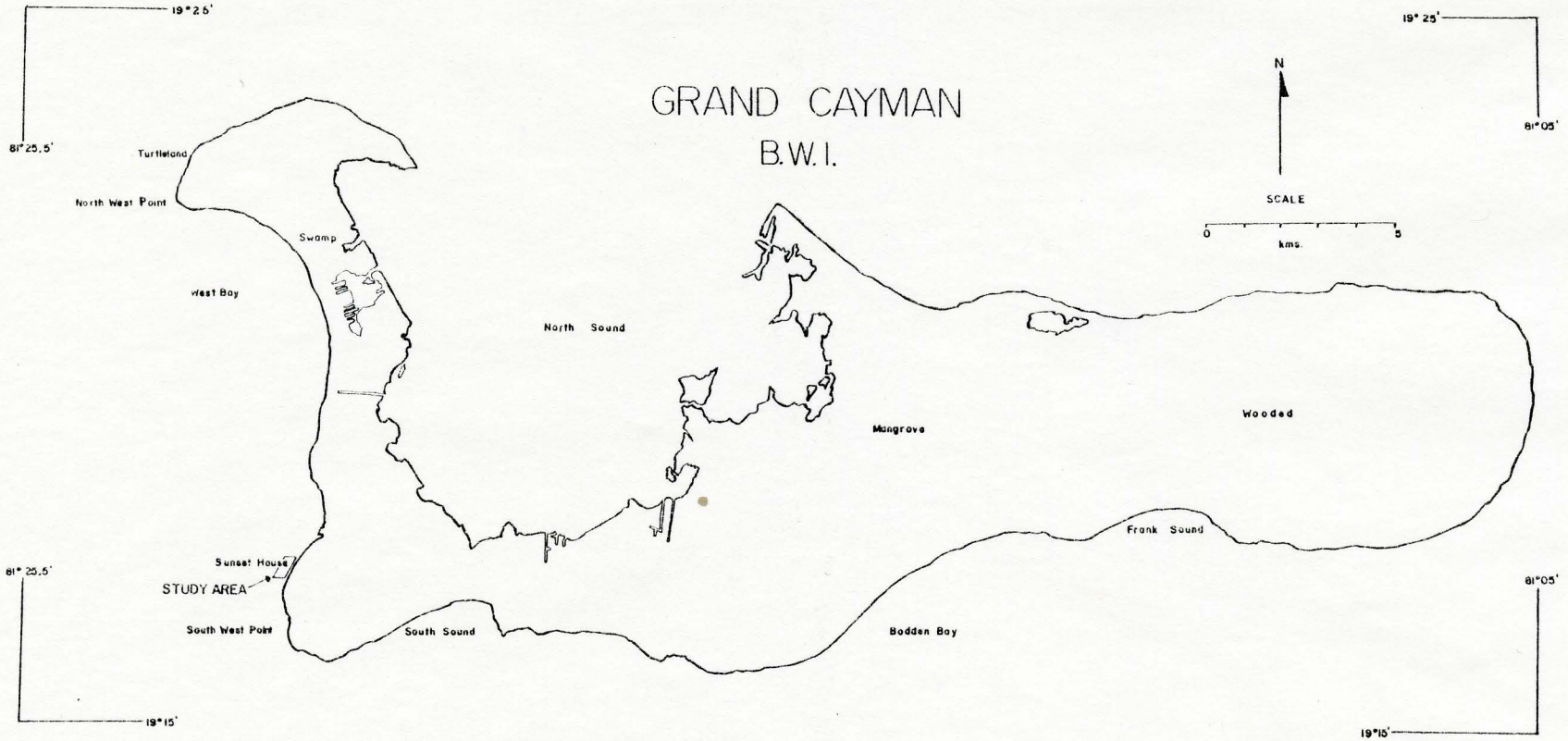

Bahamas
Cuba
Isla de Pinos
YUCATAN
PENINSULA
Grand
Cayman
Haiti
Jamaica
BELIZE
CARIBBEAN SEA
HONDURAS
NICARAGUA
COSTA
RICA
PANAMA
COLOMBIA
N
0
200
400
600
km

Plate 1.1 Grand Cayman Island and surrounding reef.
View to the South-east.
Study area shown.

Fig. 1.2 Map of Grand Cayman Island, B.W.I., showing Sunset House study area.


GRAND CAYMAN
B.W.I.
19° 26'
81° 25.5'
19° 25'
81° 05'
N
SCALE
0
5
kms.
Turtleland
North West Point
Swamp
West Bay
North Sound
Mangrove
Wooded
Frank Sound
Sunset House
STUDY AREA
South West Point
South Sound
Bodden Bay
81° 25.5'
81° 05'
19° 15'
19° 15'

Resources for the island

1.3 Geology of the Area

The following discussion follows after Roberts (1977). The island of Grand Cayman is comprised almost entirely of Recent and Pleistocene carbonates. It forms an emergent reefal structure rooted on the submarine ridge originating in South-Eastern Cuba. To the South of the ridge, the Cayman trench reaches a depth of 5487 m while the Yucatan basin to the North has water depths of up to 4572 m.

The Cayman Islands were part of Jamaica during the Miocene (Butterlin, 1956 in Roberts, 1977) but faulting in the Pliocene separated the islands and formed the Bartlett trough. Elevated Pleistocene shorelines suggest uplift during the Pleistocene with later modification by wave erosion during the late Tertiary or early Pleistocene (Doran, 1954 in Roberts, 1977). This has produced an island of relatively low relief (mean elevation +3 m; highest point + 18 m) and small scale karst topography due to dissolution of the calcareous bedrock.

The two best exposed formations are the older Bluff Limestone (Miocene), which forms raised marine cliffs, and the younger Ironshore Formation (Pleistocene), which mostly surrounds the island as an emergent coastal platform. Shallow recent fringing reefs surround the island on the North, South and East where the wave energy is high. There are two terraces, one at 8 m and another at 20 m. The deeper terrace ends at a wall which drops precipitously into the basin.

Average annual precipitation on the island is 1740 cm (Rigby and Roberts, 1976 in Cortès 1981). The climate is relatively stable with average air temperatures of 25.2°C (winter) and 28.6°C (summer). The water is very clear with salinity ranges of 35-38‰ and an average tidal range of 23 cm. The shallowest parts of the reef show little coral development which has been attributed to destruction by people (Risk, personal communication, 1982). The deeper ranges of the reef are healthy with a low amount of suspended sediment and a high biotic diversity.

The spurs and grooves present in the study area have been dubbed radial grooves, and extend seaward from the Ironshore platform. Cloud (1954) hypothesizes that these are Pleistocene surge channel systems formed by erosion following a fall in sea-level which exposes the reef flat as a barrier to trans-reef water movement. Thus, there is erosion of grooves to form channels for the water. The spur and groove systems have also been interpreted to be the most effective baffle to dissipate the destructive energy of waves and at the same time bring a constant supply of fresh water to a maximum surface area (Stoddart, 1969). Therefore, there is likely to be a high degree of sediment transport down the grooves by currents. Most of the grooves observed in the study area were almost completely devoid of sediment. The spurs meander

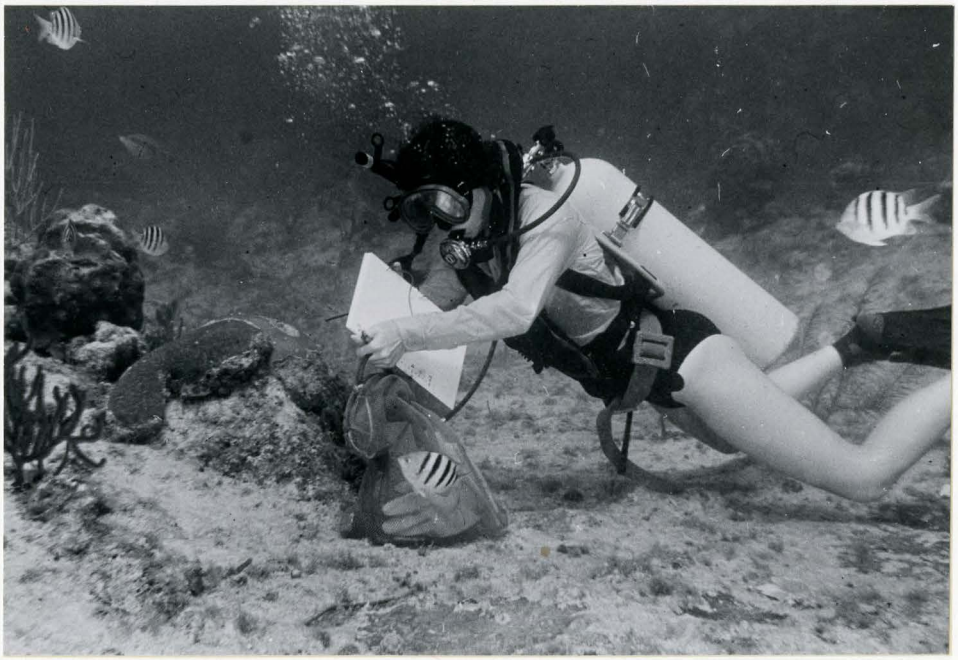
and branch off with depth and finally taper off into a sand plain with small patch reefs at approximately 18 m depth. The spur relief varies from 1-3 m.

1.4 Experimental Procedure

The field research involved the use of SCUBA in an estimation of the percentage sponge coverage of the substrate, sampling of the sponge and infested coral and sampling of the sediments (Plate 1.2).

Sponge coverage was estimated using transects and several reconnaisance dives. Transect lines across the spurs were located at regular 5 or 10 m intervals. The nylon line usually stretched from the base of the wall of one spur to the base of the wall on the other side of the spur for a total of 5-10 m depending on the width of the spur. In cases where the spur bifurcated or tapered off, a representative area of the spur was transected. A square quadrat of 2500 cm^2 area was repeatedly placed on the substrate along the line and the area within the quadrat covered by overgrowing *Cliona* was estimated. This was done along the length of the spur from a depth of approximately 1 m to 10 m where the spurs tapered off into coral rubble and a sand plain and where the sponge coverage was less than one percent. This constituted a distance of 165 m from the Ironshore Bluff. In addition to sponge coverage and type of substrate, the colony size and shape were noted.

Plate 1.2 SCUBA diving: one of the grooves.



Sponge-infested coral samples were obtained with an underwater jackhammer and great diligence as the samples often totally crumbled. The samples were placed in numbered bags, fixed in formaldehyde and dried for the trip home.

The perimeters of typical colonies were measured and markers were emplaced in the sponge colony for later measurements of the growth rate.

Sediment samples were collected at various depths down to 28.3 m wherever sediment remained in the groove. The tops of the spurs were usually clean of sediment. The sediment samples were collected in clear plastic, four ounce, numbered jars. These samples were also dried for the trip home. Clear plastic tubing of seven cm diameter and seven cm length, with caps for both ends, was used for core sampling. The cores were frozen to preserve the stratigraphy. The direction of sediment transport was also evaluated.

In the laboratory, the depth of penetration by the sponge was measured. Light microscope slides and scanning electron microscope stubs of the spicules were prepared, using the method outlined by Ruetzler (1974), to examine the spicule morphology.

To determine the biomass of the sponge relative to the depth of penetration and the amount of coral removed, small portions of the sponge-infested substrate were weighed dry then placed in hydrogen peroxide (H_2O_2) for four to five days

to dissolve the organic matter. Care was taken to use cubes bored only by Cliona. After drying, the cubes were reweighed and the difference, or amount of sponge tissue, was calculated.

These same cubes were later washed in an ultrasound bath, dried and placed on SEM stubs to examine the excavated gallery morphology.

The percentage of coral removed was determined using Archimedes' Principle; the weight of water displaced by the sample can be converted to sample volume. Small portions of the unbored substrate were prepared in the same manner as for the biomass calculations. Care was taken to use cubes that appeared to be unbored. These cubes were used to determine the specific gravity of the unbored substrate. The cubes, bored and unbored, were quickly dipped in very hot paraffin to displace any trapped air. Paraffin was chosen because of its very low viscosity and similar specific gravity to water. The cubes were weighed dry, with paraffin, and then again when suspended in water. The unparaffined weight divided by the volume of the cube is the specific gravity.

$$\frac{\text{weight of cube (unparaffined) (g)}}{\text{volume } (cm^3)} = \text{specific gravity } (g/cm^3)$$

To find the percentage of the coral removed by the sponge, the following equation was applied to each coral sample.

$$\frac{\gamma \text{ of unbored cube} - \gamma \text{ of bored cube}}{\gamma \text{ of unbored cube}} \times 100 = \% \text{ substrate removed}$$

where γ = specific gravity.

To prepare the sediments for sieving, approximately 50 g of each sample were placed in beakers with hydrogen peroxide (H_2O_2) for at least two days to remove any organic matter. The samples were then flooded with water and the sediment left to settle out. The process was repeated four times. The samples were then dried and weighed. The coarser samples were dry sieved and the 3.25 ϕ, 3.75 ϕ and 4.00 ϕ fractions extracted and weighed. The finer grained samples were wet sieved using Calgon as a dispersant to prevent flocculation. Again, the various phi fractions plus the silt fraction were extracted, dried and weighed. Approximately ten SEM photographs of each phi fraction of each sample were taken. These were later used to count the percentage of sponge chips in the sediment.

Only the sediments from the upper surface of the cores were examined. These were not sieved and an attempt was made to determine the percentage of sponge chips in the surface sediment.

All the data obtained and lists of samples collected are contained in the appendices.

CHAPTER 2

TAXONOMY AND DISTRIBUTION

2.1 Taxonomy

The genus *Cliona* was erected by Schmidt (1862) to describe a boring sponge found in the Adriatic Sea. He designated the sponge *Cliona viridis*. In 1882 Carter described another clionid sponge, *Cliona caribboea*. Several other genera of *Cliona* have since been described (Topsent, 1900, 1932; Hechtel, 1965; Pang 1971, 1973b and Ruetzler, 1974). Trace fossils made by boring sponges have been found in rocks from the Cambrian (Kobluk, 1981) but the clionid family has origins dating back only to the Silvrian (Lawrence, 1969). The extent of bioerosion by clionids has been used most commonly to assess shell exposure during the various phases of an oyster's environmental history and as a paleoenvironmental indicator based on the different salinity tolerances of the various species (Lawrence, 1969).

Cliona inhabits the tropical Atlantic, Mediterranean, Adriatic and Red Seas as well as the Great Barrier Reef of Australia. *Cliona viridis* has been noted in the Mediterranean (Schmidt, 1862; Ledenfeld 1897; Topsent, 1900); the Caribbean (Hechtel, 1965) and the Great Barrier Reef Province (Risk and Sammarco, 1982; Bergman, 1983).

Two forms of encrusting Cliona were found on the Grand Cayman reef, both later determined to be the same species. They differed in colour, oscular size, symbiosis with hydrozoa and location relative to light intensity.

A main point of contention in the naming of the Caribbean encrusting Cliona is whether it should be designated C.viridis or C.caribboea. In an attempt to resolve this dispute in the nomenclature, Topsent suggested the name Cliona viridis (Schmidt) Gray var. caribboea but this was later rejected based on the different growth habits of the two (Pang, 1971). To complicate matters, Carter found that C.celata was more similar to C.caribboeathan to C.viridis although there were differences in spiculation. Hechtel (1965) suggested lumping them all together into the Cliona viridis complex on the grounds that the differences between the three were ecologically or environmentally controlled. Ruetzler (1975) and Pang (1971) feel that this should not be the case.

The different morphologies of these species along with spicular dimensions are summarized in Table 2.1. None of the species shows papillary fusion and all have randomly scattered, spherical to elliptical oscula with raised rims. The tylostyles of all the species are very similar: a thin, fusiform shaft, pin-like, smooth, curved to straight with a constriction preceeding a spherical to spatuate or ovate head. The thickest

Table 2.1 Morphology of Different Cliona Species

	C. celata	C. viridis	C. carriboea	This study
tylostyles	globular to ovate head ≈ 500μ (2)*	spherical to spatuate head 195-384μ×5-12μ(3)	spherical to globular head 361-451μ×9.4-12.1μ(4)	spherical head 252.8-387.5μ×4.6-10.3μ
spirasters	none (2)	straight to multiangular 3-4 bends (3)	straight or w-shaped 4-7 bends (5)	w-shaped to multiangular 2-5 bends
colour	yellow (2)	yellow to dark green (4)	ocherous orange (1) to yellow (4)	dark green/brown to light brown
growth habit	not specified	overgrows substrate (4)	no tendency to overgrow substrate (4)	overgrows substrate

*
references
1. Carter (1882)
2. Hancock (1867)
3. Hechtel (1965)
4. Pang (1971)
5. Ruetzler (1974)

part of the shaft is about as wide as the head and it terminates in a sharp point.

C.viridis, C.caribboea and the Cliona of this study all possess spirasters of the same morphology, whereas C.celata does not possess flesh-spicules (Hancock, 1867). The encrusting habit and dark colour are only displayed by C.viridis. None of the cited species share the dark brown to light brown colour of the Grand Cayman Cliona. On the basis of this evidence, the Grand Caymanian encrusting Cliona has been designated C.viridis.

2.2 Species or Varieties?

The two forms of encrusting Cliona that were found were both markedly similar in their growh habit and morphology but different in colour.

The dark brown variety had few, large, prominent oscula (2-4 mm in diameter) and a tendency towards symbiosis with white to green hydrozoa. The lighter brown variety possessed very small, abundant osculae (1-3 mm in diameter) and only very rarely displayed the symbiosis. The dark Cliona became more abundant, relative to the lighter variety, with depth. It also occurred more commonly on the vertical sides of the spurs and the hardground of the grooves where swept clean of sediment. In contrast, the lighter Cliona was found relatively more abundantly in the better lit regions such as the tops of the spurs.

The tylostyle dimensions for both varieties are summarized in Table 2.2 and illustrated on Plates 2.1, 2.2, 2.3 and 2.4. Their spirasters are also equivalent (Plates 2.5, 2.6 and 2.7).

When the two varieties interface there is a thin mucus line separating the two, such that they never actually touch (Plates 2.8 and 2.9). This mucus is excreted by the sponge as a defence mechanism. In some cases, the two varieties seem to compete for space but it is very difficult to tell if one wins over the other. One example is schematically represented in Fig. 2.1, where the dark sponge completely envelopes the lighter sponge. This may be an instance of dark winning over light, however, the light sponge shows no sign of demise but seems, instead, to invade deeper into the coral head providing increased deflation of the substrate. Perhaps when forced to by some barrier, the sponge will advance down into the substrate rather than laterally.

If the light and dark colours of the two sponges were only due to differing degrees of symbiosis with zooxanthellae or the expulsion of the zooxanthellae when the sponge begins to die, then a gradational range would be expected. The lack of colour gradation and the similarity of tylostyle morphology and growth habit suggest that the light and dark sponges are simply varieties of the same species.

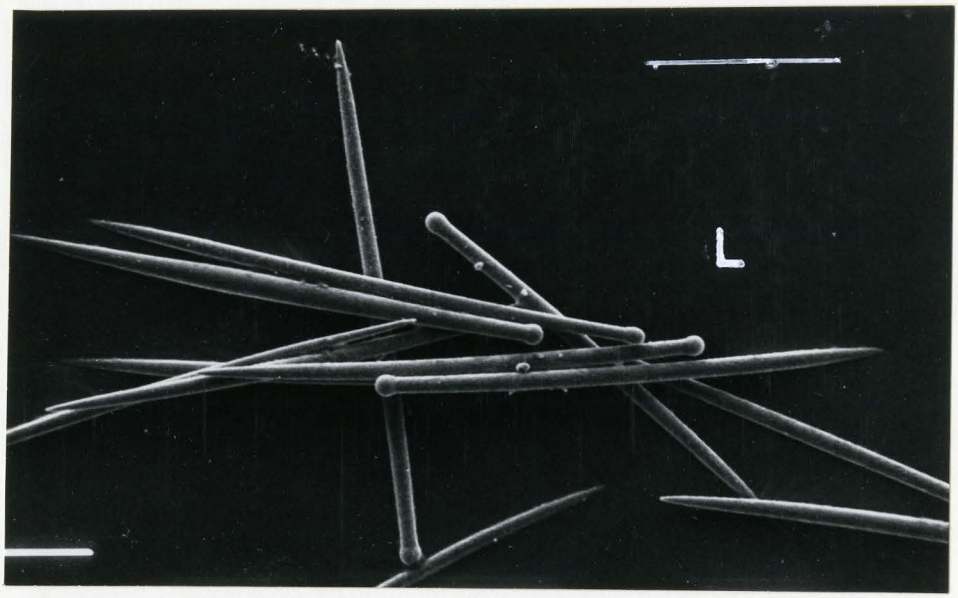
Table 2.2 Tylostyle Dimensions of Light and Dark *Cliona viridis**

		Dark length	Dark width (n = 120)		Light length	Light width (n = 120)
#31	$\bar{x}$	379μ	9μ	#27	378μ	10μ
	σ	30	2		26	3
#33	$\bar{x}$	387μ	10μ	#12	330μ	8μ
	σ	23	2		70	3
#22	$\bar{x}$	253μ	5μ	#15	262μ	6μ
	σ	30	1		13	1
#26	$\bar{x}$	375μ	9μ	#35	262μ	6μ
	σ	18	3		22	1

*Sample slides are labeled according to sample number and can be found in the archives of the Dept. of Geology, McMaster University.

Scanning Electron Microscope Micrographs showing morphology of the tylostyles for the light and dark varieties, *Cliona viridis*.

Plate 2.1 L = light
Plate 2.2 D = dark
Scale bar = 100μ


L

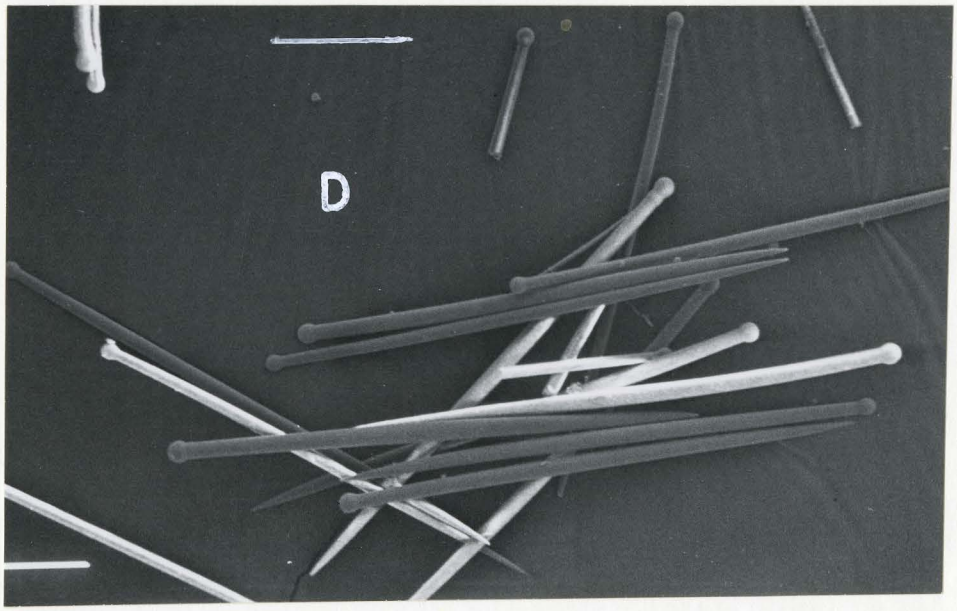
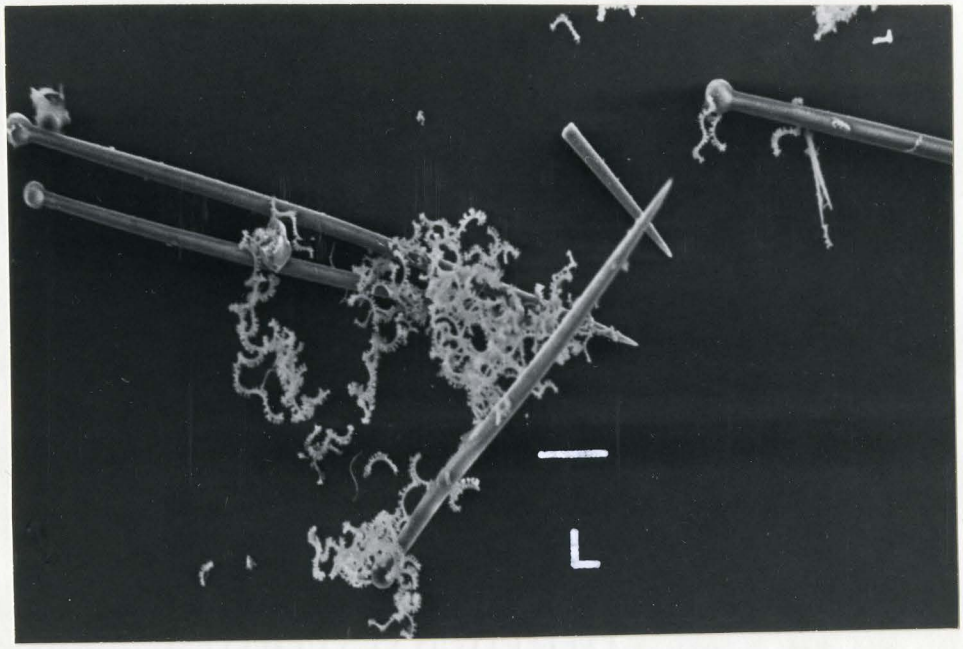

D

Plate 2.3 SEM micrograph. Cliona viridis.
Tylostyle with spirasters - light variety.
Scale bar = 20µ

Plate 2.4 SEM micrograph. Cliona viridis
Various dimensions of tylostyles.
Thinner tylostyles may be immature
versions of larger tylostyles.
Light variety.
Scale bar = 10µ



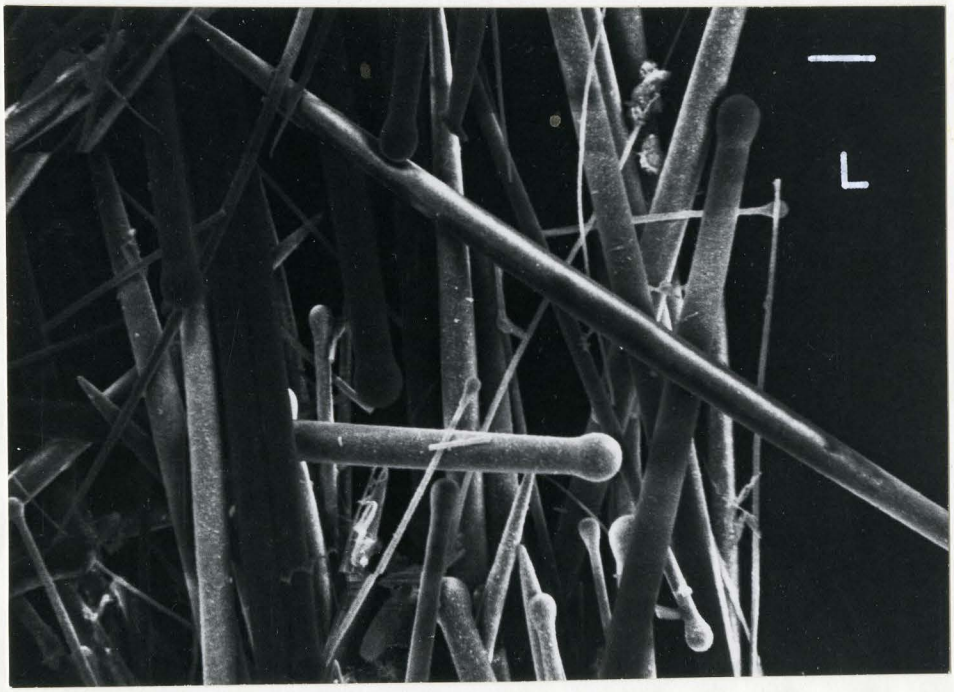
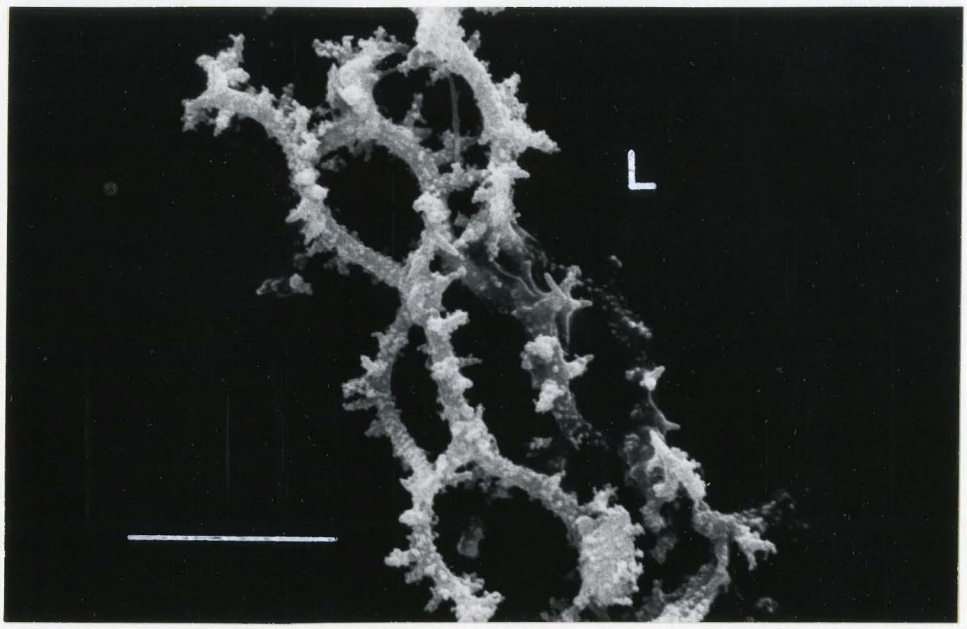
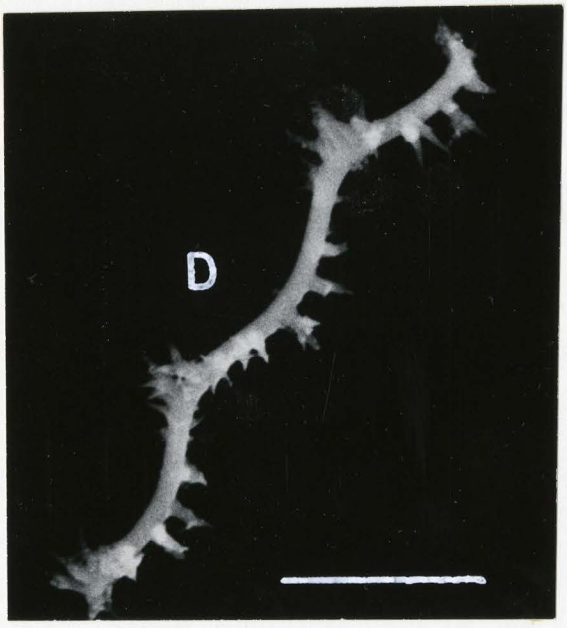


Plate 2.5 Spirasters of the light variety *Cliona viridis*. Note similar morphology to dark variety spirasters below. Scale bar = 10μ

Plate 2.6 Spiraster of the dark variety *Cliona viridis*. Scale bar = 10μ

Plate 2.7 Spirasters of the dark variety *Cliona viridis* with tylostyle in background. Scale bar = 10μ


L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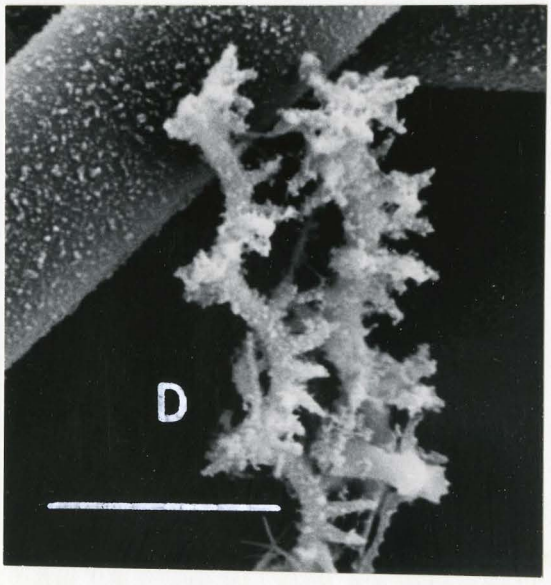
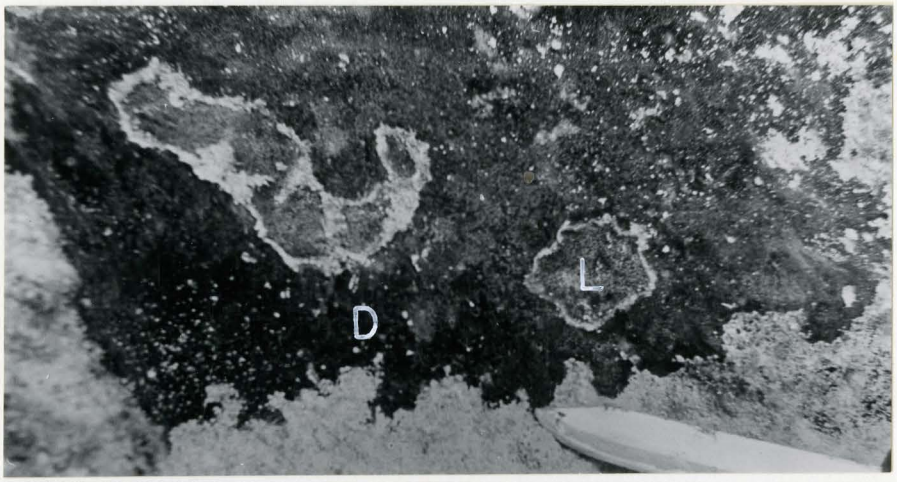

D

Plate 2.8 Light and dark varieties of C. viridis in contact. Note mucus rim.

Plate 2.9 Dark variety surrounding light variety of C. viridis.


L
D


L
D

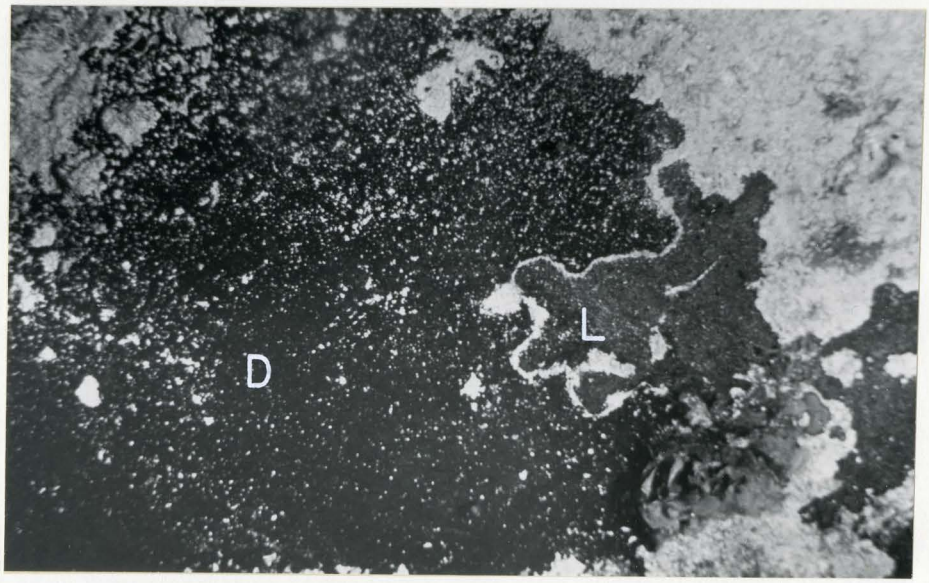
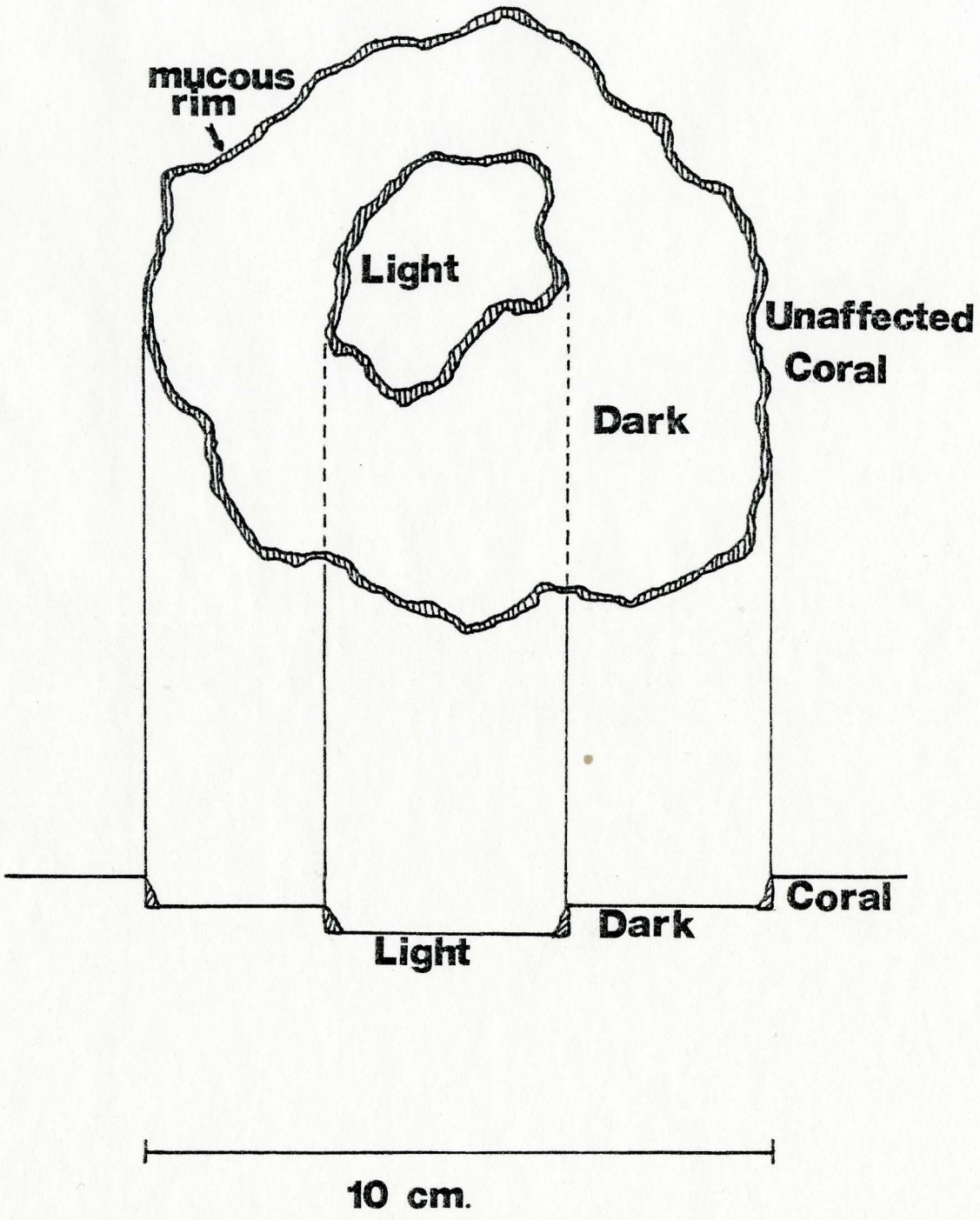

L
D

Fig. 2.1 Schematic drawing of light variety C. viridis surrounded by dark variety C. viridis infesting coral. Cross-sectional view shows deflation of the substrate.


mucous rim
Light
Unaffected Coral
Dark
Coral
Dark
Light
10 cm.

2.3 Spatial Distribution

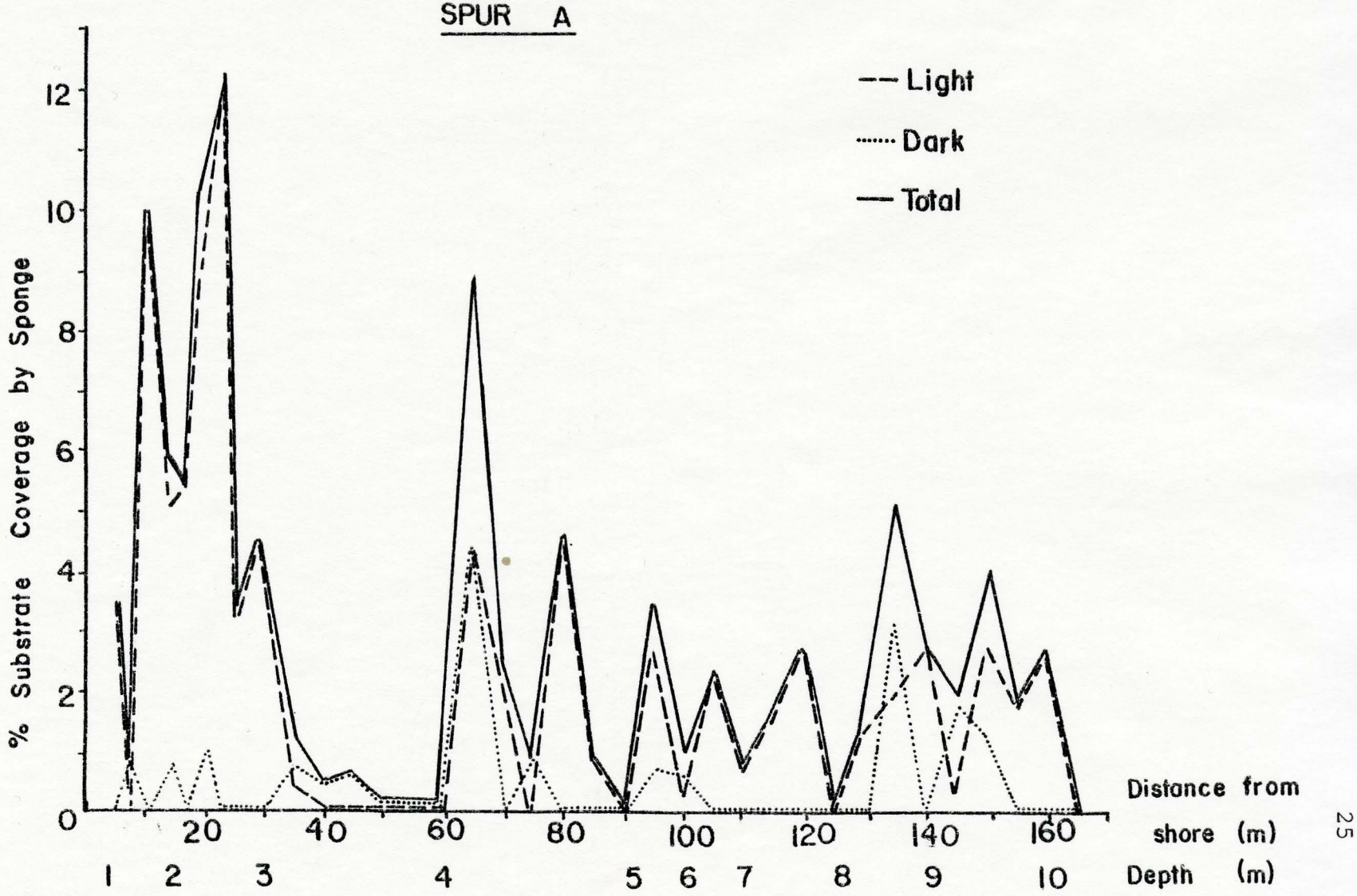
On the Grand Caymanian reef the ratio of dark to light increases with depth (Figs. 2.2, 2.3, 2.4 and 2.5). Overall abundance of Cliona viridis, however, shows no significant change with depth (Fig. 2.6) until approximately 18 m depth where the spurs taper off into a sand plain. The patch reefs on the plain are only minimally infested with Cliona viridis and this amount decreases even further at 28 m (top of the wall leading to the Cayman trench) where the sponge coverage was estimated at less than 1%. Hartman (1957) found C.viridis to be the dominant species in the littoral zone but less common and restricted to coralline algae from 15-35 m depth.

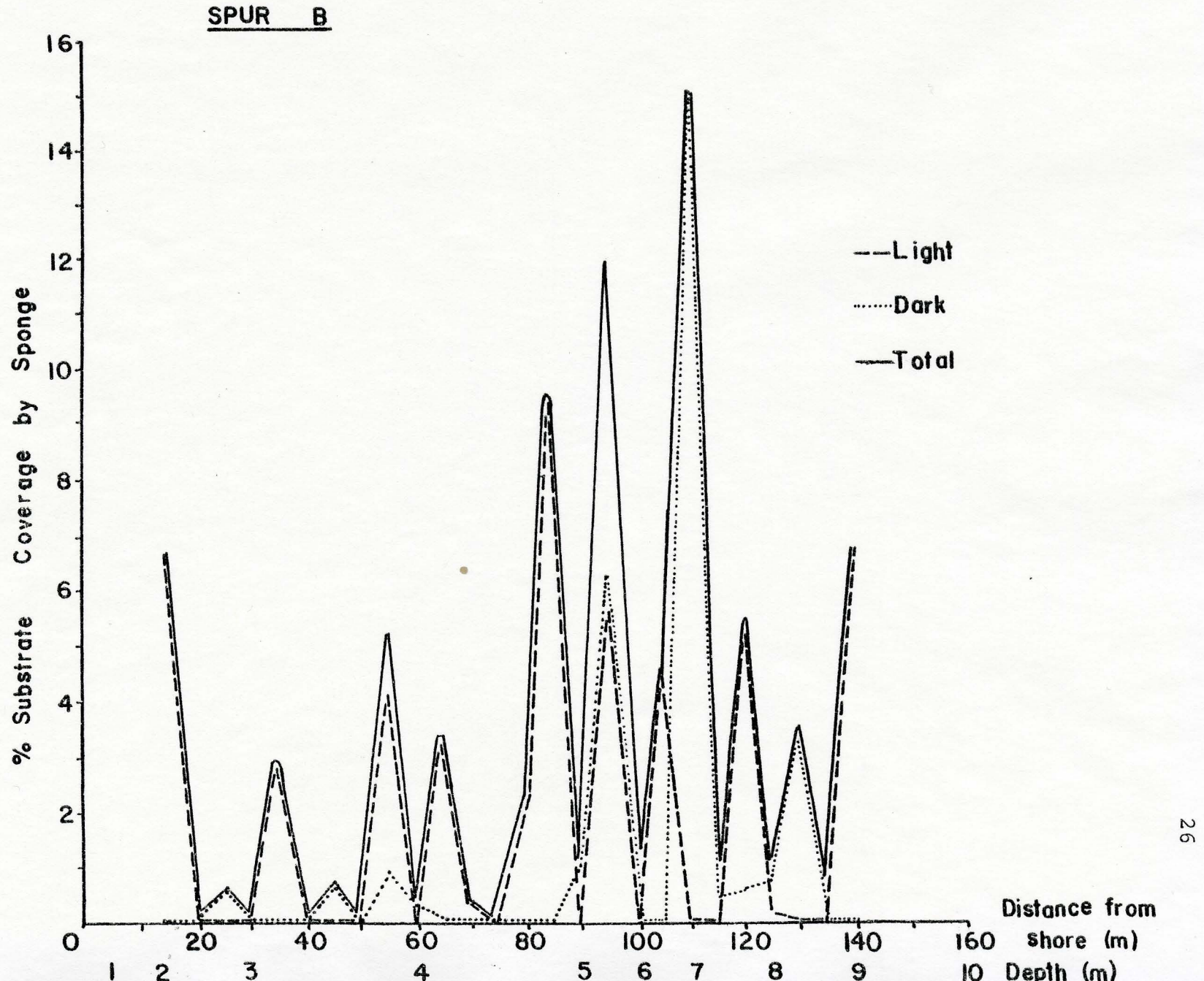
The relative increase in the dark variety with depth is coincident with its occurrence in more poorly-lit areas at shallow depths.

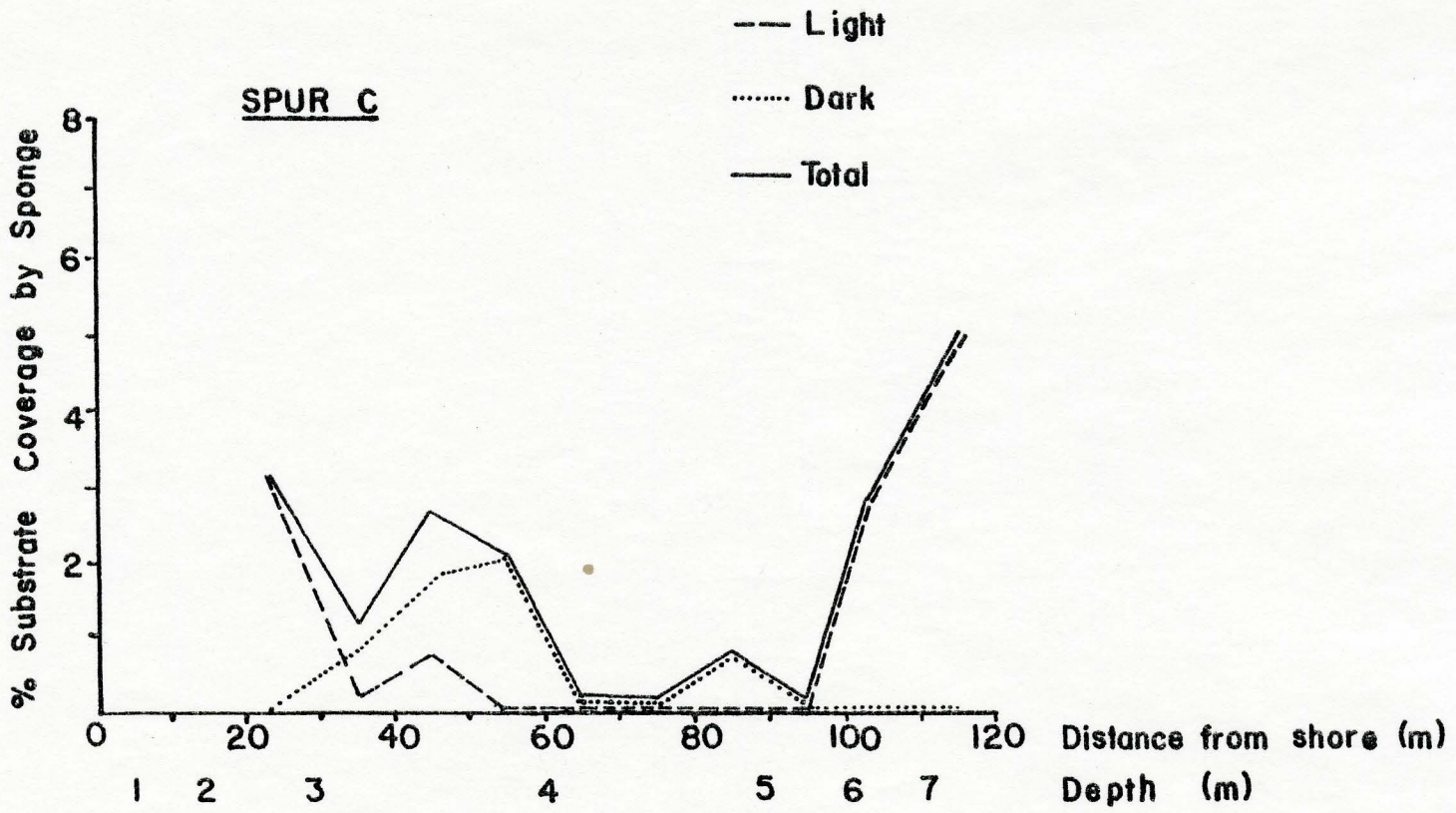
At Turtleland, where the water was very murky, neither sponge was found in excess of 1% substrate coverage. C.viridis did not occur preferentially on any particular substrate. This is mirrored in the lack of pronounced C.viridis coverage change as the dominantly dead coral changed very abruptly to live coral at approximately 7 m depth. 20% live coral coverage at 6.5 m and 50% live coral coverage at 7.5 m was estimated.

The sponge may grow on both the hardground and an adjacent live coral head at the same time. Previous studies on boring sponges in general and Cliona specifically (MacGeachy, 1977; Hein and Risk, 1975) have found that the sponge bores

Figs. 2.2, 2.3, 2.4, 2.5 Percentage substrate coverage by *Cliona viridis* as a function of distance from shore and depth-transect data (refer Appendix C).


SPUR A
Light
Dark
Total
% Substrate Coverage by Sponge
0
2
4
6
8
10
12
20
40
60
80
100
120
140
160
1
2
3
4
5
6
7
8
9
10
Distance from shore (m)
Depth (m)


SPUR B
% Substrate Coverage by Sponge
16
14
12
10
8
6
4
2
0
---Light
.....Dark
——Total
20
40
60
80
100
120
140
160
Distance from shore (m)
1
2
3
4
5
6
7
8
9
10
Depth (m)


SPUR C
Light
Dark
Total
% Substrate Coverage by Sponge
8
6
4
2
0
20
40
60
80
100
120
Distance from shore (m)
1
2
3
4
5
6
7
Depth (m)

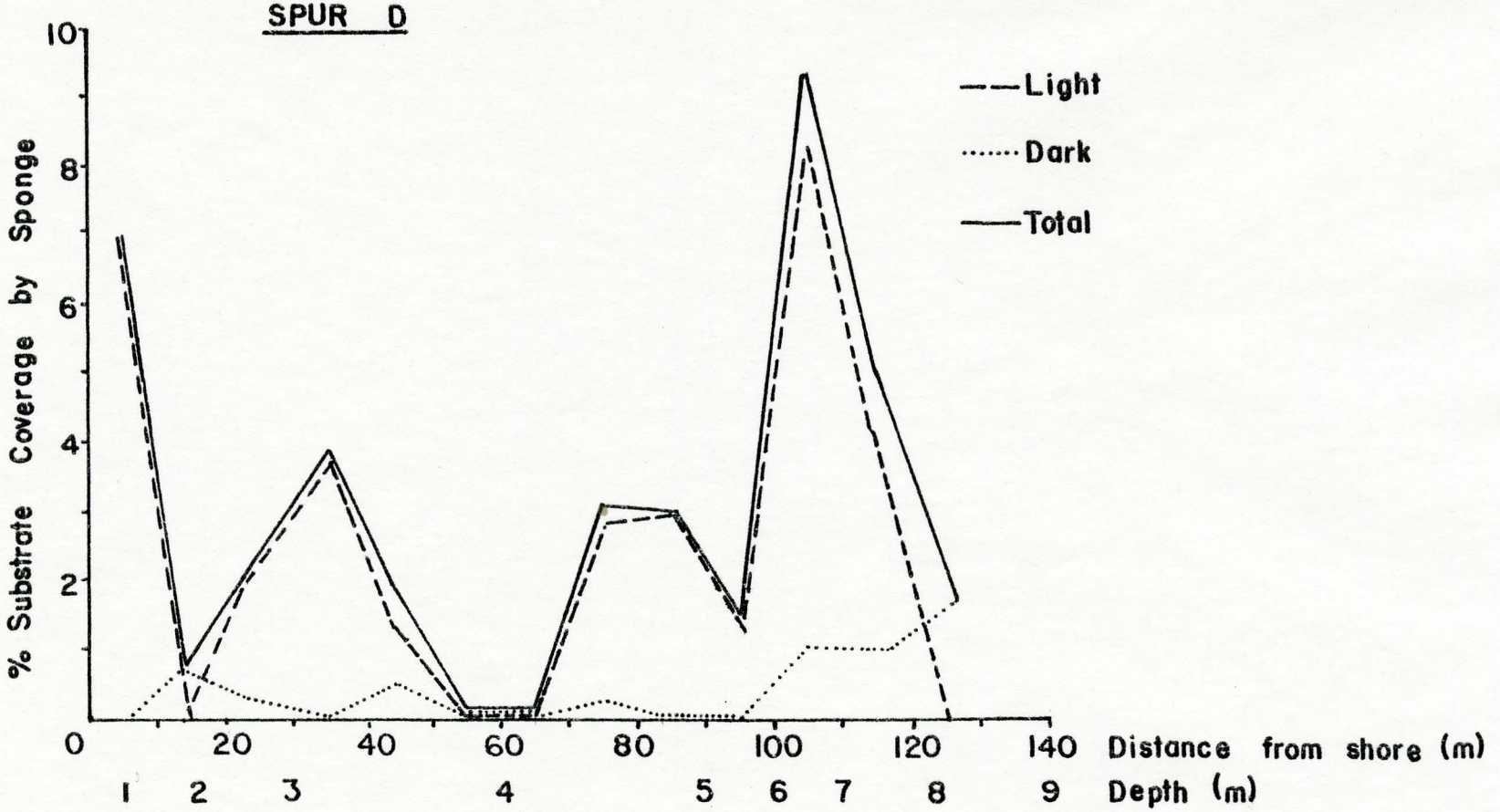
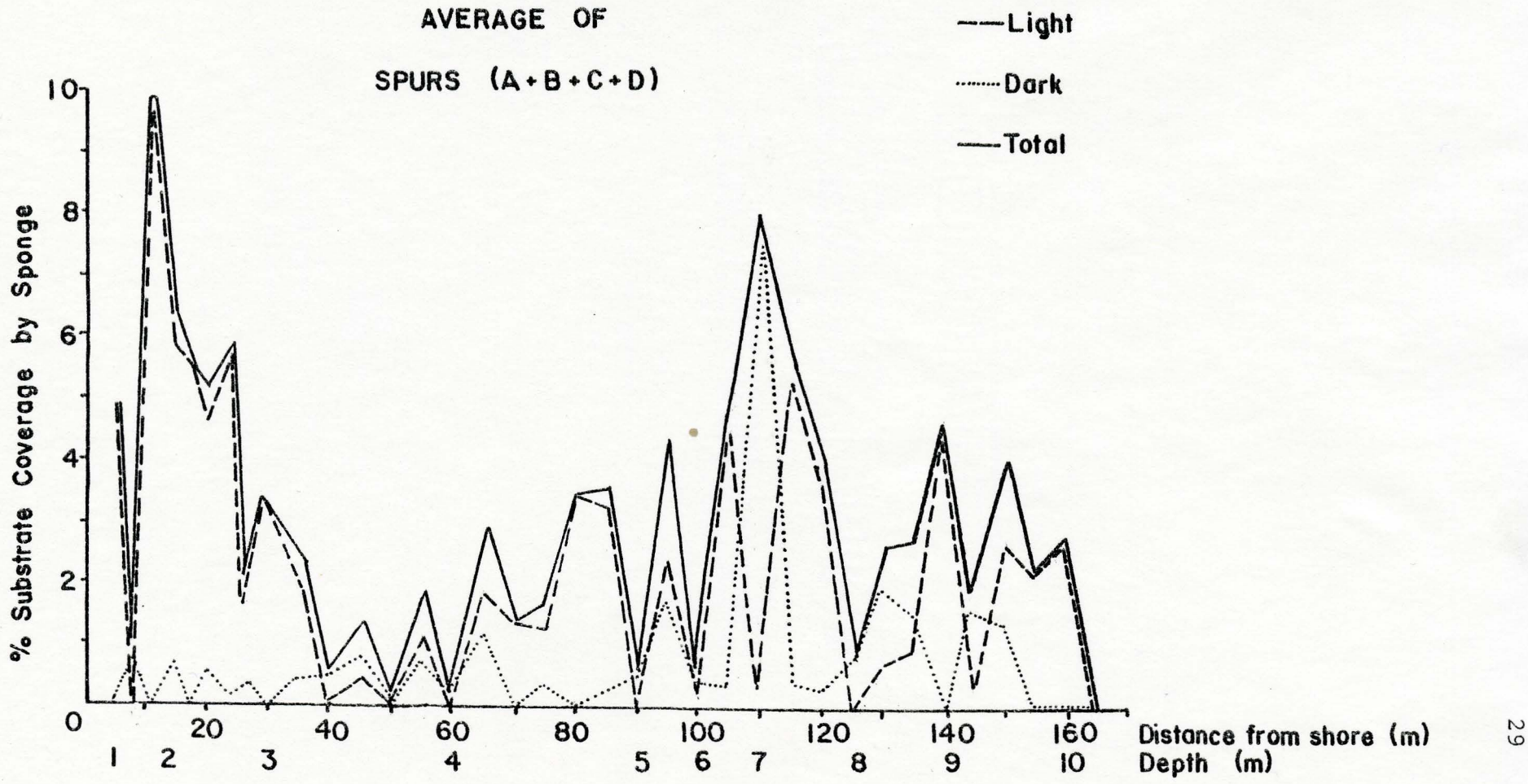

SPUR D
% Substrate Coverage by Sponge
10
8
6
4
2
0
Light
Dark
Total
20
40
60
80
100
120
140
Distance from shore (m)
1
2
3
4
5
6
7
8
9
Depth (m)

Fig. 2.6 Average of spurs (A+B+C+D): percentage substrate coverage by Cliona viridis as a function of distance from shore and depth.


AVERAGE OF
SPURS (A+B+C+D)
Light
Dark
Total
% Substrate Coverage by Sponge
0
2
4
6
8
10
0
20
40
60
80
100
120
140
160
Distance from shore (m)
1
2
3
4
5
6
7
8
9
10
Depth (m)

more often on the dead undersides of coral heads or the bases which would provide the largest area of dead substrate. In Grand Cayman, however, Cliona viridis seemed to more often inhabit the tops and sides of coral heads where the coral is alive. In these cases, Cliona often invades and kills the coral head. MacGeachy (1977) suggested that this is only possible if the live coral surface were previously damaged in some manner and that the sponge larvae settled on and invaded the spot before the coral could heal itself.

Upon first examination, the sponge seemed to occupy topographic highs and to grow downwards along the substrate. Where Cliona had invaded the hardground, however, it seemed to occupy a topographic low or depression. Hypothesizing substrate deflation as well as lateral expansion, these depressions could have been formed by the sponge. If there is a barrier of suitable material in the way of lateral expansion of the sponge, it may grow up the obstacle rather than around.

Most of the Cliona colonies were found on the edges of the spurs rather than on the flat, horizontal spur top. Very few occupied the vertical spur walls or the central axis of the groove.

2.4 Biotic Associates, Predators and Competitors

Various coral species were encountered on the spurs including Montastrea annularis, Montastrea cavernosa, Siderastrea siderea, Diploria labyrinthiformis, Dichoenia stokeski,

Agaricia agaricites, Acropora cerviconis and Acropora palmata. In addition, various polychaetes and holothurians were found at depths starting at 5 m. Gorgonians were first noted at 13 m and became more abundant with depth. The sand plain at 18 m out to the top of the wall at 24 m was littered with Halimeda flakes and other flocculent debris. Bryoza, arthropods and fish life were plentiful, molluscs were rare. Sponges were ubiquitous and grew to dimensions of 3-5 m on the wall.

Parrot fish were the only directly observable predators. They grazed the sponge, scraping off large quantities. Randall and Hartman (1968) suggest that the sponges may comprise over 95% of the food of some fish (ie.angelfish). Upon examination of stomach contents, they found Cliona in only one fish, and postulated that the defensive characters of the sponge - mineralized sclerites, noxious chemical substances and tough fibrous components - are highly effective in discouraging predation. Some Cliona colonies were dead but showed no evidence of predation. Perhaps disease also plays a role in population control.

Competition for suitable substrate between the sponges and other borers provides a control on the population. Hartman (1957) found that Cliona, once well rooted in the substrate, prevents any other borer from exploiting the same substrate, Goreau (1966) found the same exclusivity in his study of the encrusting sponge Mycale laevis. Hartman also found that the

various Cliona species inhabit different depth zones on the reefal complex. He found Cliona viridis to be the dominant species in the littoral terrace. If two species occupy the same depth zone then they will inhabit different substrates within that zone. Therefore, there is little interspecies competition. This may be an overgeneralization on Hartman's part as it was occasionally observed, on Grand Cayman, that two different species of Cliona, at the same depth, inhabited the same type of substrate although usually not the same coral head. There is also, of course, competition for food. Hartman proposes that the filter-feeding sponge, Cliona, feeds on unicellular algae, flagellates, bacteria and particles of detritus.

CHAPTER 3

BIOEROSION BY *CLIONA*

3.1 Bioerosion

3.1.1 Method of Bioerosion

The burrows which *Cliona* excavates and inhabits have variously been described as dendritic, dividing dichotomously and anastomosing to form a congeries of small galleries and tunnels through which communication is maintained with the external environment. Boring consists of establishing new galleries and enlarging old ones.

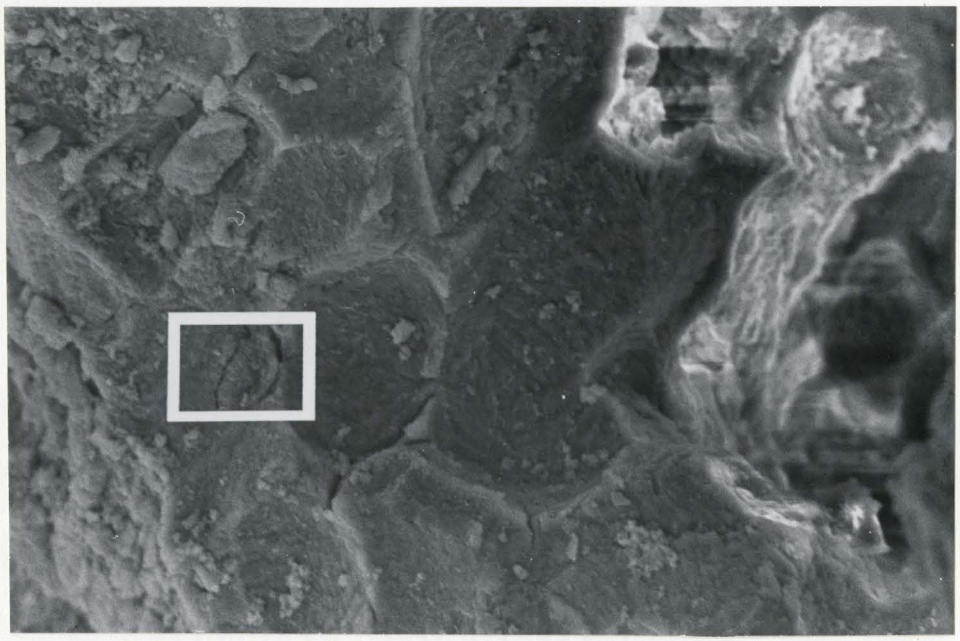
The boring mechanism has been intensively studied, however, many questions remain. Hancock (1867), suggested that the spicules grind away the substrate. He could not conceive of simple sponges performing chemical feats. Letellier (1894) found that the tissues of *Cliona* were not acidic and that the edges of the sponge chips were not corroded. This led him to believe that the sponge sets up torsions to break off bits of the substrate and that no acid was used. Nassanov (1883) found larval clionids actively boring before they had developed spicules. The presence of sponge chips suggested to him that the process involved a combination of chemical and physical erosion. Topsent (1887) postulated the presence of contractile cells, boring by purely physical means. This was

the only way of explaining the erosion of both carbonate and conchiolin substrates. Vossmaer (1933) resolved this problem by suggesting that Cliona uses both acid to dissolve the carbonate and enzymes to attack the conchiolin. Warburton (1958) proposed that the boring was done only by means of an acid, which formed the etchings he saw on the calcite substrate.

There have been various duplications and combinations of the above hypotheses presented in the literature. The most widely accepted method proposes the use of a special amoebocyte cell which releases an etching agent to erode the chip, then penetrates and enlarges the crevice and contracts around the chip to free it. The chip is removed via amoeboid transport and expelled with the exhalant water current (Hein and Risk, 1975). A partially removed chip is shown on Plate 3.1. Plate 3.2 shows an area heavily excavated by Cliona. The scalloped surface is produced by removal of the chips (Plate 3.3 and 3.4). The nature of the etching agent has not yet been determined, although Ruetzler (1975) suggests that it may be a carbonic anhydrase. Pomponi (1979) found acid phosphatase to be the agent. Cobb (1969) explains that the release of the etching agent is precisely regulated and that the dissolution is restricted to a narrow zone of contact between the cell edge and the substrate. It has been calculated that only 2-3% of the eroded substrate is removed in dissolved form (Ruetzler and Reiger, 1973). Excavation by purely physi-

Plate 3.1 A partially removed chip which has been etched but not yet removed. Scale box width = 12μ

Plate 3.2 Coral surface heavily excavated by *Cliona viridis*. The scalloped surface remains after removal of the chips. Scale bar = 100μ



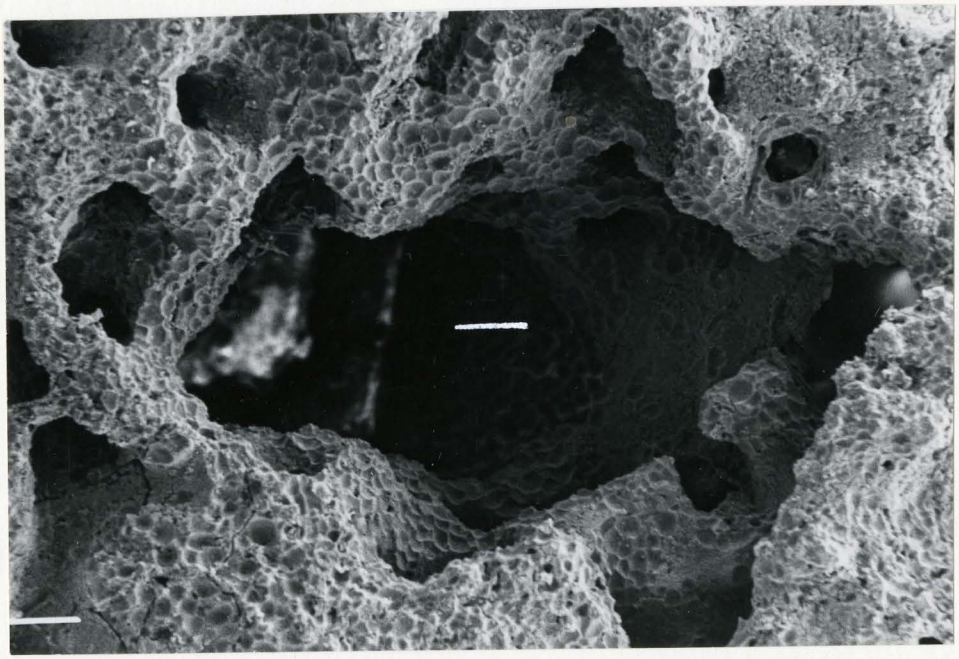
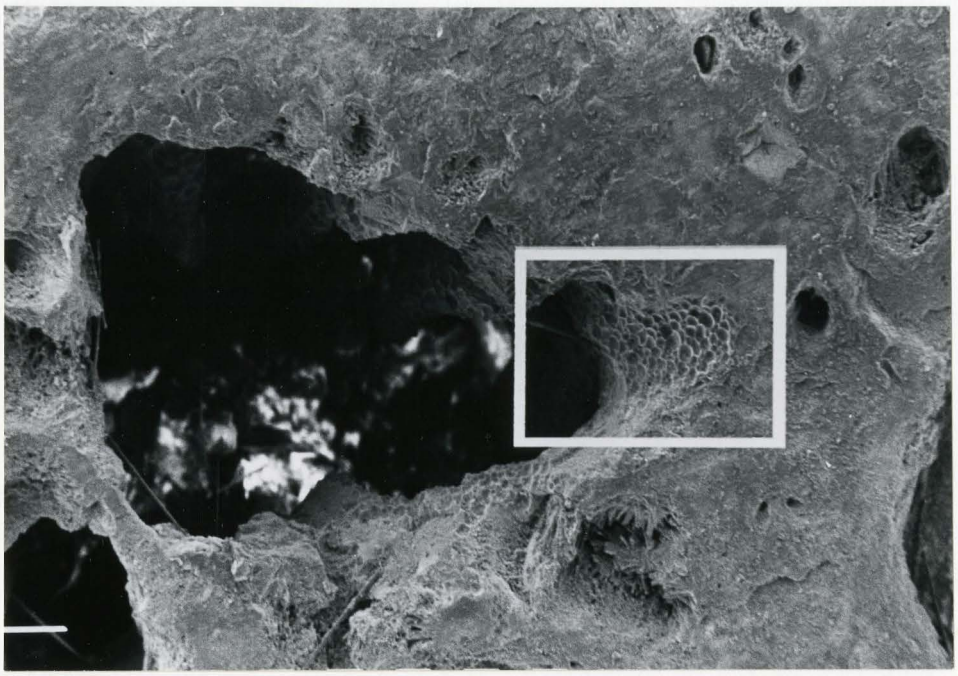
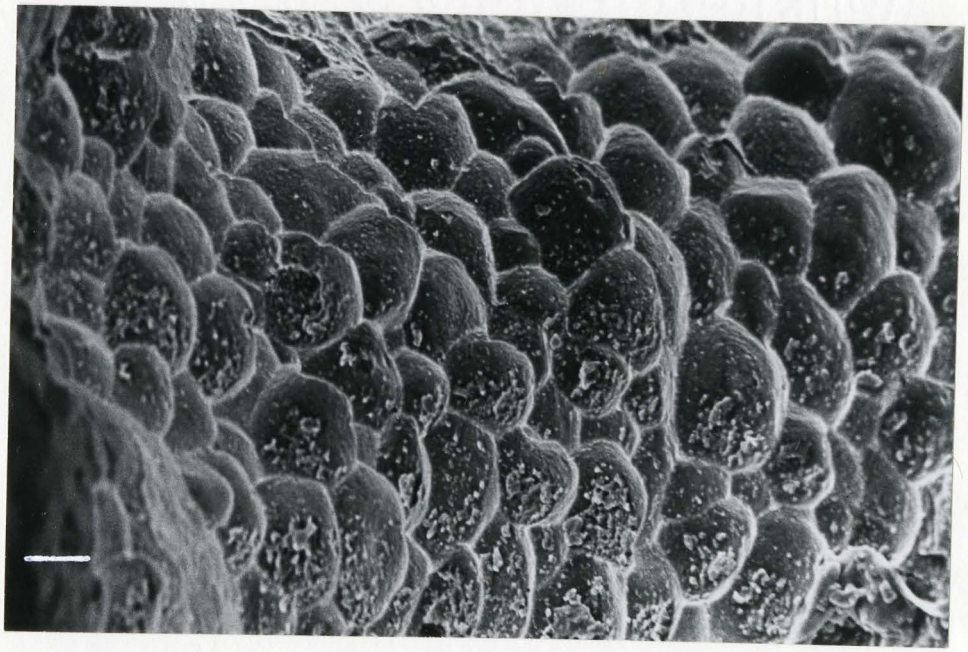


Plate 3.3 Excavated gallery with scalloped rim.
Scale box width = 660μ

Plate 3.4 Enlargement of Plate 3.3 showing scalloped rim.
Scale bar = 20μ





cal means would not produce the right morphology for the chip (Warbuton, 1958).

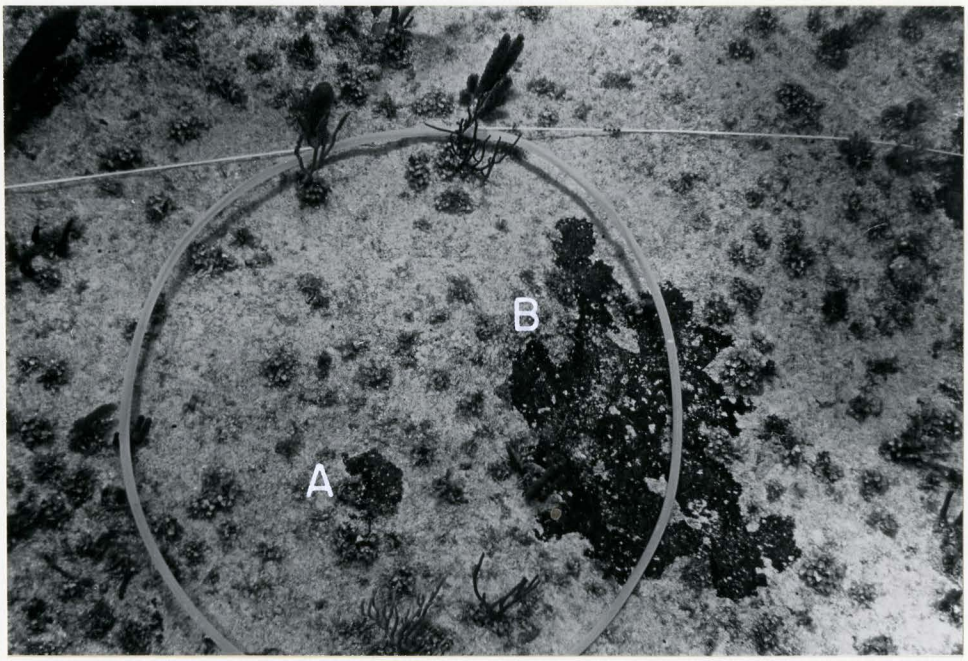
MacGeachy (1977) lists the factors which control the amount of boring. He includes the amount of suitable substrate, the coral growth rate, the sponge boring rate and the sponge biomass. He explains that the corals that calcify the quickest are the least dense and, therefore, the most easily and intensely bored. Highsmith (1981) and Bergman (1983) both found an increase in the amount of substrate removed with an increase in the density of the substrate. Highsmith explains that high density skeletons provide more protection. This correlation was not explored in this study.

3.1.2 Colony Form

The colonies of Cliona viridis found in Grand Cayman were commonly highly irregular to dendritic in shape, with sutured or scalloped boundaries. A few of the smaller colonies were oval to circular in shape. They usually grew up instead of around obstacles so there did not seem to be any topographic control on the shape of the colony. Quite often there were localized patches of several colonies growing adjacently. When these bordered on each other they were separated by a mucus rim.

Smaller colonies were generally subcircular, while the larger colonies tended to a highly dendritic form (Plate 3.5). It is possible that this strategy is analogous to the

Plate 3.5 Smaller circular form of colony (A) versus larger dendritic form (B). Quadrat from a different study of the same area.

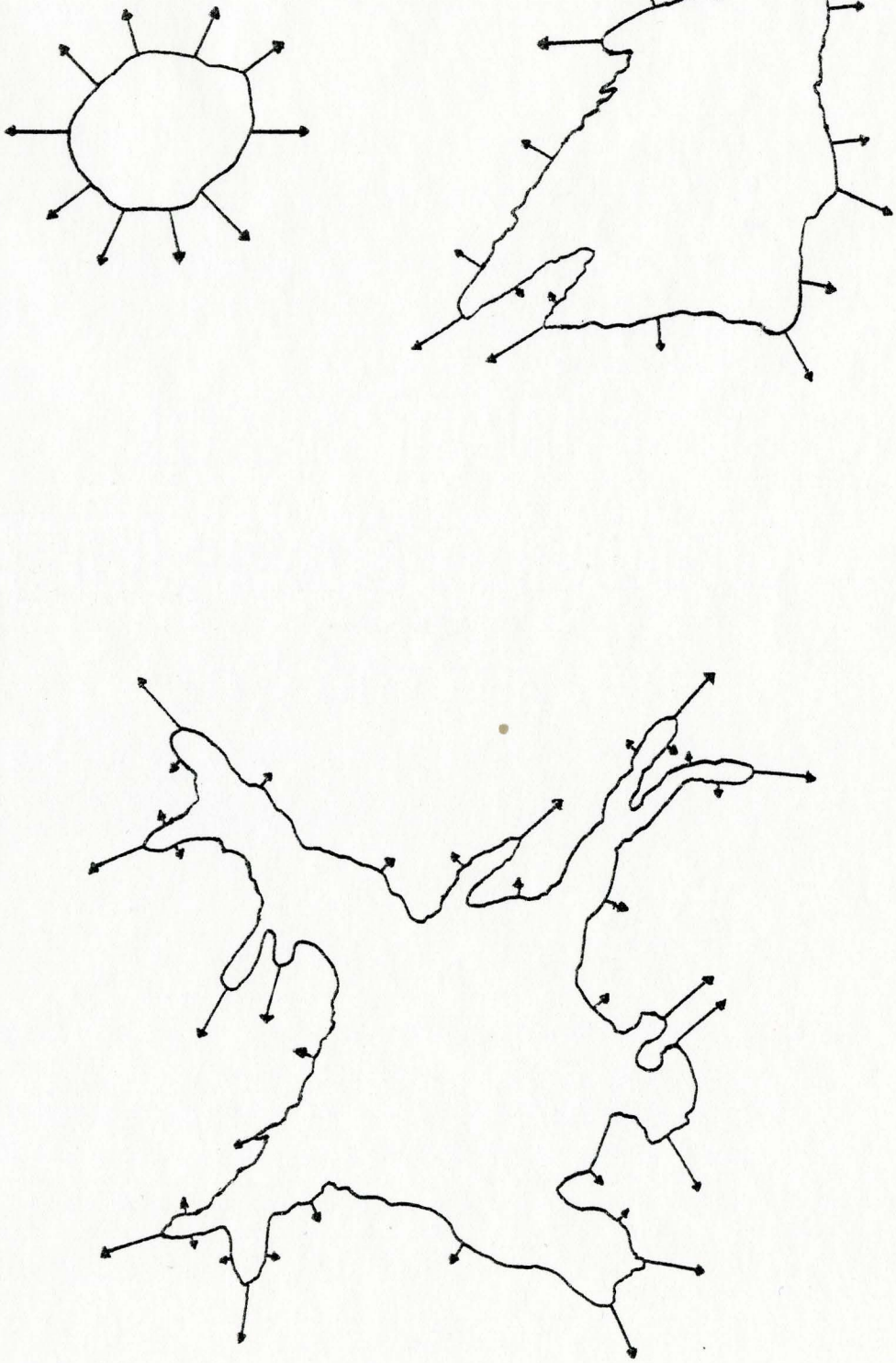

B
A

growth habit of the corals Montastrea and Acropora which grow protrusions and then later fill-in between the limbs (Dustan, 1975). If a circular form is maintained at a constant growth rate, the area of each growth increment contributes proportionally less to the total area of the sponge colony. Thus, the sponge cannot exploit the substrate as rapidly as if it took a dendritic form, in which case the length of the perimeter would be larger relative to the area of the sponge. An average crenulation factor of 2.75× was determined by measuring the perimeter of a section of a typical dendritic sponge colony, from a to-scale photograph, and comparing this to the perimeter of the same size section of a non-dendritic, subcircular colony. The large perimeter means an increase in the area of contact between the substrate and the periphery of the sponge which is where the most active exploitation takes place (Fig. 3.1).

This growth form might also be a defensive strategy. If one branch of the colony is attacked by predators or disease the rest of the colony may survive. A circular form, however, would propagate the disease more rapidly and would provide a larger target for predators.

Warburton (1958) suggested that the colonies spread by either growing across the boundary between the inhabited substrate and a bordering substrate, or by spawning and producing swimming larvae which may settle and infest new substrates.

Fig. 3.1 Schematic drawing of hypothetical phases in the growth of a colony from a small circular form to a larger dendritic form. The length of the arrows signify direction and relative rates of lateral expansion.



3.1.3 Direction of Expansion

In addition to lateral expansion, there may also be vertical deflation of the substrate. The substrate surface inhabited by the sponge, especially in live coral, was seen to be deflated below the uninfested adjacent substrate surface by up to 1 cm. This observation has not been cited in previous literature, possibly because it is a process unique to *C. viridis* and this study area. The 1 cm relief was often vertical but in some cases it was a gradual slope from uninfested coral down to the middle or oldest part of the colony to form a shallow bowl. If the deflation were to go deeper than 1 cm it would be a self-defeating process because the more recessed the sponge surface is, the more difficult it would be for the sponge chips to be carried away by currents. There is no convincing reason why the deflation occurs primarily on live substrates, except that perhaps it is more difficult for the sponge to expand laterally and compete with the live coral than to simply penetrate deeper into already inhabited substrate. Therefore, there is probably both lateral and vertical expansion involved although the maximum deflation observed was 1 cm. Even this observed 1 cm deflation represents a minimum for the bioerosion.

3.1.4 Growth Rate

As explained previously, the sponge growth rates were not available. In one case, however, a light colony was seen to be surrounding a 10 cm gorgonian and extending 5 cm past it. Since gorgonians grow at approximately 5 cm yr^{-1}, a lateral expansion rate of 2.5 cm yr^{-1} for the sponge might be feasible. Bergman (1983) found a 1 cm yr^{-1} growth rate for C. viridis in Australia.

3.1.5 Depth of Penetration

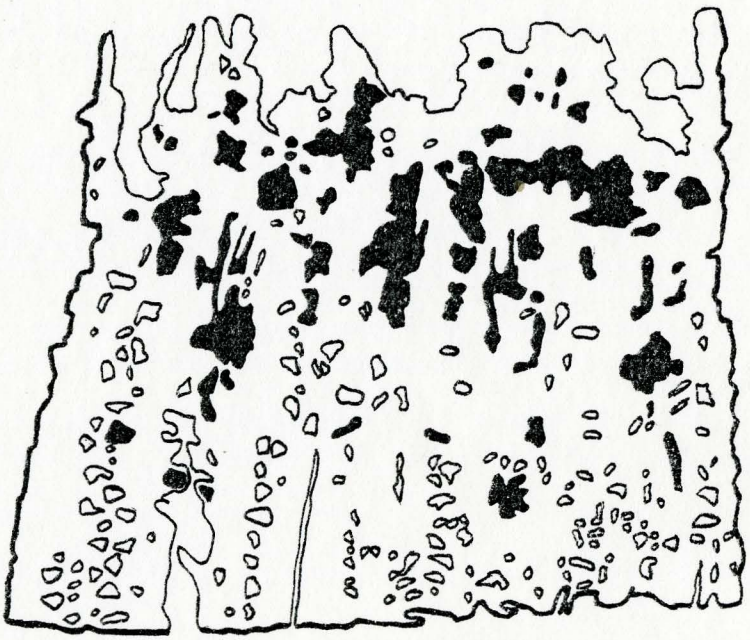
The depth of penetration into the substrate by Cliona viridis was highly variable, even within the same coral head, 0.41-1.37 cm (mean 8.7 cm , see Appendix). The majority of the boring takes place within the upper 0.6 cm and tapers off with depth into the substrate (Figs. 3.2 and 3.3 and Plate 3.6). Bergman (1983) found Cliona viridis boring to a mean depth of 1.3 cm on the Great Barrier Reef.

3.1.6 Gallery Morphology

The colonial sponges live within the galleries they excavate but will occupy available openings in the substrate before making new ones (Neumann,1966; see Plate 3.7 and Figs. 3.2 and 3.3). Individual galleries of Cliona veridis tend to be spherical to highly irregular, closely spaced and isolated with little tendency to coalesce and with very few connecting tunnels. The galleries were measured at 0.8 - 2.0 mm (mean

Fig. 3.2 Cross-section of bored portion of substrate. Solid black areas represent excavated galleries whereas outlined areas represent natural substrate porosity. Note relative decrease in excavation with depth into substrate. Ragged upper surface represents 100% removal.

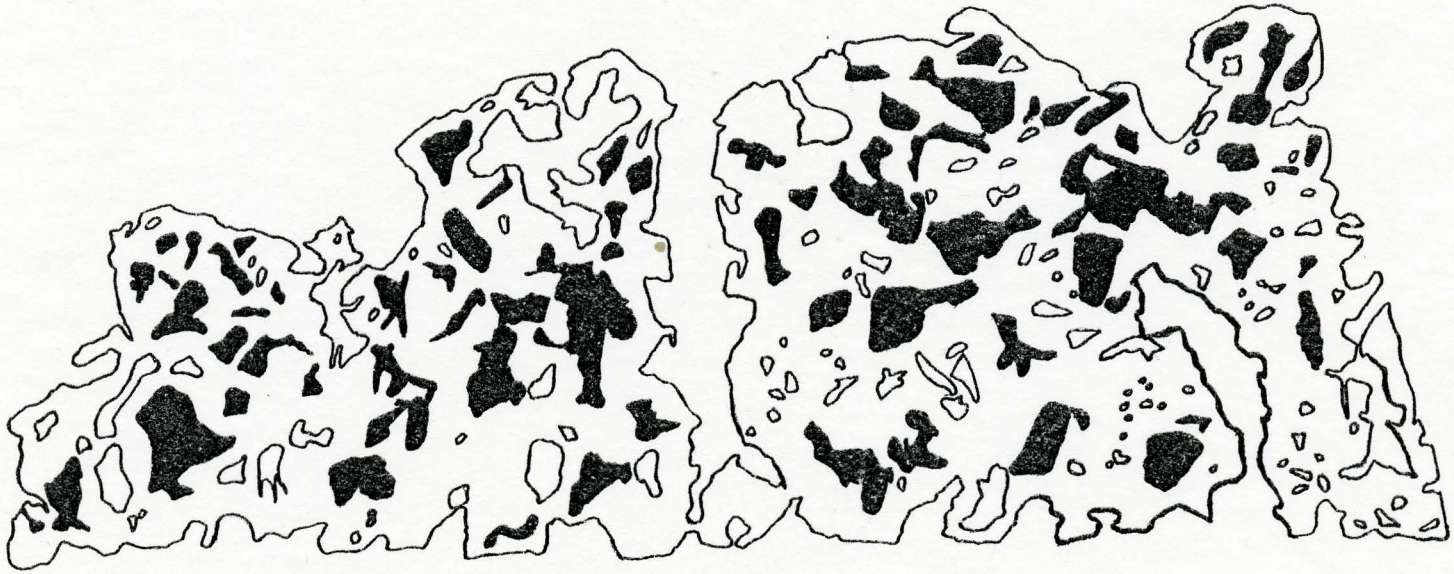
Sample no. 38



1 cm.

Fig. 3.3 Cross-section of bored portion of substrate. Note extensive removal of upper surface. Solid black areas represent excavated galleries whereas outlined areas represent natural substrate porosity.

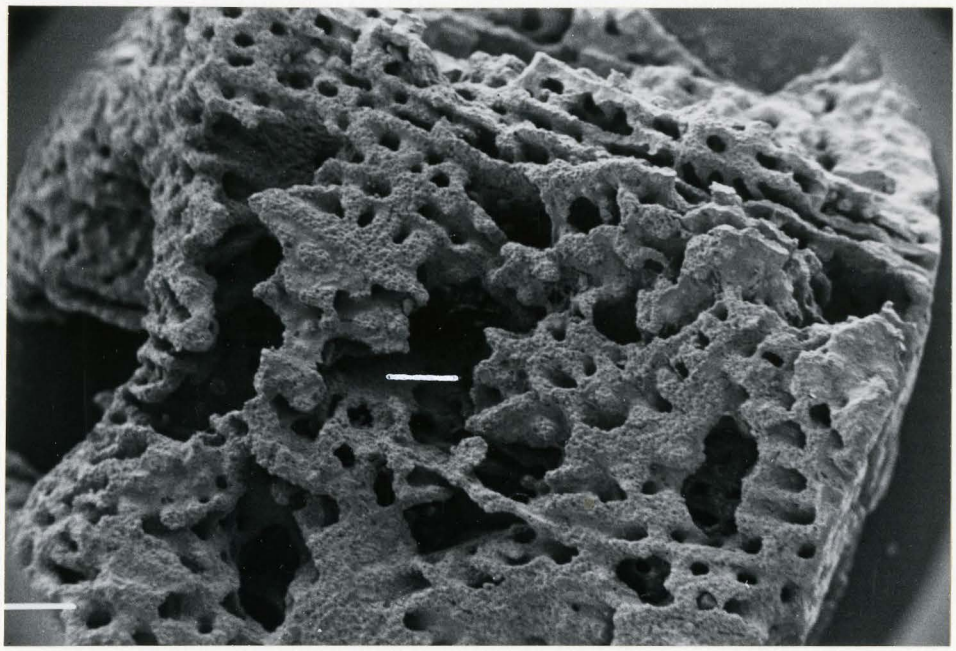
Sample no. 1



1 cm.

Plate 3.6 Cross-sectional view of substrate excavated by *Cliona viridis*.

Plate 3.7 Excavated coral surface showing gallery morphology and primary porosity.



1.4 mm) in diameter. Bergman (1983) estimated the galleries of C. viridis of Australia to be 2.00 mm in diameter on average. Hechtel (1965) in Jamaica, found the galleries of Cliona viridis var caribboea to be 1 - 3 mm in diameter.

3.1.7 Shedding Debris

Warburton (1958) described the chips expelled by the sponge as gleaming-white piles surrounding the oscula like a cone of volcanic debris. These cones were not seen in Grand Cayman possibly due to their removal by currents.

It is assumed that the sponge expels the chip with enough force to lift it above the sponge surface and into any existing current which would then sweep the chip away. In Grand Cayman, the currents are relatively strong and the sponge chips very small. Predators and other free-swimming biota may also brush the chips off the sponge surface. The shedding of sediment would only be a problem for the relatively small fraction of sponge colonies which grew on completely horizontal surfaces.

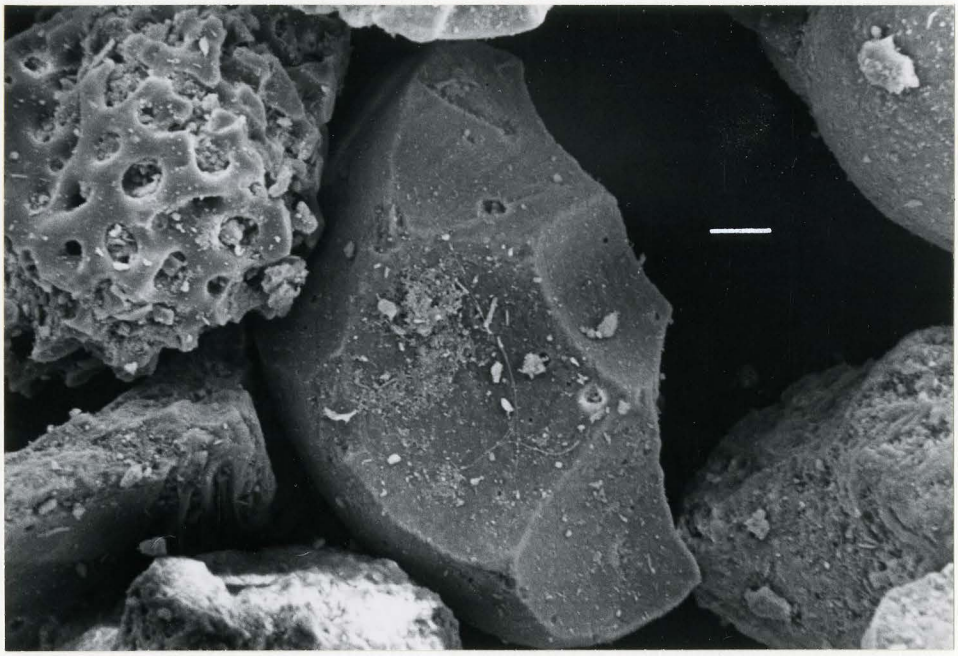
3.2 Morphology of Chips

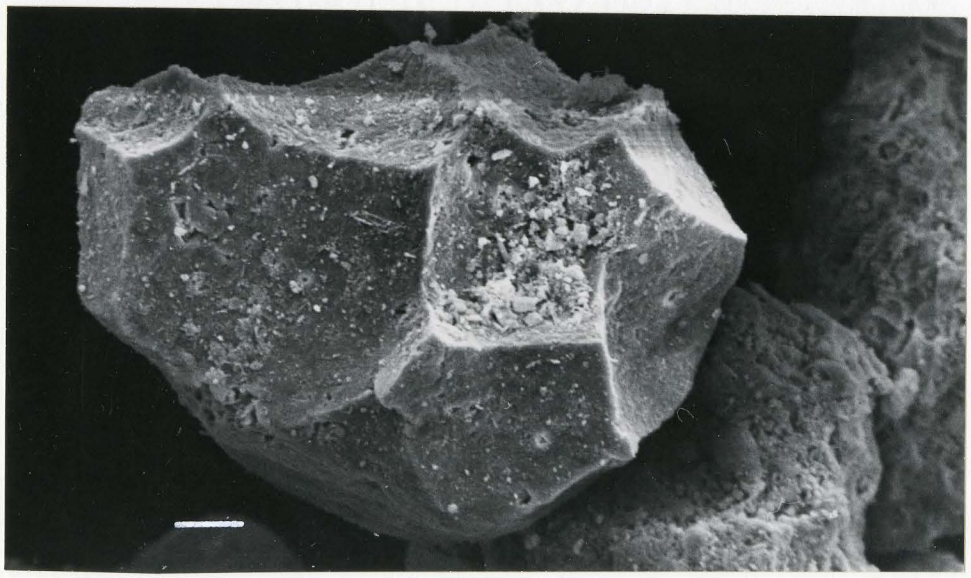
The chips produced by the sponge during excavation of the substrate are highly distinctive and easily identifiable by SEM if they have not been abraded or biogenically altered (Plates 3.8 and 3.9).

The chips are generally circular to ellipsoidal, although they can be highly irregular in shape. The chip surface

Plate 3.8 Sponge-produced chip. Note concave facets and sharp edges. Scale bar = 10μ

Plate 3.9 Sponge-produced chip. Scale bar = 10μ





is composed mostly of concave facets which are pits left by previously removed adjacent chips. One large face is usually convex and represents the portion of the chip that has been excavated from untouched substratum. The faces meet in sharp edges.

Cobb (1969) found that the chip morphology was independent of the type of substrate, although the size of the chip varied somewhat. Futterer (1974) claimed that the outline of the chip is identical regardless of the substrate from which it comes from. Thus, the shape of the chip tells nothing of its origins although ghost features on the surface of the chip may be relict from the original substrate.

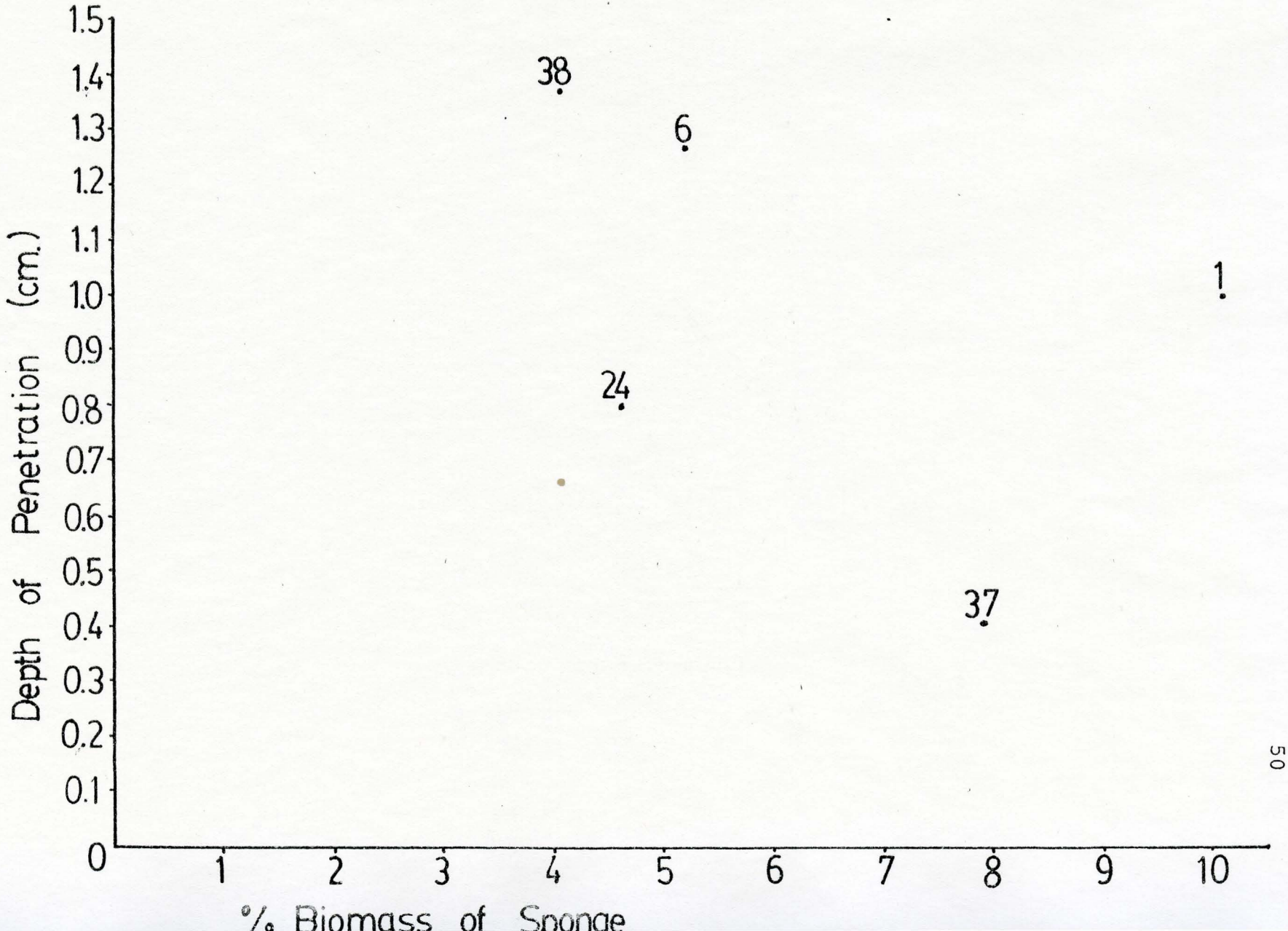
3.3 Sponge Biomass

To calculate the sponge biomass, five to eight cubes (approximately 1 cm^3 each) of the bored portion of the substrate plus sponge, were cut in a random pattern from each of five colonies. The weight difference before and after peroxiding gives the amount of sponge biomass.

The sponge biomass, calculated as a percentage of the bored portion of the substrate, did not show a significant correlation with the depth of penetration (Fig. 3.4) but was roughly correlative with the percentage of substrate removed.

The sponge biomass expressed as a percentage of the bored substrate was found to be 6.46±3.15. Bergman (1983)

Fig. 3.4 Depth of penetration of Cliona viridis versus the sponge biomass expressed as a percentage of the bored portion of the substrate.


Depth of Penetration (cm.)
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
38
6
1
24
37
1
2
3
4
5
6
7
8
9
10
% Biomass of Sponge

found the percentage biomass of C. viridis in Australia to be 9.84%±2.7.

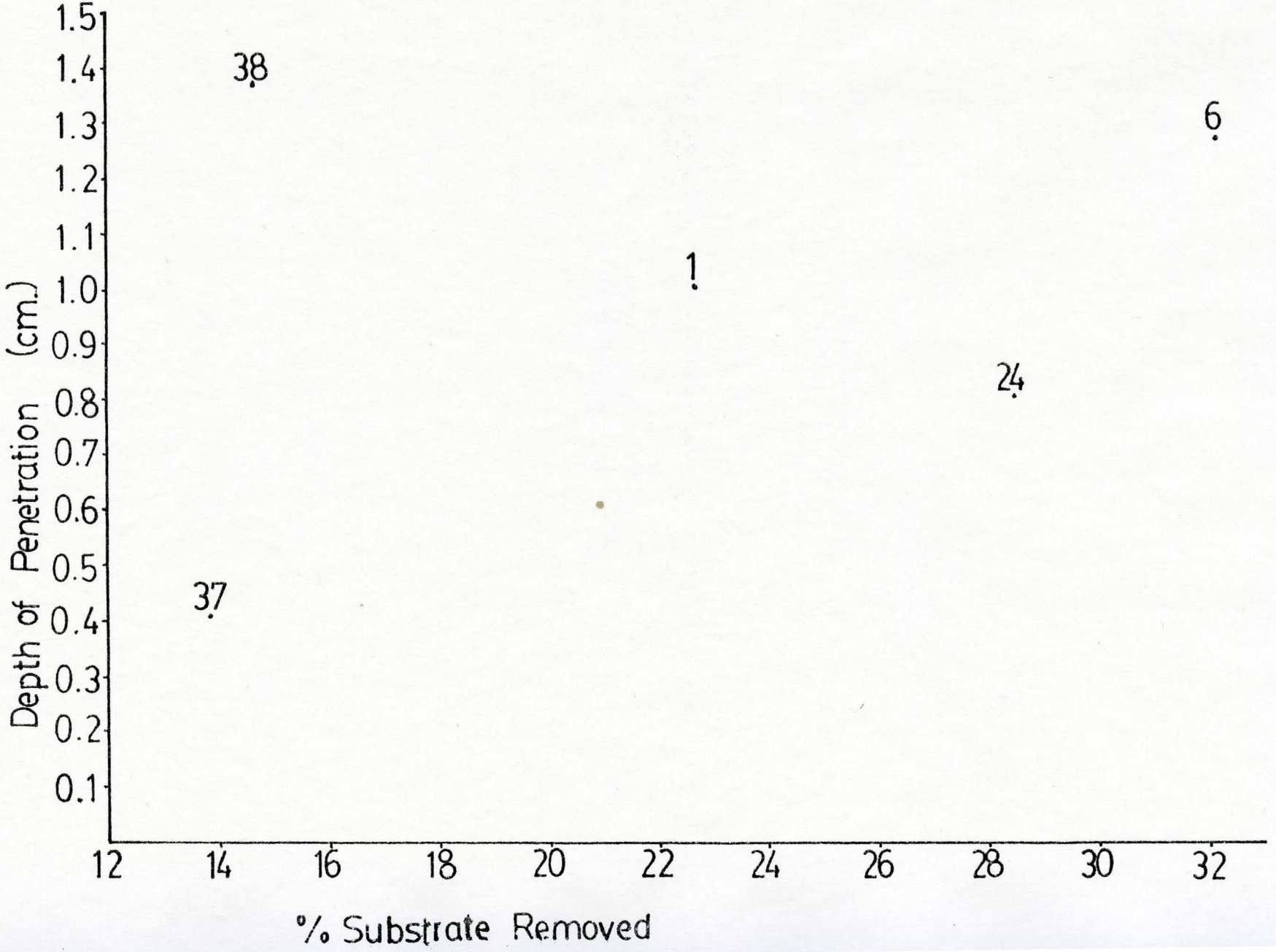
The lack of correlation between sponge biomass and depth of penetration is to be expected if some areas are heavily bored and then partially abandoned or left dormant as the sponge concentrates its energy dominantly on lateral expansion. The very rough trend that is evident shows a decreasing sponge biomass with increasing depth of penetration. This would support the idea that the sponge proportions more of its mass to areas of high activity, such as the perimeter of the colony, where the depth of boring has not yet reached its maximum.

3.4 Amount of Substrate Removed

To test for the amount of substrate removed, the speccific gravities of the bored cubes used in the biomass experiment were compared to the specific gravities of totally unbored cubes from the same substrate samples. Five cubes each of bored and unbored substrates were used from each of the five samples.

The amount of substrate removed varied from 13.9% to 32.2% (mean 22.4%) of the bored portion of the substrate. The variance did not seem to be a function of either substrate nor variety of Cliona viridis. The depth of penetration was plotted against the percentage of substrate removed (Fig. 3.5) but no significant trend was found. This is consistent with

Fig. 3.5 Depth of penetration by *Cliona viridis* versus the percentage of the substrate removed.


Depth of Penetration (cm.)
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
38
6
1
24
37
12
14
16
18
20
22
24
26
28
30
32
% Substrate Removed

the idea that even once the sponge has attained its maximum depth of penetration, it is still actively enlarging old galleries.

3.5 Sediment Production

If a lateral expansion rate of 1 cm yr^{-1} (Bergman, 1983) is assumed and the depth of penetration by the sponge, the colony perimeter length and the percentage of substrate coverage by the sponge are measured, then an absolute minimum sediment production rate can be determined.

The average density of the unbored substrate was calculated, in the biomass experiment, to be 1.7 g cm^{-3}. If the percentage substrate removal is 13.9% to 32.2% then 9.23 g cm^{-3} to 0.54 g cm^{-3} of the substrate is removed. Therefore, if the colony expands laterally by 1 cm yr^{-1} along the length of its perimeter, then it removes 0.23 g to 0.54 g for every 1 cm of perimeter.

An average of 5% substrate coverage was determined from the transect data (figs. 2.2 to 2.6). Drawings of typical colonies that represented 5% substrate coverage were taken from the field notes. The crenulation factor of 2.75× was applied to the lengths of the perimeters in order to obtain a more representative perimeter length (the field sketches of colonies were of necessity drawn without the elaborate crenulations). The amount of sediment produced was then calculated in two ways; as a function of the area of a sponge colony and as a function of the area of substrate.

The former method involved estimating the areas of the typical colonies and calculating the perimeters. Then the amount of sediment produced was expressed as a function of the area of sponge. In order to express the amount of sediment produced as a function of the area of substrate, several transects representing 5% sponge coverage were taken from the field notes. This usually involved two to three colonies. The perimeters of the colonies were measured and the crenulation factor applied. This length of perimeter was then expressed as a function of the transect area.

13.9% to 32.2% substrate removed gives 2.5 kg m^{-2} yr^{-1} ±1.5 to 5.8 kg m^{-2} yr^{-1} ±3.5 of sponge and 0.6 kg m^{-2} yr^{-1} ±0.3 to 1.4 kg m^{-2} yr^{-1} ±0.7 of substrate (n = 5). The data are summarized in Tables 3.1 and 3.2. Other authors have estimated rates of sediment production, expressed in terms of substrate area, for Cliona; Neumann (1966), 23 kg m^{-2} yr^{-1}; Ruetzler (1975), 7 kg m^{-2} yr^{-1}; Bergman (1983), 0.9 kg m^{-2} yr^{-1} (Cliona viridis in Australia).

From Multer's (1977) Holocene sea-level rise curves for the Florida Keys and the Bahamas, a rate of spur deflation can be calculated. If the average rate of substrate removal is 1 kg m^{-2} yr^{-1} (at 50% substrate coverage) and the average density of the unbored substrate is 1.7 g cm^{-3} then 600 cm^3 m^{-2} yr^{-1} is removed and the substrate deflation rate is approximately 0.6 mm yr^{-1}. Thus, in 2000 years, the spurs would deflate by 1.2 m if Cliona viridis was the only cause of reef

Table 3.1 Amount of Sediment Produced as a Function of Sponge Colony Size (at 5% substrate coverage)

Colony Perimeter (cm)	Colony Area (m^2)	Perimeter (cm m^{-2} sponge)	13.9% Removal (0.23g cm^{-1} parameter)	32.2% Removal (0.54 g cm^{-1} perimeter)
452	0.050	9040	2.1 kg m^{-2} yr^{-1}	4.9 kg m^{-2} yr^{-1}
325	0.065	5000	1.2 kg m^{-2} yr^{-1}	2.7 kg m^{-2} yr^{-1}
259	0.055	4709	1.1 kg m^{-2} yr^{-1}	2.5 kg m^{-2} yr^{-1}
270	0.020			
413	0.020	18127	4.2 kg m^{-2} yr^{-1}	9.8 kg m^{-2} yr^{-1}
314	0.015			
300	0.033			
281	0.012	17250	4.0 kg m^{-2} yr^{-1}	9.3 kg m^{-2} yr^{-1}
454	0.015			
			average = 2.5 kg m^{-2} yr^{-1} $\pm$1.5	5.8 kg m^{-2} yr^{-1} $\pm$3.5

Table 3.2 Amount of Sediment Produced as a Function of Substrate Area (at 5% substrate coverage)

Colony Perimeter (cm)	Substrate area (m^2)	Perimeter (cm m^{-2} substrate)	13.9% Removal (0.23g cm^{-1} perimeter)	32.2% Removal (0.54 g cm^{-1} perimeter)
452	0.20	2260	0.5 kg m^{-2} yr^{-1}	1.2 kg m^{-2} yr^{-1}
325	0.20	1625	0.4 kg m^{-2} yr^{-1}	0.9 kg m^{-2} yr^{-1}
259	0.25	1036	0.2 kg m^{-2} yr^{-1}	0.6 kg m^{-2} yr^{-1}
270, 413, 314	0.25	3988	0.9 kg m^{-2} yr^{-1}	2.2 kg m^{-2} yr^{-1}
300, 281, 454	0.25	4140	1.0 kg m^{-2} yr^{-1}	2.2 kg m^{-2} yr^{-1}
			average = 0.6 kg m^{-2} yr^{-1} $\pm$0.3	1.4 kg m^{-2} yr^{-1} $\pm$0.7

destruction and if a constant rate of substrate removal is assumed. This means that 2250 years ago the spur tops were 1.35 m higher than they are at present and the sea was 0.65 m lower than present (Multer, 1977). In other words, 2250 years ago the sea level was coincident with the shallowest parts of the spurs which now stand at least 2 m below sea-level. The spur-groove relief varies from 1 m to 3 m. It would take 2000 to 5000 years more to completely decimate the spurs if Cliona viridis provided the only mechanism for reef destruction.

The 30% of the substrate removed by the sponge has the result of greatly weakening the substrate making the substrate very susceptible to further removal by grazers, browsers and physical erosion. The sponge activities may therefore result in 100% substrate removal. To test the amount of substrate removed in this situation, the original level of the substrate would have to be established or the sponge plus substrate removed to a closed system.

A plot of sponge biomass versus percentage substrate removed (Fig. 3.6) gives a fairly good correlation. Table 3.3 summarizes the data found by Least Mean Square Analysis.

The two differing correlations exhibited by the plot may be coincidental; environmentally controlled. It is not a function of depth, substrate type nor variety of Cliona viridis.

Fig. 3.6 The amount of sponge biomass expressed as a percentage of the bored portion of the substrate as related to the percentage of substrate removed.

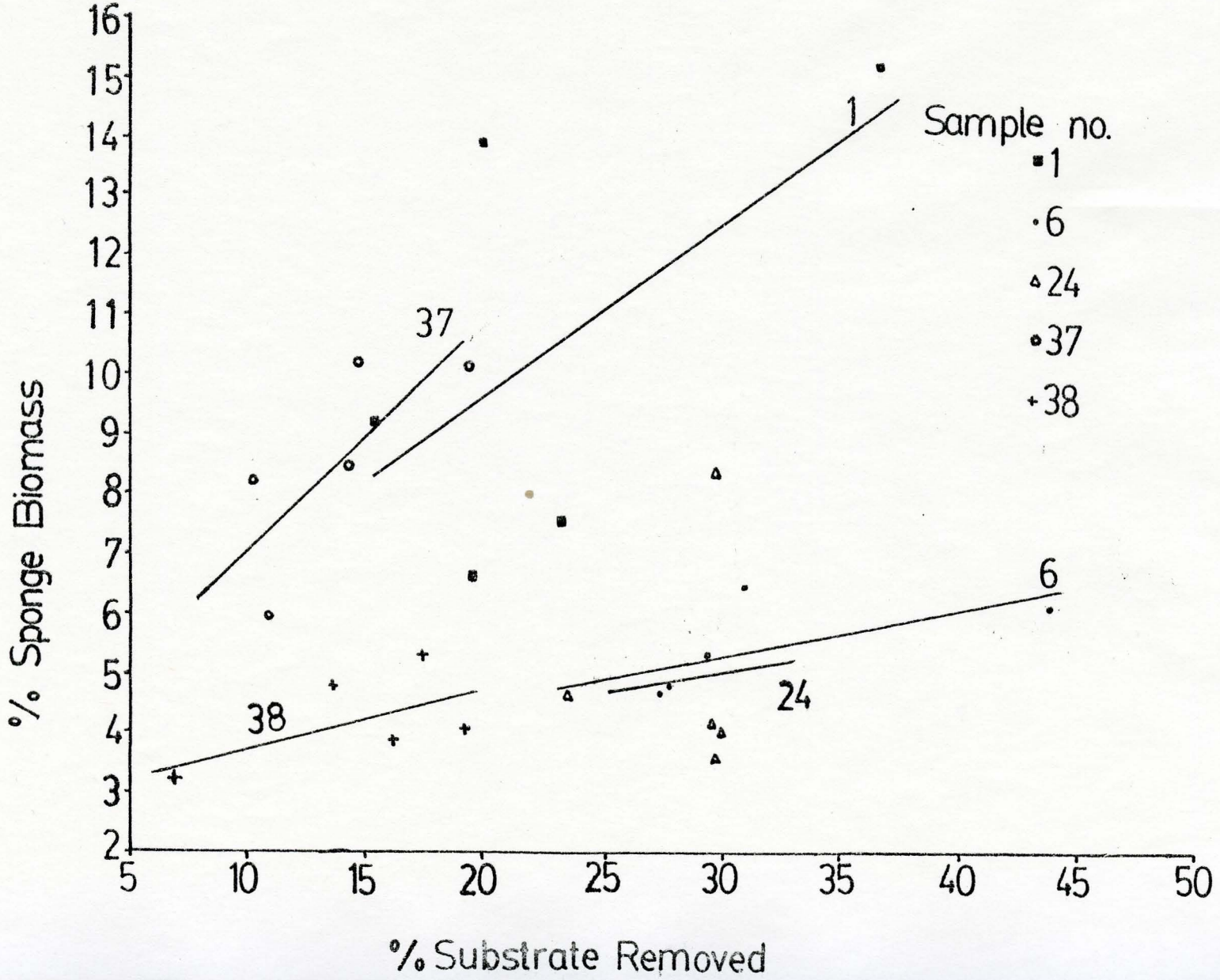

% Sponge Biomass
% Substrate Removed
Sample no.
1
6
24
37
38
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
5
10
15
20
25
30
35
40
45
50

Table 3.4 Data for Fig. 3.7

Sample No.	Correlation Coefficient	Linear Equation
1	0.62	y = .028×+3.91
6	0.60	y = 0.07×+3.26
24	0.08	y = 0.07×+2.98
37	0.77	y = 0.37×+3.51
38	0.57	y = 0.10×+2.80

*Data can be found in the appendix.

CHAPTER 4

SEDIMENTOLOGICAL DATA

4.1 Sediment Transport

Sediment produced by Cliona contributes significantly to the fine fraction of sediments within reefs.

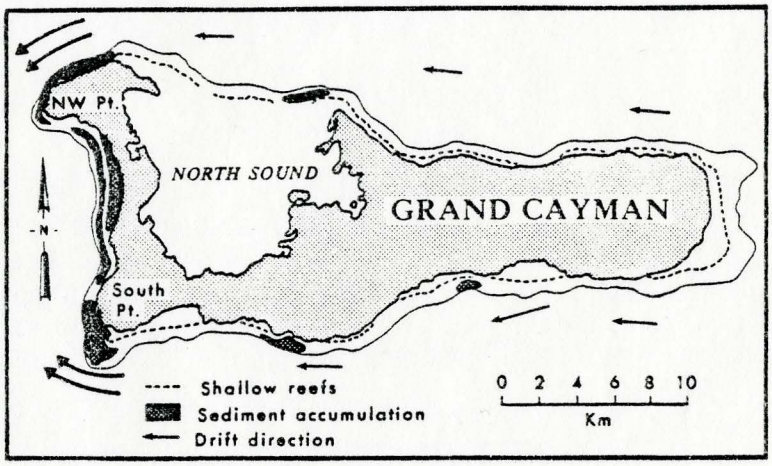
In Neumann's (1966) study area, there was very little wave energy present to transport in the fine-grained sediments so they must have been produced in situ, within the reefal structure. The opposite is likely true of the Grand Cayman study; wave energy may be high enough to sweep most of the sediments over the wall, into the basin.

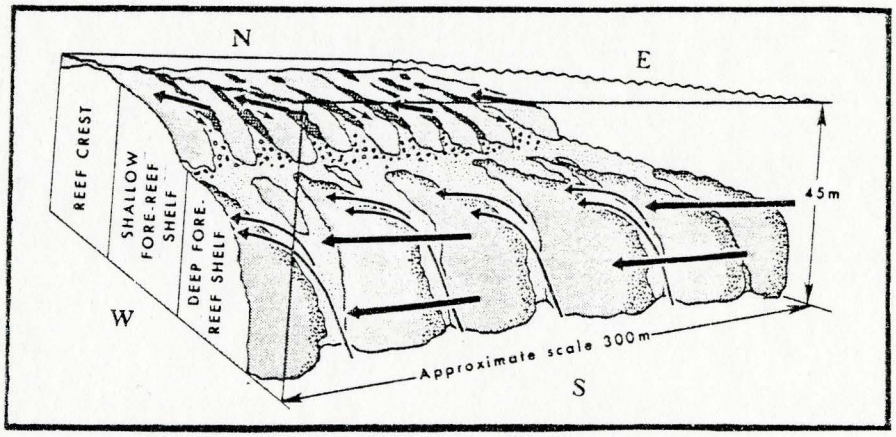
> "A general lack of clionid silt in the shallow zones of the reef indicated to the authors that clionid debris from the reef was being transported in suspension across the forereef and deposited by gravity settling at the top of the slope, or perhaps, transported into the deeper part of the basin by density currents." (Moore and Shedd, 1977).

Thick accumulations of coarse-grained sediment were found on the terrace at 18 - 20 m depth. However, there were no significant sediment accumulations within the spur and groove system. Roberts (1977) shows the current pattern around the island of Grand Cayman and the accumulation of sediment on the leeward (Western) side (Fig. 4.).

Fig. 4.1 Distribution of significant areas of sediment accumulation and shallow reef growth as related to a generalized current pattern around the island (Roberts, 1977).

Fig. 4.2 A schematic drawing of the Grand Cayman fore-reef shelf showing the strong shelf edge currents that are directed onshore through deep shelf-margin grooves. Shallow shelf currents are considerably weaker and somewhat more variable with regard to direction. The return current sweeps clean the grooves (Roberts, 1977).


NW Pt.
NORTH SOUND
GRAND CAYMAN
South Pt.
N
Shallow reefs
Sediment accumulation
Drift direction
0 2 4 6 8 10
Km


N
E
W
S
REEF CREST
SHALLOW FORE-REEF SHELF
DEEP FORE-REEF SHELF
45m
Approximate scale 300m

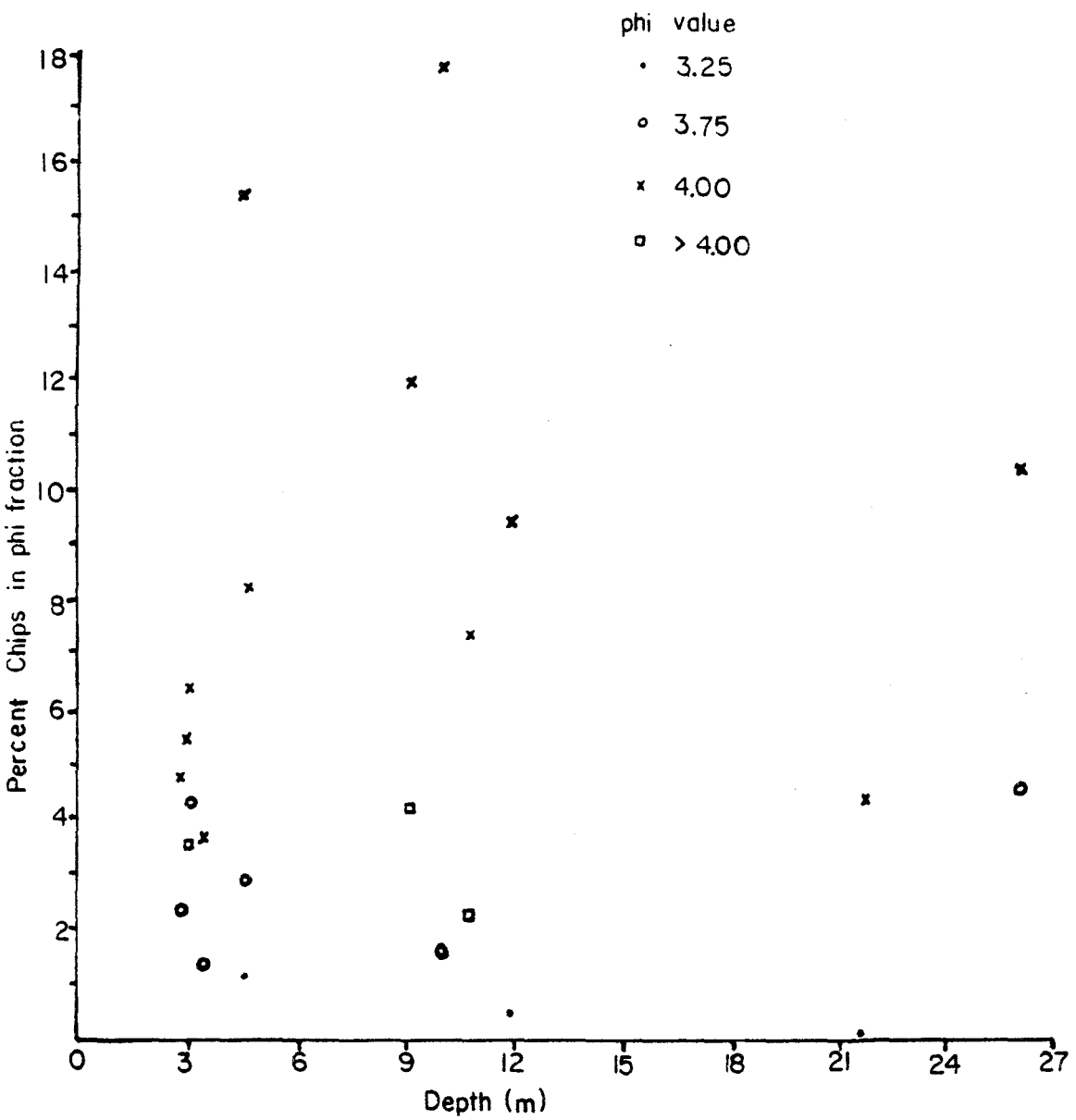
Roberts also shows that the general marine current pattern for the fore-reef areas of Grand Cayman has most return water transport moving from the reef crest seaward, downslope (Fig. 4.2). Thus, most clionid debris would be swept ultimately into the basin. The spur and groove system of the fore-reef would also be swept clean in the bi-annual periods of storm activity.

To test the direction of sediment movement, a layer of carborundum was placed on the floor of a groove in a measured square shape. At first Sergeant fish feasted on the carborundum but soon left it alone. When the patch was re-examined two days later, a lobe of the material had moved downslope approximately 25 cm. The surface of the carborundum was not pocked, therefore, it is unlikely that the fish moved it while feeding. Further evidence for the downslope movement was the ponding of sediment in the lee of boulders and in the downslope end of small valleys on the tops of spurs. It was only in these areas that sediment sampling was possible.

4.2 Percentage Clionid Chips in the Sediment

Twenty-eight samples in all were collected and twelve of these were point-counted for sponge chips (Fig. 4.3; Appendix G). The majority of the chips were found in the 4 phi fraction (62.5 - 74μ). There is a definite bimodality in the grain size distribution of different sediment samples but it

Fig. 4.3 The percentage of sponge chips found in each phi fraction as a function of depth (see Appendix G for data).


phi value
3.25
3.75
4.00
> 4.00
Percent Chips in phi fraction
Depth (m)
0
3
6
9
12
15
18
21
24
27
2
4
6
8
10
12
14
16
18

does not seem to be a function of depth. In the coarser grained samples the percent sponge chips in the sediment ranged from 0.0122% to 0.442%. For the finer grained sediments higher values of 0.250% - 1.250% were found.

These values represent a definite minimum in the actual percentage of sponge chips in the sediment. Many of the chips were seen to be riddled with holes presumed to be formed by boring algae. It was decided that most of the boring of the chips took place after their removal from the substrate. On the surface of the chip, the excavated tunnel began as a cone shaped hole, rapidly narrowing to a cylindrical tunnel just below the surface of the grain. If the burrowing had been executed while the chip was still deep within the substrate then the cone, which precedes the tunnel, would not be seen. This observation lead to the inference that algae are actively breaking down the chips thereby minimizing further the percentage of chips found in the sediment. Tudhope and Risk (1982) found that boring algae contributed significantly to the breakdown of sand size particles to very fine-grained particles.

Weakening of the substrate, by Cliona, leaves the skeleton more susceptible to destruction via physical abrasian and grazing. Thus, indirectly, Cliona contributes even further to the amount of bottom sediments.

On Fanning Island, in an area of very low sediment transport, Futterer (1974) found that 30% of the sediment was

composed of sponge chips. Ruetzler (1975) also found the distinct bimodality in grain size in his sediments. His highest count was 22% sponge chips although, in the mud sample (125-16μ) 41% of the sediment was sponge chips.

A relative estimate of the percent sponge chips in the surficial sediments, as supplied by the cores, was determined but no trend was found.

CHAPTER 5

RESULTS AND CONCLUSIONS

5.1 Discussion

Cliona viridis is represented by two varieties on the Grand Cayman reef. The light and dark varieties showed no evidence of competition for space and differed only in colour, oscula size and symbiosis with hydrozoa. The dark variety became relatively more abundant with depth. Transect data showed that the average substrate coverage was approximately 5% and this fraction tapered off with depth. Both varieties were almost exclusively found on the spurs although a small proportion of the dark colonies inhabited the margins of the grooves.

Cliona viridis bores by etching out chips from the substrate and then removes the chips via amoeboid transport. The chips are expelled with the exhalant currents and carried away by water currents.

The colonies were observed to adopt a dendritic form as they expanded. The reason for this shape change is unknown but it may be to maximize the colony perimeters, to more effectively exploit new substrate, and to provide a defence mechanism against predation and disease.

The sponge colonies expand laterally, overgrowing the substrate, at a rate of approximately 1 cm yr^{-1} (Bergman, 1983). They also deflate the substrate to an observed maximum of about 1 cm, with respect to the surrounding uninfested substrate. The sponge excavated and inhabited galleries to an average depth of 0.8 cm with progressively less material removed with depth into the substrate.

Individual chambers within the colonies averaged 1.4 mm in diameter and formed sub-circular to dendritic, semi-isolated, closely-spaced cavities with few connecting tunnels through which communication with the surface was maintained.

Many of the colonies were situated on sub-vertical to sub-horizontal substrates so that the excavated chips were shed from the sponge surface by gravity settling. In other cases, currents were responsible for chip removal.

C. viridis was found to rework at least 13.9% to 32.2% and possibly as high as 100% of the substrate as evidenced by the depression of the substrate where inhabited by the sponge. Sediment was produced at a rate of 1 kg m^{-2} yr^{-1} at 5% substrate coverage.

The very low percentage of the chips found in the sediments may be explained in several ways. Fore-reef currents, as explained by Roberts (1977), regularly sweep the grooves clean of sediments. The chips are very fine-grained and thus are easily transported over the wall, into the basin. Boring

algae and abrasion may be responsible for the physical degradation of the chips until they are unrecognizable as being sponge-produced.

Thus, the percentage of sponge chips found in the shallow sediments does not represent the amount of sediment produced by Cliona viridis. The coarser-grained samples were comprised of 0.0122% to 0.442% sponge chips while the finer-grained samples were composed of 0.250% to 1.250% sponge chips. The majority of the chips were found in the 62.5μ-74μ size range, where they made up 3.74%-17.72% of the silt fraction.

5.2 Application to the Geological Record

Bioerosion by Cliona spans from the Silurian until present (Kobluk, 1981). Cliona is responsible for a significant portion of the porosity and permeability now found in ancient carbonate deposits. Their importance as potential reservoir or aquifer engineers is evident.

The characteristic chips are often identifiable in ancient deposits and, thus, are good as fossils for ecological and paleoecological significance. Kobluk (1981) found sponge chips in lower Cambrian cavities in carbonate deposits. Although he cannot directly attribute these to Cliona, he speculates that the bioerosion by endolithic sponges has contributed significantly to sediment production in the reef interior as far back as the lower Cambrian.

At a constant sediment production rate of 1 kg m^{-2} yr^{-1}, a very large volume of sediment would have been contributed by C. viridis to the geologic column since the Silurian.

Scleractinians first appeared in the Triassic. If molluscs and carbonate rocks provided the only abundant suitable substrates for Cliona to bore in pre-Triassic times, then there may have been a distinct increase in the amount of fine-grained carbonate sediments beginning in the Triassic with the addition of Scleractinians as substrates. This assumes that the amount of available substrate is the most important control on the sponge population.

5.3 Sources of Error

Several assumptions were made that may add an increment of error. The growth rate of the Grand Cayman Cliona viridis was assumed to approximate the growth rate found by Bergman (1983) for Cliona viridis in Australia. It was also assumed that the rate of bioerosion is constant with time, depth and maturity of the sponge colony. The growth rate was assumed to be constant around the length of the perimeter.

Sediment trapped in or by the sponge, that was not removed during washing of the sample, was included in the weight of the sponge plus coral cubes. Peroxiding to remove the sponge biomass released much of the sediment at the same time. Therefore, the sponge biomass calculations took into account trapped sediment also. This was particularly true of sample no. 1 which

contained a relatively large amount of trapped sediment.

The use of paraffin to seal the cubes and displace air, in order to calculate the amount of water displaced by the cubes, may have introduced error. The specific gravity of paraffin is slightly less than that of water. This may have caused the cubes to be slightly buoyant, thereby decreasing their weight in water and, ultimately, their specific gravity.

The difficulty in recognizing the sponge-produced chips under the Scanning Electron Microscope induced a significant underestimate of the percentage of sponge chips in the sediment. The chips were totally indistinguishable under reflected light or transmitted light.

The majority of the infested substrate samples obtained were Montastrea annularis and cemented coral rubble. This was due both to the relative abundance of these substrates and to the possibility of obtaining comparatively good samples. This sampling bias may have, in turn, prejudiced the results.

5.4 Suggested Further Studies

Growth rates of Cliona viridis colonies of Grand Cayman would add to this study. A detailed study of the growth rates at different points around the perimeter relative to the dendritic form would permit more precise estimates of the rate of sediment production and of deflation of the spurs.

Also important are the growth and infestation strategies of the sponge. If the sponge deflates the coral surface rather than just removing enough of the substrate to create a habitat, then the rate of sediment production and spur deflation is substantially increased. Measurements of substrate deflation with time must be estimated.

Sediment traps strategically placed at different depths, just above the sediment surface, and at the top of the wall may provide a better indication of the percentage of chips in the sediments as well as the degree of transport of chips into the basin.

APPENDICES

APPENDIX A

SUBSTRATE AND SPONGE SAMPLE DISTRIBUTION

Substrate Sample Number	Substrate Type	Sponge Variety	Depth (m)
1	*Siderastrea siderea*	Dark	15.0
6	*Montastrea annularis*	Light	?
7	*Dichocoenia stokesi*	Light	2.2
12	Cemented Rubble	Light	2.3
13	*Montastrea annularis*	Dark	?
14	Hardground	Light	3.3
15	Hardground	Light	4.6
16	Cemented Rubble	Light	3.0
22	*Siderastrea siderea*	Dark	3.3
24	Coral Rubble	Light	5.3
26	*Montastrea annularis*-dead	Dark	2.0
27	*Siderastrea siderea*	Light	5.0
29	Coral Rubble	Dark	2.0
30	Coral Rubble	Light	2.0
31	*Montastrea cavernosa*-dead	Dark	26.6
33	*Siderastrea siderea*-dead	Dark	21.6
35	Cemented Rubble	Light	10.0
37	*Montastrea annularis*-dead	Dark	9.3
38	*Montastrea annularis*-dead	Dark	16.6
39	*Montastrea annularis*-dead	Dark	11.3

APPENDIX B

SEDIMENT SAMPLE AND CORE DISTRIBUTION

a) Sediment Sample Distribution

Sample Number	Depth (m)
1	10.0
2	5.0
4	3.6
6	3.0
7	3.0
8	5.0
10	11.0
12	13.0
14	19.3
15	3.3
18	10.0
19	11.6
21	4.6
23	28.3
25	23.6

b) Core Distribution

Core Sample Number	Depth (m)
1	3.0
2	4.0
4	17.3
5	20.3

APPENDIX C

PERCENT SUBSTRATE COVERED BY CLIONA - FROM TRANSECTS

Distance from Shore (m)	Depth (m)	Transect A Light %	A Dark %	B Light %	B Dark %	C Light %	C Dark %	D Light %	D Dark %
5	1	3.5	0					7.0	0.0
8	1.5	0.0	0.8						
11	1.8	9.7	0.03						
14	2.0	5.1	0.8	6.7	0.0			0.0	0.6
17	2.3	5.5	0.0						
20	2.4	9.2	1.0	0.0	0.0				
23	2.6	11.9	0.0			3.1	0.0	1.8	0.3
26	2.8	3.4	0.0	0.0	0.5				
29	3.0	4.5	0.0	0.0	0.0				
35	3.2	0.4	0.8	3.0	0.0	0.2	0.9	3.7	0.0
40	3.4	0.0	0.5	0.0	0.0				
45	3.6	0.0	0.6	0.0	0.5	0.8	1.8	1.3	0.4
50	3.8	0.0	0.0	0.0	0.0				
55	4.0	0.0	0.0	4.3	0.9	0.0	2.0	0.0	0.0
60	4.0	0.0	0.0	0.0	0.3				
65	4.0	4.4	4.5	3.3	0.0	0.0	0.0	0.0	0.0
70	4.0	2.5	0.0	0.3	0.0				
75	4.5	0.0	0.9	0.0	0.0	0.0	0.0	2.8	0.2
80	4.5	4.4	0.0	2.3	0.0				
85	4.5	0.9	0.0	9.4	0.0	0.0	0.6	2.9	0.0
90	5.0	0.0	0.0	0.0	1.0				
95	5.5	2.7	0.7	5.7	6.3	0.0	0.0	1.3	0.0
100	6.0	0.3	0.6	0.0	0.0				
105	6.5	2.2	0	4.6	0.0	3.1	0.0	8.3	1.0
110	7.0	0.7	0	0.0	15.1				
115	7.5	1.6	0	0.0	0.4	5.0	0.0	3.9	1.0
120	8.0	2.6	0	4.6	0.6				
125	8.0	0	0	0.2	0.7			0.0	1.7
130	8.5	1.3	0	0.0	3.5				
135	9	2.0	3.1	0.0	0.0				
140	9	2.7	0	6.6	0.0				
145	9	0.4	1.6						
150	9	2.7	1.3						
155	10	1.8	0						
160	10	2.7	0						
165	10	0	0						

APPENDIX D

DEPTH OF PENETRATION

Substrate Sample No.	mean (cm)
1	1.01±0.50
6	1.27±0.48
7	0.66±0.16
13	0.41±0.16
14	0.45±0.20
16	1.25±0.36
24	0.80±0.21
27	0.70±0.09
29	0.73±0.27
30	0.50±0.11
37	0.41±0.22
38	1.37±0.25
39	0.62±0.24

APPENDIX E

PERCENTAGE BIOMASS OF SPONGE IN CORAL

Sample No.	Biomass %	Sample No.	Biomass %
1A	15.041	6D	5.363
1B	7.484	6G	6.446
1C	6.449	6H	4.745
1E	9.221	6I	4.650
1H	13.857	6J	6.064
1AA*	12.693	6AA	3.965
1BB	8.681	mean	5.206±0.934
1CC	14.013		
1DD	4.147		
mean	10.182±3.849**	37A	8.448
		37B	10.138
		37C	6.021
24AA	4.941	37D	6.815
24BB	3.904	37E	8.151
24CC	3.749	37F	10.190
24DD	4.934	37AA	5.863
24EE	4.048	37BB	7.669
24F	4.151	mean	7.912±1.670
24G	4.057		
24H	3.552		
24I	4.665	38A	3.228
24J	8.469	38B	4.745
mean	4.646±1.425	38C	4.070
		38E	5.285
		38J	3.857
		38AA	2.735
		38BB	3.448
		38CC	5.112
		mean	4.060±0.921

*Double-lettered samples are extra and were not correlated with percent substrate removed.

**High variance due to large amount of incorporated sediments that were washed out during peroxiding of sample no. 1.

APPENDIX F

PERCENTAGE SUBSTRATE REMOVED

Sample No.	% Substrate Removed	Sample No.	% Substrate Removed
1A	36.69	6D	29.48
1B	23.16	6G	31.02
1C	18.64	6H	29.11
1E	15.02	6I	27.38
1H	19.86	6J	43.88
mean	22.67±7.47	mean	32.17±5.97
24F	29.69	37A	14.29
24G	29.36	37B	19.44
24H	29.75	37E	10.18
24I	23.60	37F	14.74
24J	29.81	37G	10.63
mean	28.44±2.43	mean	13.86±3.35
38A	6.86		
B	13.78		
C	19.19		
E	17.31		
J	16.05		
mean	14.64±4.27		

APPENDIX G

PERCENTAGE CLIONA CHIPS IN EACH SAMPLE

Sample #	Depth (m)	3.25		3.75		4.00		Sitt		Total seds. % chips
		% chips	% ϕ of total seds	% chips	% ϕ of total seds.	% chips	% ϕ of total seds.	% chips	% ϕ of total seds	
6	3.0			2.39	0.22	4.82	0.04			0.007
7	3.3			4.35	0.41	5.48	0.10			0.024
15	3.3					6.42	4.16	3.70	18.24	0.950
4	3.6			1.40	0.35	3.74	0.11			0.009
8	5.0	1.14	30.29			15.39	0.60			0.442
2	5.0			2.99	0.56	8.24	0.04			0.021
18	10.0					11.97	7.20	4.26	9.21	1.250
10	11.0			1.36	0.13	17.72	0.12			0.250
19	11.6					7.32	3.30	2.31	11.51	0.506
12	13.0	0.45	2.88			9.41	0.23			0.034
25	23.6	0.17	2.50			4.38	0.18			0.012
23	28.3			4.56	3.13	10.38	6.40			0.80

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