DISTRIBUTION AND ECOLOGICAL SIGNIFICANCE OF *CLIONA VIRIDIS*
THE DISTRIBUTION AND ECOLOGICAL SIGNIFICANCE
OF THE BORING SPONGE CLIONA VIRIDIS
ON THE GREAT BARRIER REEF, AUSTRALIA

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TITLE: The Distribution and Ecological Significance of the Boring Sponge Cliona viridis on the Great Barrier Reef, Australia.  

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ABSTRACT

Production of fine sediments in reef environments is a poorly understood but probably significant process. On the Great Barrier Reef, *Cliona viridis* is locally abundant. The sponge has been found from Lizard Island in the north, down to the southern part of the Central Region, and it is likely even more widespread. Although on individual reefs the sponge may occur almost anywhere, it is most abundant on lagoon patch reefs ("bommies" in Australian), where it overgrows the substrate and bores to a constant depth of about 1.3 cm.

Sponge infestation reaches a maximum at a depth of 4 m, covering almost 8% of the vertical sides of bommies. It is frequently the dominant benthic organism. Serial underwater photography demonstrates that colonies can expand laterally at a rate of about 1 cm yr\(^{-1}\) removing approximately 40% of the substrate. This species is a major producer of fine sediment on the Great Barrier Reef.
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1.1 Bioerosion

"Bioerosion" was first proposed by Neumann (1966), to describe the removal of consolidated mineral or lithic substrates by organisms, causing a weakening of the matrix and subsequent dissolution of the skeleton of living organisms (e.g., corals, bivalves), or hard substrates (e.g., cemented reef framework, limestones). Bioerosion is a widespread phenomenon involving many different phyla in a variety of environments. Relatively little quantitative work has been done on this important process and much of what is known comes from research on coral reefs. Scoffin et al. (1980) demonstrated that bioerosion was a destructive process almost equal to the constructive process of reef growth. A recent review (Warme, 1977) of modern Caribbean coral-algal reefs and Jurassic Moroccan Scleractinian reefs implied that carbonate substrates exposed to bioeroders may be ultimately reduced to lime mud unless bioerosion is arrested by another process, such as burial, submarine cementation, vigourous framework growth, or effective incrustation. Coral skeletons particularly are affected by bioerosion of the dead parts of the skeletons. Borers create cavities of varied geometry with boring diameters from a few microns to a decimetre or more.
Bertram (1936), working in the Red Sea, recognized that any slight damage to the envelope of live polyps on a coral head (e.g., scarid bite) or other entry into the skeleton (vacated worm tube), provided an opportunity for infestation by borers that could ultimately destroy the coral.

Bioeroders are known from all five kingdoms. Most groups (apart from the bacteria, fungi, and algae) dissolve little of the material excavated; rather, they produce mud- and silt-sediment. The sedimentological products of bioerosion by sponges (Cobb, 1969), parrot fish (Darwin, 1842), urchins (Hunt, 1969) and a few other groups, are obvious and well documented. The sediment loosened in this manner can have several fates (Warme, 1977):

a) it can fall and be directly incorporated into the abundant reef crevices and cavities,
b) it can become part of the inter-reef sediment,
c) it can be further removed into oolite tracts and other environments,
d) it may be moved downslope and completely out of the shallow reef system if sufficient relief exists.

The main sources of loose clasts in lagoonal sediments are skeletal material, physical erosion of hard surfaces by waves and currents, and bioerosion. Quantification should be attempted in more complicated coral-algal rock where incrustation, cementation, and sedimentation are all factors. The relative importance of bioeroders, at least in some cases, may be greater than other erosive agencies; however, the absolute rate may be harder to assess. The
estimate of potential bioerosion may be represented by the following equation proposed by Hodgekin (1964):

\[
\text{estimate of} = \text{volume of average} \times \text{density of} \times \text{life span or potential excavation borers generation bioerosion time}
\]

The extent to which boring reduces coral strength can be estimated crudely from density measurements that treat boreholes as an increase in porosity (Highsmith, 1981). The ratio of the difference between the density of solid aragonite (2.94) and the density of the coral to the density of aragonite is an estimate of the coral porosity. If \( \sigma \) is used to estimate the breaking strength then:

\[
\sigma = \sigma_0 e^{-n\nu}
\]

where \( \sigma_0 \) is the strength of the material without pores, \( n \) is some constant between 4 and 7, and \( \nu \) is the porosity. This is an oversimplification. It is necessary to differentiate between borings that act throughout the cross-sectional area and ones which act on the periphery or in the centre. Only if the borings act throughout the cross-sectional area will this method work. On the other hand, borings on the periphery of a cylindrical coral, acting in effect to reduce the radius, will have a profound effect on the strength, because the resistance to breakage of a cylinder is a function of the cube of the radius (Hein and Risk, 1975). This principle was verified experimentally by Tunnicliffe (1982) by measuring in situ the breaking strength of Acropora palmata due to physical action (i.e., waves) as a
function of bioerosion. This latter method is preferred, as no known eroder has a constant effect across the cross-sectional area of the coral. Borers may have weakening effects similar to cracks as opposed to increased porosity (Highsmith, 1981).

Incrustation, sedimentation, and cementation are processes which add to the volume and mass of reefs. It is necessary, however, to evaluate the processes which remove material -- boring, chemical solution, physical erosion -- in order to understand the growth history of any organic buildup. Otter (1936) diagramatically represented the inter-relationship of these parameters in the destruction of a coral reef. Biological penetration is much greater than physical or chemical submarine weathering, and is an important factor in shaping the seabed (Warme, Scanland and Marshall, 1971). Borers not only effectively penetrate the rocks, but also bare new rock surfaces to physical and chemical deterioration. Recognition of bored or otherwise degraded surfaces provides important cross-cutting relationships, yielding data on the amount, constancy, and pervasiveness of reef erosional episodes and other events that were involved in reef building (Warme, 1977). Multiple episodes of boring become a key to determining volumes of material eroded, just as unconformities are used in stratigraphy (Scoffin and Garrett, 1974). Reef borers can play important roles in reef ecology and growth, and their recognition provides important tools for understanding reef history, ecology, and preservation.
1.2 Cliona as a Bioeroder

Evidence of the activity of boring sponges has been described in rocks as old as Lower Cambrian (Poulson, 1967; Kobluk, 1981a,b). Clionolithes has been recorded as early as Upper Ordovician (Clarke, 1921; Ruedemann, 1925). Pickerill and Harland (pers. comm.) report a Mid-Ordovician sponge, but don't determine any affinities with pre-existing ichnogenera. Borings that can be attributed with any degree of certainty to the Clionidae are probably post-Jurassic (Bromley, 1970).

Boring sponges of the genus Cliona are important coral bioeroders, accounting for approximately 70 to 80% of the total skeletal damage caused by bioerosion (Bak, 1976). Sponges typically make small chambers (galleries) ranging from 1-12 mm in diameter, located 2-3 mm below the skeletal surface. Galleries of the boring sponge Cliona are defined as ramifying galleries of varying diameters with pitted surfaces (Hein and Risk, 1975).

The larvae of clionids settle only on dead portions of coral skeletons (Hartman, 1977), chiefly at the bases. Although the Clionidae are not notably host specific, some species appear to restrict their "attack" to specific host morphologies (Pang, 1973a), whereas other congeneric species do not. The excavating activities weaken the attachment points of the corals, promoting dislodgement by wave action in shallower waters (Goreau and Hartman, 1963). In deeper parts of the reef, large flattened colonies may topple under their own weight, especially if they are overgrown by other attached
organisms that add to the load on the weakened bases (Hartman, 1977).

Boring clionid sponges penetrate calcium carbonate substrates by a sequence of chemical and mechanical processes, producing a lime mud (Cobb, 1969; Hein and Risk, 1975). Ruetzler and Reiger (1973) estimated that only 2 to 3% of the material excavated goes into solution; the remainder is passed through the excurrent canal system and voided to the environment as chips. Chips which have been etched out of the substrate are angular and possess several flat, concave or convex facets which meet to form ridges or points (Fig. 1). Neither the polymorphic form of the calcium carbonate, nor the presence of organic material within the substrate, alters the basic pattern of cellular penetration (Cobb, 1969). Chips are between 15 and 100 µm (coarse-silt to fine-sand), with a pronounced maximum (55%) within the 20-40 µm fraction (Fuetterer, 1974). Fuetterer (1974) also observed that the size distribution of the boring pits (25-82 µm) on Cliona celata corresponded perfectly to the size distribution determined from grain size analysis of lagoonal sediments. As the sediments of most reefs are derived from the reefs, these sponges are an important factor in the sediment budget.

Clionid bioerosion rates have been found to be directly linked to substrate availability (Ruetzler, 1975) and to the texture of the carbonate substrate (Neumann, 1966). Substrates on reefs vary from massive mollusc shells, through a range of different skeletal types to highly porous corals. This variation in structure seems to have little influence on the distribution of endolithic species, but exerts a strong influence on the morphology of the boring (Bromley,
Figure 1. SEM micrographs of sponge chips. Notice the scalloped texture of the grains. These are characteristic clionid bioerosion by-products. Scale bar = 10 μm.
This is particularly true of the sponges, which commonly occupy and modify existing voids. Neumann (1966) felt, from the observation of naturally infected material, that the depth of penetration of the sponge into a calcareous host is limited by the effectiveness of the water circulating system of the sponge.

A few studies, using a variety of techniques have attempted to determine the bioerosion rates of Cliona. Neumann (1966) measured rates of bioerosion by Cliona lampa by measuring weight loss of blocks which had been attached to sponge bearing material for 100 days; he calculated that Cliona-infested substrates can lose as much as 6.7 kg m\(^{-2}\) 100 days\(^{-1}\). In areas of prolific reef development, however, such as St. Croix and Jamaica, Ruetzler (1975) proposed a maximum sustained rate of 7 kg m\(^{-2}\) yr\(^{-1}\).

Moore and Shedd (1977) used the by-products of clionid bioerosion, the volume of clionid burrows preserved in the record of reef accretion, and the sediment produced by boring activity as a measure of effective clionid bioerosion. In general, areas of rapid accretion (e.g., reef fronts) have prolific coral growth and thus relatively low substrate availability; areas of low accretion have little coral growth and therefore relatively high substrate availability. In those cores with low accretion rates 41% of the core was lost by clionid activity, while in cores with high rates of accretion only 32% was lost. Their calculated bioerosion rates ranged from 0.19 to 3.29 kg m\(^{-2}\) yr\(^{-1}\), illustrating the effect of substrate availability through time on bioerosion rates.

Goreau (1963) proposed, that in a situation where clionids
are attacking living corallines, it may be that the rapid rate of calcification of coralline algae can modify the shape and nature of the galleries by rapidly healing areas attacked by Cliona. It is possible to link sponge activity patterns to certain environmental factors: mechanical stimuli, high light intensity, strong currents, and possibly low temperature accelerate the boring process (Ruetzler, 1976). Depth per se does not appear to affect the boring rate (Scoffin and Garrett, 1974; McGeachy and Stearn, 1977); however, the above-mentioned parameters vary with depth and may be responsible for the evidence of increased bioerosion observed by Warme (1977) in shallower zones (15 m) of the reef. The importance of grazing fish as a control on the distribution of shallow-water sponges was emphasized by Bakus (1964) for Fanning Island, and by Risk and Sammarco (1982) for the Great Barrier Reef. Randall and Hartman (1968) concluded, however, that fish predation was probably not a limiting factor in sponge distribution in the West Indies.

The result of the activity of boring sponges is two-fold:

1) direct production, by the boring activity, of fine-grained material,

2) loss of stability to the organism under attack, making it more susceptible to continual mechanical breakdown.

1.3 Setting and Scope

The Great Barrier Reef Province extends 2,000 km along the Queensland Coast, from latitude 24o 07'S to latitude 9o 22'S. The province is typically divided into three main regions (Fig. 2):
a) NORTHERN REGION - includes all reefs north of 16oS, and is characterized by shallow depths (generally < 40 m).

b) CENTRAL REGION - includes the area from 16oS to 21oS on the mainland; 20oS on the shelf edge. The water depth ranges from 40 to 60 m.

c) SOUTHERN REGION - includes the area from 21oS to 24oS. This is the deepest area of the reef province, ranging to 160 m. The Continental Shelf slopes eastward to the outer reef zone and then drops down to the Continental Slope. The Shelf can be divided into inner-, mid-, and outer-shelf areas along the 40 and 100 metre contour lines.

The present study was done on Davies reef, a mid-shelf reef located in the Central Region of the Province (Fig. 3). This kidney-shaped reef is 10 km in length and 5 km from front to back (Fig. 4). There is a well-developed reef front, a large, relatively protected lagoon (containing a large area of patch reef (bommie) development), a well-developed sand-spit, an area of reef-derived sediment containing little coral growth, and extensive back reef development. The bommies rise vertically from a sandy lagoon floor from 10 m to 80 m. The reef tops are irregular. The framework surface is only partly covered with living corals, and the hard substrate is encrusted with calcareous algae and many attached soft animals and plants.

The bommies are densely populated with boring sponges of the genera Cliona and Siphonodictyon. One of these sponges — Cliona viridis — was so abundant, it was nicknamed "plague". Because of the nature of the growth habit, this is an ideal
Figure 2. Map of the Queensland Coast, showing the division of the Great Barrier Reef Province into regions. Contour line (200 m) marks the edge of the continental shelf.
Figure 3. Aerial photograph of Davies Reef, mid-shelf reef, Great Barrier Reef, Australia.
Figure 4. Diagrammatic representation of Davies Reef showing, reef-front, back-reef, lagoon, and sand-spit.
experimental animal. The purpose of this study was to determine the distribution of *Cliona viridis*, and its bioerosional capabilities.

1.4 Previous Reports of Clionid Bioerosion in the Great Barrier Reef Province

To date, very little has been done either taxonomically or ecologically on boring sponges in the Great Barrier Reef Province. A few early reports of the presence of boring sponges on the barrier reef exist (Gardiner, 1903; Otter, 1936) however, there is no mention of the presence of *Cliona*. Hopley (1982) briefly discussed clionids in a general chapter on bioerosion on the Great Barrier Reef.

Risk and Sammarco (1982), proposed that bioerosion was greatly accelerated by reduction in grazing pressure within defended territories, as a result of one or more of the following:

a) increased success of larval settlement,

b) reduced grazing and predation on macroborers,

c) increased food supply due to algal turf.

They also suggested that the crypticity exhibited by most of the boring sponges on the Great Barrier Reef is a result of intense grazing pressure.

A systematic survey of the boring sponges present on the Great Barrier Reef is still required.
Chapter 2 - Taxonomy

2.1 Introduction

A detailed systematic survey of the boring sponge fauna present on the Great Barrier Reef is still required. Plague was one of the many boring sponges observed on the Great Barrier Reef and was later identified as *Cliona viridis* (Schmidt, 1862). A brief description of this organism is given, along with a discussion of its taxonomic status.

2.2 Materials and Methods

Samples were collected from various localities and depths from Davies Reef Lagoon, and fixed in 70% (V/V) EtOH. Permanent slides of clean spicules were prepared by boiling tissue in concentrated nitric acid, rinsing in water, and dehydrating in alcohol (100% V/V). Spicules were mounted on glass microscope slides and examined under phase contrast microscopy (Zeiss Photomicroscope), and on SEM stubs, gold sputter coated and examined under a Philips SEM 500.

Internal structures of the borings and penetration depths were examined by cutting samples on a diamond saw.

Measurements given are means and standard deviations (ranges
in parentheses). Spicule sizes are based on 50 measurements per dimension for each sample.

2.3 Taxonomic Description

COLOUR: In life, the rims of the papillae are yellow, while the rest of the outer surface is dark brown; the internal tissue is yellow brown. In EtOH (70% V/V) the sponge is dull yellow green.

SUBSTRATES: massive corals, reef framework.

DEPTHS: collected from 0-12 m.

MATERIAL: Samples were collected from the vertical sides of bommies in Davies Reef Lagoon. Small samples of tissue were preserved and mounted (method described by Ruetzler, 1974) for spicule examination.

SPICULES: 1) Abundant straight to slightly curved tylostyles (Fig. 5a). The shaft tapers gradually to a point. The head is sub-globose to globose; it is rarely subterminal. Occasionally a secondary swelling may be present immediately below the head. Maximum diameter of the head is 8.8 μm ± 1.8 (4-14 μm); length is 10.8 μm ± 2.1 (4-16 μm). Tylostyle length: 284 μm ± 42 (184-376 μm). Tylostyle width: 5.6 μm ± 1.6 (2-8 μm). N = 4 specimens. 2) Abundant spiny spirasters (Fig. 5b); usually having 3-4 bends (1-8 bends). The spines are thorn-like
Figure 5. Spicules of *Cliona viridis* (Schmidt) Gray.

a) Tylostyles with abundant spirasters, 256 X.

b) SEM micrograph of spiraster. Note location of spines on convex side of the main axis. Endings of spines bifurcate or trifurcate. Scale bar = 10 μm.
in appearance, and found predominantly on the convex side of the axis. The spines are bifurcate to trifurcate. Spiraster length: 23.6 µm ± 7.5 (8-41.6 µm). N = 4 specimens.

SURFACE: The sponge was only found in the Beta stage; tendency to overgrow the substrate (Fig. 6). The tops of the papillae are yellow, while the rest of the surface is greenish to yellowish brown, probably due to the presence of symbiotic algae (zooxanthellae). The papillae are 1-1.5 µm in diameter, 1-2 mm high, contractile with no evidence of papillary fusion.

EXCAVATIONS: The sponge excavates 1.3 cm ± 0.2 into the substratum, producing irregular frequently fused chambers 1-3 mm in diameter (Fig. 7). Boring progresses via lateral extension of the surface and then downwards. The organism was found boring into massive substrates only.

LOCATION: Plague was found in the Northern and Central Regions of the Great Barrier Reef and across the Shelf (Fig. 8). The following reefs were studied:

A/ Northern Region -- Lizard Island (mid-shelf)
B/ Central Region -- 1) Inner-Shelf
   Magnetic Island
   Pandora Reef
   2) Mid-Shelf
   Davies Reef
   Britomart Reef
Figure 6. Surface of plague,  

a) boring through a coral, 5 X; 

b) in a coxcomb oyster shell, 5 X; c) showing both surface and internal aspects of plague, 5 X 

and d) magnified osculum (contactile), 10 X.
Figure 7. SEM micrograph of inside of boring chamber. Note the scalloped texture of the walls. a) view of the inside of the main gallery. Scale bar = 100 µm. b) pioneer filament chamber, 8 X (a).
Figure 8. Map of the Queensland Coast. Stippled areas indicate where plague has been observed.
Plague was found in the lagoon of all of these reefs, with the exception of Pandora. In some of the reefs (e.g., Britomart Reef) plague was occasionally found on the false front.

DISCUSSION: The taxonomic status of Cliona viridis (Schmidt) and Cliona caribboea Carter (1882) has been reviewed by Topsent (1900; 1932), Hechtel (1965), Pang (1971; 1973b), and Ruetzler (1974). Pang (1971) has summarized the salient taxonomic features of the two species, from the description of the type specimen of C. caribboea and material from Discovery Bay, Jamaica. C. viridis has been described from Port Royal (Hechtel, 1965) and the Mediterranean (Schmidt, 1862; Topsent, 1900).

Vioa viridis Schmidt (1862) was originally described from the Adriatic and transferred to the genus Cliona by Gray (1867). The type specimen possessed tylostyles with distinctive sub-terminal knobs. Pang (1971) observed the same sub-terminal heads in some Mediterranean specimens.

The validity of C. caribboea Carter (1882) has been debated since its erection. Carter recognized that the general characters of his species were almost identical with those of C. celata, although marked differences existed in the spiculation.

Topsent (1900) considered C. caribboea and C.
subulata Sollas (1878) to be a simple synonymy of *C. viridis* (Schmidt), based on the spiculation, the same complement of spherular cells (possibly zooxanthellae) which are supposed to be specific for *C. viridis*, and growth habitat. The description of *C. subulata* Sollas (1878) presents no description of the spicules or their dimensions, and thus may be dismissed. Topsent (1932), however, revised his ideas on *C. caribboea* and proposed the name *Cliona viridis* (Schmidt) var. *caribboea* Carter. The idea of a simple synonymy was rejected based on the differences in growth habitat. The name *C. caribboea* was not accepted due to the marked similarities in the spiculation. De Laubenfels (1936), comparing sponges at the Pacific and Caribbean ends of the Panama Canal, found *C. caribboea* to be a characteristic West Indian species, unless it was considered to be conspecific with *C. celata*.

In the most recent taxonomic reviews (Hechtel, 1965; Pang, 1971, 1973b; Ruetzler, 1974), no satisfactory conclusions have been drawn on the validity of *C. caribboea*. Hechtel (1965) felt there was not enough information available to separate the *Cliona viridis* complex. Pang (1971) thought that although *C. caribboea* was obviously similar to *C. viridis*, it was best to retain *C. caribboea* at least tentatively, for the widely distributed West Indian clionid. Ruetzler (1974) supported Pang's (1971) conclusion.

Clearly, no satisfactory decisions have been reached on the specific status of *C. caribboea* and the species definition of *C. viridis*. An in-depth systematic study is required before any
concrete decisions may be made. *C. viridis* is known from the Caribbean, but whether this is conspecific with *C. caribboea* cannot yet be confirmed. The growth forms of *C. caribboea* more closely resemble *C. celata* (Carter, 1882; de Laubenfels, 1936) than *C. viridis*. Whether the differences are genetically or ecologically determined requires further study.

The diagnostic features of *C. viridis* and *C. caribboea*:

1) absence/presence of zooxanthellae,

2) morphology of the substrate bored,

3) colony type (i.e., Alpha or Beta).

These differences, however, may simply be environmentally-controlled variations within one species. In other words, it is entirely possible that *C. caribboea* and *C. viridis* could be put into synonymy, in which case *C. viridis* would take precedence. At present, I feel that the name *C. caribboea* should refer *sensu stricto* to Carter's original description of 1882, and that the overgrowing sponge described in this study, which is common in both the Great Barrier Reef and the Caribbean, should be called *C. viridis*.
Chapter 3 - Aerial Distribution

3.1 Introduction

To date, little is known of the aerial distribution of boring sponges or the factors controlling this distribution. Systematic studies provide information about geographical location and ecological limits of the organism indirectly by habitat, depth and location data. What little ecological work has been done is summarized by Sara and Vacelet (1973). De Laubenfels (1947, 1950) was the first to use an ecological approach to consider the effects of light intensity, water movement, current velocity and chemical characteristics of the water on sponge distribution.

This study attempts to ascertain the spatial distribution and abundance of plague, with respect to both depth and lateral position on Davies Reef.

3.2 Materials and Methods

Bommies were chosen from an aerial photograph, such that all areas of the reef were studied from reef front to back reef (Fig. 9). With the use of SCUBA, vertical transects were run from the top to the base of each bommie, such that both windward and leeward
Figure 9. Diagram of Davies Reef showing the location of the bommies used in transect sediment studies.
Figure 10. Diagrammatic representation of bommie surface showing the relative position of transects.
faces were surveyed (Fig. 10). Anywhere from four to six transects were done per bommie, depending on the depth of water in which the bommie was located.

A 1/2 m² quadrat, subdivided into 25, 5 cm² units was placed in the centre of the transect line at 1 m intervals. The lateral coverage within the quadrat was determined and recorded as percent abundance. Depths were corrected for tide state (Official Tide Tables for the Queensland Coast, 1981).

3.3 Results and Discussion

The aerial coverage at each depth was obtained by calculating the percent abundance across the reef at each of the respective depths, and plotting percent abundance versus depth. The total percent abundance was then divided into its windward and leeward components, and each component plotted as a percent of the total abundance with respect to depth. A horizontal profile of depth distribution was determined by projecting bommies (Fred, 1,2,3,5,6,7,8, George and Linda) onto a NW-SE (reef front to back reef) line, and plotting the percent abundance of plague per bommie on a horizontal position versus depth graph.

Plague occurs mostly between three and eight metres (Fig. 11), with the maximum peak occurring at four metres, a total of 7.7% (Table 1). Below eight metres, there is an abrupt drop in coverage. The peak occurring at twelve metres is due to a single occurrence of plague on an especially deep bommie. The presence of this peak suggests that plague may occur at depth in deeper lagoons.
Table 1. Summary of the distribution of plague with depth on Bommies in Davies Reef Lagoon.
<table>
<thead>
<tr>
<th>Depth</th>
<th>TOTAL</th>
<th>LEEWARD</th>
<th>WINDWARD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Transects</td>
<td>% Abundance</td>
<td>Transects</td>
</tr>
<tr>
<td>0</td>
<td>18</td>
<td>0.89</td>
<td>10</td>
</tr>
<tr>
<td>1</td>
<td>43</td>
<td>5.53</td>
<td>23</td>
</tr>
<tr>
<td>2</td>
<td>52</td>
<td>6.88</td>
<td>28</td>
</tr>
<tr>
<td>3</td>
<td>54</td>
<td>7.63</td>
<td>28</td>
</tr>
<tr>
<td>4</td>
<td>59</td>
<td>7.69</td>
<td>30</td>
</tr>
<tr>
<td>5</td>
<td>62</td>
<td>7.06</td>
<td>30</td>
</tr>
<tr>
<td>6</td>
<td>58</td>
<td>4.55</td>
<td>28</td>
</tr>
<tr>
<td>7</td>
<td>42</td>
<td>7.02</td>
<td>20</td>
</tr>
<tr>
<td>8</td>
<td>36</td>
<td>7.42</td>
<td>13</td>
</tr>
<tr>
<td>9</td>
<td>29</td>
<td>2.96</td>
<td>11</td>
</tr>
<tr>
<td>10</td>
<td>22</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>11</td>
<td>13</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>12</td>
<td>7</td>
<td>2.00</td>
<td>4</td>
</tr>
<tr>
<td>13</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>14</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>15</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>TOTAL</td>
<td>72</td>
<td>38</td>
<td>34</td>
</tr>
</tbody>
</table>
Figure 11. Relationship of plague abundance (%) as a function of depth.
Although overall maximum abundance occurs at depths of three to eight metres, there is a slight abundance decrease observed at five metres. If the total abundance is divided into its windward and leeward components (Fig. 12), the contributing source of the peaks may be determined.

The windward component has greater aerial coverage and a greater depth range (0-12 m), while the leeward component range is less (0-10 m), with less aerial coverage at almost every depth. On the windward side, two peaks occur: a small one at two metres and a larger one at eight metres. The leeward component peaks at five metres and decreases gradually with depth. Thus, the peak at four metres in the percent total abundance is due to a combination of both the windward and leeward components, while the seven metre peak is comprised almost entirely of the windward component.

The abundance trends observed on Davies Reef are roughly in agreement with those observed by Neumann (1966), at Harrington Sound, Bermuda. Neumann found that the erosive process in the area of the "notch" (level of lowest low tide) appeared to be more effective than those at greater depth, or in the intertidal zone. At Harrington Sound, lowest low water marked the distinct upper limit of the borers.

The distribution of plague across the reef with depth is shown in Fig. 13. No plague was found on the reef front, or crest, or on the windward face of bommie Fred, which is adjacent to the reef crest. Plague first appears on the lee side of bommie Fred.

Across the reef, windward abundance is greater than leeward abundance, with exception of the bommies occurring near the reef
Figure 12. Windward-leeward components of plague abundance (%) as a function of depth.
Figure 13. Relative windward-leeward abundance (%) of plague across Davies Reef as a function of depth. Bommies are represented by a central line with windward to the right of this line and leeward to the left. Horizontal dashes on the central line indicate the corrected depth boundaries windward-leeward for each of the bommies.
crest (bommie Fred, 1, and 6). Generally, the depth at which plague is found in the lagoon decreases from reef front to back reef. However, the depth of the lagoon decreases as well (Fig. 13). Plague occurs at greater depths on the windward face of the bommie than on the leeward face, with the exception of the bommies adjacent to the reef crest.

The absence of plague on the reef front and crest, and its decreased abundance on the windward faces of bommies Fred, 1, and 6, is probably due to two main factors:

a) prolific coral growth,

b) morphology of the corals present.

Pang (1973a) felt that the morphology of the coral skeleton was a more important factor than the actual species. Plague bores preferentially into vertical, flat, substrates exposed to the light; coral growth at the reef front consists primarily of the branching corals Acropora spp., and Pocillopora spp. This works to exclude plague from this area by:

a) decreasing the substrate availability,

b) reducing the ambient light by shading effects.

The increase in abundance on the leeward face of these bommies is possibly due to stronger current action in this area than on the leeward face of back reef bommies.

The general decrease in abundance towards the back reef area, and the greater abundance on the windward face, is possibly due to water movement. Andrews and Mueller (1983), working on Britomart Reef, Great Barrier Reef, found that currents were established around bommies which created positive and negative
gradients of nutrients, and that the patterns of concentration rotated tidally. As plague is both a filter-feeder and a primary producer (it has symbiotic zooxanthellae), location in an exposed rather than a sheltered habitat will result in more prolific growth.

In front of the sand-spit plague does well; relatively abundant windward and leeward. Behind the spit, however, there is a marked decrease in abundance and the depth at which it was present. The spit may act as a barrier to water flow, thereby limiting the availability of nutrients. In the back reef area, much of the available substrate is colonized by calcareous algae and other encrusting organisms, which would protect the framework to some degree from subsequent bioerosion.

Clearly, the abundance, position, and depth relationships are the result of several processes. In order to elucidate the contributions of each of these parameters controlling the distribution of the organisms on reefs, further ecological studies are required, monitoring known parameters affecting the organisms' growth. Quantification of the surface areas can provide useful parameters for comparative studies in ecology. This is especially true in coral reefs where the morphological complexities are so great as to make other techniques unfeasible (Dahl, 1973). The production, occupation, and destruction of reef surfaces are fundamental reef processes.
Chapter 4 - Biomass and Substrate Removal

4.1 Introduction

Relatively little has been done on the ecological aspects of boring sponges. Some work has been done on aerial coverage (Scoffin and Garrett, 1974; McGeachy and Stearn, 1976), but this has involved the number of individuals and an estimate of the rates of substrate removal. There have been no attempts made to quantify the sponge biomass. Although rates of substrate removal have been calculated (Neumann, 1966; Ruetzler, 1975; Warme, 1977), little mention is made of the percent substrate removed and parameters controlling substrate removal.

The purpose of this study was to examine the relationship(s) between the percent biomass and the amount of substrate removed.

4.2 Materials and Methods

Sponge colonies were collected using SCUBA from various places and depths on Davies Reef, and subsequently fixed in 95% EtOH to prevent bacterial degradation. These samples were used to determine both biomass and amount of substrate removed. The colonies were cut into small cubes using a diamond blade saw. The depth of penetration of the sponge was measured on the fresh cut surface. Twenty-five measurements were made per sponge colony.
4.2A Biomass Determination

For each sponge colony 15 cubes were cut, such that there was no unbored coral present (Fig. 14a). The cubes were then placed in preweighed beakers, dried in a drying oven at 90°C, and weighed on a Mettler Balance. The cubes were then covered with H₂O₂ (35% V/V) for four days to remove the organics. They were then rinsed in distilled water, dried (90°C) and reweighed.

4.2B Density Determination

The density of the samples was determined for bored and unbored substrates. A total of 15 cubes were cut such that 10 were completely bored by plague and 5 showed no visible signs of boring (Fig. 14b). The cubes were placed in crucibles in a drying oven (90°C) for 24 hours and weighed on a Mettler Balance. Each cube was dipped in hot paraffin to displace the trapped air within the sample. The volume of each cube was determined using Archimedes’ Principle. A Mettler Balance, modified to determine submerged weights, was used to determine the volume of the samples. The dry weight of the sample with paraffin was determined both in air and water to determine the volume of the sample. This volume was then divided by the actual dry weight of the sample to determine the density of the substrate.
Figure 14. Samples used in %Biomass and Density Determinations:

a) example of completely bored sample used in %Biomass determination, 2 X;  
b) example of completely bored and unbored samples used in density determinations, 2 X.
4.3 Results and Discussion

The sponge bores to an average depth of 1.3 cm ± 0.3, with an average percent biomass of 9.84 ± 2.7 and removes 0.8 gm cm⁻³ ± 0.4 of substrate (Table 2). Two Stepwise Regressions (BMDP.2R) were done to determine any possible correlations between the parameters %substrate removed, %biomass, penetration depth, density of original substrate, and depth. In the first regression %substrate removed was the dependent variable, and in the second regression %biomass was the dependent variable. The only correlation found was between the %substrate removed and the density (P > 0.01). The %substrate is directly proportional to the density (Fig. 15). There was no correlation with %biomass. Ruetzler (1975) found that substrate availability determined the amount of boring that occurs. Generally the sponge bored until approximately 50% of the substrate was removed. This was supported in this study as the maximum values of percent substrate removed were around 50%, although on average only 37% ± 13.8 of the substrate was removed. The main factor determining the percent substrate removed, however, was the initial density of the substrate.

There was no correlation with depth or windward-leeward positioning with respect to %biomass, %substrate removed, depth of penetration, or initial density of the substrate. Substrate density appears to be species specific, and affects only the amount of substrate removed by plague.

The lack of correlation within the data is not surprising.
Table 2. Summary table of the measured parameters of plague.

Note: where density values could not be calculated the original density of the substrate was assumed to be 2.6.
<table>
<thead>
<tr>
<th>Sample #</th>
<th>Location</th>
<th>Bearing</th>
<th>Depth (m)</th>
<th>Substrate</th>
<th>Biomass of Plague</th>
<th>Penetration Depth (cm)</th>
<th>Density of Original Substrate (gm/cc)</th>
<th>Substrate Removed by Plague</th>
<th>%Substrate Removal</th>
</tr>
</thead>
<tbody>
<tr>
<td>D201</td>
<td>1 Bommie</td>
<td>180W</td>
<td>10</td>
<td>mollusc shell</td>
<td>10.05 ± 2.52 completely bored</td>
<td>2.6</td>
<td>1.87 ± 0.08</td>
<td>71.92</td>
<td></td>
</tr>
<tr>
<td>D202</td>
<td>1</td>
<td>240L</td>
<td>8</td>
<td>coral rubble</td>
<td>5.67 ± 1.19 1.704 ± 0.358</td>
<td>2.6</td>
<td>1.39 ± 0.08</td>
<td>53.49</td>
<td></td>
</tr>
<tr>
<td>D203</td>
<td>1</td>
<td>200W</td>
<td>4</td>
<td>oyster valve</td>
<td>10.12 ± 1.87 completely bored</td>
<td>2.6</td>
<td>1.43 ± 0.05</td>
<td>54.91</td>
<td></td>
</tr>
<tr>
<td>D210</td>
<td>1</td>
<td>OL</td>
<td>8</td>
<td>coral</td>
<td>15.73 ± 3.69 0.968 ± 0.163</td>
<td>1.15 ± 0.04</td>
<td>0.54 ± 0.03</td>
<td>35.49</td>
<td></td>
</tr>
<tr>
<td>D212</td>
<td>1</td>
<td>300L</td>
<td>4</td>
<td>oyster</td>
<td>4.29 ± 1.73 0.948 ± 0.315</td>
<td>1.07 ± 0.15</td>
<td>0.46 ± 0.10</td>
<td>24.65</td>
<td></td>
</tr>
<tr>
<td>D215</td>
<td>2</td>
<td>280W</td>
<td>7</td>
<td>coral</td>
<td>8.50 ± 2.85 0.924 ± 0.265</td>
<td>2.40 ± 0.12</td>
<td>1.18 ± 0.04</td>
<td>49.31</td>
<td></td>
</tr>
<tr>
<td>D218</td>
<td>3</td>
<td>150W</td>
<td>10</td>
<td>coral</td>
<td>8.37 ± 1.69 1.276 ± 0.359</td>
<td>2.24 ± 0.06</td>
<td>1.11 ± 0.06</td>
<td>49.14</td>
<td></td>
</tr>
<tr>
<td>D220</td>
<td>3</td>
<td>240L</td>
<td>8</td>
<td>coral</td>
<td>8.99 ± 2.98 1.308 ± 0.364</td>
<td>2.20 ± 0.03</td>
<td>1.06 ± 0.02</td>
<td>47.87</td>
<td></td>
</tr>
<tr>
<td>D230</td>
<td>8</td>
<td>240L</td>
<td>3</td>
<td>coral</td>
<td>8.96 ± 1.85 1.060 ± 0.261</td>
<td>1.21 ± 0.16</td>
<td>0.09 ± 0.06</td>
<td>7.75</td>
<td></td>
</tr>
<tr>
<td>D231</td>
<td>8</td>
<td>240L</td>
<td>3</td>
<td>coral</td>
<td>9.06 ± 2.58 1.076 ± 0.427</td>
<td>1.74 ± 0.11</td>
<td>0.69 ± 0.04</td>
<td>39.66</td>
<td></td>
</tr>
<tr>
<td>D232</td>
<td>9</td>
<td>270L</td>
<td>15</td>
<td>coral</td>
<td>10.33 ± 2.04 1.468 ± 0.556</td>
<td>1.20 ± 0.06</td>
<td>0.19 ± 0.02</td>
<td>15.45</td>
<td></td>
</tr>
<tr>
<td>D233</td>
<td>9</td>
<td>bommie top</td>
<td>10</td>
<td>coral</td>
<td>8.57 ± 1.73 1.960 ± 0.643</td>
<td>1.58 ± 0.10</td>
<td>0.37 ± 0.16</td>
<td>23.66</td>
<td></td>
</tr>
<tr>
<td>DE</td>
<td>6</td>
<td>300L</td>
<td>3</td>
<td>coral</td>
<td>10.31 ± 2.72 1.176 ± 0.392</td>
<td>2.04 ± 0.15</td>
<td>0.86 ± 0.09</td>
<td>41.91</td>
<td></td>
</tr>
<tr>
<td>DF</td>
<td>6</td>
<td>270L</td>
<td>4</td>
<td>coral</td>
<td>9.68 ± 3.16 1.324 ± 0.448</td>
<td>1.70 ± 0.03</td>
<td>0.49 ± 0.02</td>
<td>28.94</td>
<td></td>
</tr>
<tr>
<td>DH</td>
<td>8</td>
<td>330L</td>
<td>3</td>
<td>coral</td>
<td>9.15 ± 2.68 1.156 ± 0.266</td>
<td>2.05 ± 0.04</td>
<td>0.74 ± 0.05</td>
<td>35.93</td>
<td></td>
</tr>
<tr>
<td>DI</td>
<td>8</td>
<td>240W</td>
<td>4</td>
<td>coral</td>
<td>12.39 ± 3.35 0.972 ± 0.273</td>
<td>1.86 ± 0.15</td>
<td>0.74 ± 0.07</td>
<td>39.95</td>
<td></td>
</tr>
<tr>
<td>DJ</td>
<td>8</td>
<td>180W</td>
<td>4</td>
<td>coral</td>
<td>15.31 ± 6.65 1.136 ± 0.218</td>
<td>1.57 ± 0.06</td>
<td>0.47 ± 0.03</td>
<td>30.25</td>
<td></td>
</tr>
<tr>
<td>DK</td>
<td>8</td>
<td>240W</td>
<td>3</td>
<td>coral</td>
<td>10.45 ± 3.34 1.380 ± 0.297</td>
<td>1.64 ± 0.17</td>
<td>0.56 ± 0.06</td>
<td>33.88</td>
<td></td>
</tr>
</tbody>
</table>
Figure 15. %Substrate Removed as a function of density.
Neumann (1966) felt that the boring rates, and hence the amount of bioerosion, were affected more by the texture of the carbonate substrate than by the mineralogy. Scoffin and Garrett (1974) and McGeachy and Stearn (1976) found no correlation in borer density or distribution with depth; however, the ratio of living coral surface to dead encrusted areas influenced the borer density and the extent of boring. This parameter, ratio of living to dead surface, was not measured in this study. The parameters controlling percent biomass of the sponge within the host are complex. Experiments with more rigorous controls on boring rates and substrate availability should be done.
Chapter 5 - Growth Rates

5.1 Introduction

Numerous methods have been used to determine the growth rates of clionids (Neumann, 1966; Hein and Risk, 1975; Ruetzler, 1975; Bak, 1976; Hudson, 1977; Moore and Shedd, 1977; de Groot, 1980; Highsmith, 1981). No estimates of boring sponge rates have been determined for the Great Barrier Reef, Australia, although Highsmith (1981), studied clionid bioerosion rates at Enewetok (only gives %substrate removed). The rest of the studies were done in the Caribbean, or off the coast of Florida.

Growth rates of Cliona viridis were determined on Davies Reef, Great Barrier Reef, using sequential photography. This sponge is an ideal experimental organism for determining growth rates, as it extends laterally across the surface and penetrates to an approximately constant depth (refer to Chapter 4).

5.2 Materials and Methods

Underwater photographs were taken with a Nikonos III equipped with an extension tube and framer. The tube magnifies the image 1.8X. Two concrete nails were hammered into the reef framework -- one just inside the edge of the plague colony, the other just outside the edge of the plague colony -- the width (7 cm)
Figure 16. Diagram of set-up used in determining lateral extension of plague. The X represents the position of the concrete nails used for ensuring the positioning of the camera.
Figure 17. Reproduction of Overlays used in Growth Rate Determinations. Stipled areas represent the lateral extension of plague in six months.
of the closeup framer (Fig. 16), in order to ensure alignment of the photographs, taken in April and June, 1981, and February and August, 1982. Slides were projected on a Caromate screen and outlines of colonies traced in order to realign successive photographs. Overlays were produced (Fig. 17), from which the lateral extension of plague was measured.

5.3 Results and Discussion

The average lateral extension of plague is $0.96 \text{ cm yr}^{-1} \pm 1.1$. From Chapter 4, the average depth of penetration is $1.3 \text{ cm} \pm 0.3$. Therefore, the rate of plague extension through the substrate is $1.2 \text{ cm}^2 \text{ yr}^{-1} \pm 0.3$. The average amount of substrate removed was $0.8 \text{ gm cm}^{-3} \pm 0.5$ (Chapter 4). Thus, the rate of substrate removal by an advancing front of *Cliona viridis* is $0.9 \text{ gm cm}^{-2} \text{ yr}^{-1} \pm 0.2$ or $900 \text{ gm m}^{-2} \text{ yr}^{-1} \pm 200$.

This number, however, cannot be applied to individual colonies. Consider the following hypothetical situation (Fig. 18). In both cases the total coverage by plague in a square metre is 10%. In case I the 10% is made up entirely by one circular colony, whereas in case II the 10% is made up of ten 1% circular colonies. The rate of substrate removal in the first case is $105 \text{ gm m}^{-2} \text{ yr}^{-1}$; in the second case, it is $329 \text{ gm m}^{-2} \text{ yr}^{-1}$. Thus, the rate at which plague removes substrate is dependent on both the perimeter of the colony and the percent coverage (i.e., two colonies may cover the same percentage of substrate, but have
Figure 18. Hypothetical Situation demonstrating the effects of varying colony morphology on substrate removal rate. Both cases cover 10% of the quadrat (see text).
different rates of substrate removal due to differences in colony perimeters).

Using X-radiography, Hudson (1977) determined growth rates of *Cliona vermifera* to be 1.4 mm yr⁻¹, 6.7 mm yr⁻¹ after establishment of the colony. The initial slow rate may be a reflection of initial settlement, with the boring rate increasing as the colony becomes established (Hudson, 1977). No attempt was made, however, to estimate the percent substrate removed by clionid boring. The lateral extension rate of *Cliona vermifera* is lower than the rate herein determined of *Cliona viridis*.

Moore and Shedd (1977) determined sediment production rates by two methods involving the use of clionid bioerosion by-products. The first method used the volume of clionid borings preserved in the reef accretion record. This method yielded a range of sediment production rates of 190 to 3,290 gm m⁻² yr⁻¹. Cores having low rates of accretion lost 41% of the substrate by clionid activity, while cores with high accretion rates lost 32%.

The second method used by Moore and Shedd (1977) involved the determination of the sediment produced by boring activity as a measure of effective bioerosion. This yielded a value of 2.7 gm m⁻² yr⁻¹ at 40 m to 1,806 gm m⁻² yr⁻¹ at 15 m.

Neumann (1966), Ruetzler (1975), and Bak (1976) used experimental blocks attached to pieces of calcium carbonate "infected" with boring sponges. Both Neumann (1966) and Bak (1976) observed high rates of substrate removal. Neumann (1966), working with *Cliona lampa*, found bioerosion rates at Harrington Sound to be from 22 to 25 kg m⁻² yr⁻¹. This number is several times
higher than the accretion rates of calcium carbonate on reefs as determined by Smith (1973). Bak (1976), working in Curacao using *Cliona peponaca* and larger experimental blocks, obtained lower rates than Neumann (1966), but the rates were almost equal to calcium carbonate accretion rates. The rate of bioerosion at Curacao was found to be 2.5 to 3.3 kg m$^{-2}$ yr$^{-1}$. Ruetzler (1975) worked with *Cliona lamppe* and *Cliona aprica* to determine bioerosion rates. His blocks were smaller than those used by Bak (1976), and the weight loss was determined after the blocks (conch and *Chama* shells) had been submerged for a year, as opposed to the 100 days used by Neumann (1966). Ruetzler (1975) determined the excavation rate to be 0.26 kg m$^{-2}$ yr$^{-1}$, which is significantly lower than the rates reported by either Neumann (1966) or Bak (1976). As discussed earlier in this thesis (Chapter, 4), however, a direct correlation exists between substrate removal and original substrate substrate density. This strongly implies substrate control of bioerosion rate.

Many explanations have been proposed as factors controlling the boring rates of the clionid sponges. Hein and Risk (1975) demonstrated that on the Florida Reef Tract the rate of destruction was related to the substrate type. Neumann (1966) felt depth played an important role in affecting the boring rate at Harrington Sound, as the rate of destruction increased in rapidly flowing waters. Both of these ideas were later supported by de Groot (1980), who found higher boring rates at 3 m and 12 m than at 27 m. There was little difference in the destruction rate between 3 m and 12 m, but the excavating rate was higher in *Acropora palmata* than in
Montastrea annularis.

Hartman (1957) and Pang (1973a) proposed that the difference in boring activities may be intraspecific. That is to say, the difference in boring rates during establishment and growth determines the rates post establishment. This view is somewhat substantiated by Hudson (1977), who found that during the first four years of growth the lateral extension rates were low, but these increased after four years. The initial slow rate may be a reflection of initial settlement; once the organism is established, growth rate increases. This may be true, but it is unlikely to account for the large discrepancies in the values reported in the literature.

Boring rates may be related to the amount of available substrate. Ruetzler (1975) found that boring activity continued until approximately 50% of the substrate was excavated. This is in agreement with the data obtained in this study (Chapter 4). Thus short term studies on fresh substrates should generally show very high boring rates, and long term studies on limited substrates should show very low boring rates (Highsmith, 1981). This is precisely the pattern reported in the literature.

The rates determined by Hudson (1977), and the amount of substrate removed as determined by Moore and Shedd (1977), correlate well with the data presented in this study. These three methods determined the rates directly either by measurement in situ or by measuring sponge-by-products. However, the rates determined by Neumann (1966), Ruetzler (1975), and Bak (1976), are all based on indirect measures of clionid boring activity by "infecting"
experimental substrates over different time periods.
6.1 Introduction

Sponges produce characteristic silt-sized chips (Fig. 1) (Cobb, 1969). The percent contribution of sponge chips to lagoonal sediments was determined by Fuetterer (1974) for the Persian Gulf, the North Adriatic Sea, and Fanning Island Lagoon, Line Islands. No comment was made however, as to the distribution of chips on the reef.

The purpose of this study was three-fold:

a) to determine the percent composition of clionid chips in lagoonal sediments,

b) to determine if there is any significant difference with respect to windward-leeward sides of bommies,

c) to determine if there is any difference across the reef in chip distribution.

6.2 Materials and Methods

Sediment samples were collected across the reef lagoon Davies Reef, from windward and leeward sides of the same bommies as the abundance transects (Chapter 3) using SCUBA. Samples were collected in 500 ml Nalgene jars, by running the mouth of the jar through the surface of the sediment until it was full. After the sediment had settled out the excess water was decanted and 95% EtOH
was added to arrest bacterial degradation.

Samples were coned and quartered and approximately 100 gm (wet weight) of sediment were placed in a 500 ml beaker. Hydrogen peroxide (100 ml) was added to the samples to eliminate the organics, and left to stand for 48 hours with occasional stirring. Samples were flooded with distilled water, the sediments were allowed to settle and the water was decanted (as much as possible without disturbing the sediment). The samples were washed 4 to 5 times more. After decanting the last wash, the sediments were transferred into preweighed beakers, dried at 90°C for 48 hours, cooled in a desiccator and weighed.

The various fractions comprising the total were separated by wet sieving through a series from 0¢ to 4¢ screens. Calgon was added to the sediment prior to sieving to prevent clumping of the grains. No attempt was made to collect the grains smaller than 4¢. The sieves were dried at low temperatures and the fractions transferred into preweighed beakers and weighed on a Mettler Balance.

The percentage of sponge chips in the silt fraction (3¢ and 4¢) was determined by grain counting from SEM micrographs. Double sided tape was stuck to the SEM stub, the other side was touched to the sediment sample. The stubs were gold sputter coated, and observed on a Philips SEM 500 at 40X magnification. Sequential photographs were taken of one traverse across the stub and two stubs were examined for each grain size.
Figure 19. SEM micrograph of 30 fraction used for grain counting.

Boxed area shows sponge chip. Scale bar = 100 \( \mu \text{m} \).
6.3 Results and Discussion

The percentage of fine-grained material produced by Cliona spp. on Davies Reef is $1.2\% \pm 0.8 \ (0.23\%-4.02\%)$ (Table 3, Fig. 19). This is significantly lower than the results obtained by Fueterer (1974) for Fanning Island Lagoon, Line Islands, but corresponds well with the results obtained for the Persian Gulf and the Northern Adriatic Sea (Fueterer, 1974). Chip production in Fanning Island Lagoon amounts to 30% of the total sediments, while in the Persian Gulf and Northern Adriatic Sea chip production represents only 2-3% of the total sediment.

The conditions at Fanning Island Atoll are relatively simple. There is no flux of exogenous sediment to the lagoon (i.e., sediment is produced and deposited in the lagoon), and the sedimentation rate is greater than 1 mm yr$^{-1}$ (50% porosity) (Smith et al. 1970). Fanning Island Atoll illustrates how significant the boring sponges are to the origin of the fine-grained fraction of the lagoonal systems (Fueterer, 1974). The Fanning Island data however, cannot be extrapolated to incorporate the conditions present on Davies Reef. The reef is subject to unequal semi-diurnal three metre tides. Sedimentation rate is lower and there is a net flux of sediment across the lagoon.

The percentage of silt in the total fraction and the percentage of chips in the total fraction (Fig. 20) vary with respect to windward-leeward sides of the bommie (Fig. 21). The percents of both are greater on the leeward side ($P > 0.01$; signed rank test). The aerial coverage of plague however, is greater on the windward
Table 3. The distribution of sediment and sponge chips windward-leeward across Davies Reef.
<table>
<thead>
<tr>
<th>Sample</th>
<th>Location</th>
<th>Depth (m)</th>
<th>Sample Wt (gm)</th>
<th>%Silt Fraction</th>
<th>% Chips in Silt Fraction</th>
<th>% Chips in Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>D1</td>
<td>FRED</td>
<td>6</td>
<td>77.9292</td>
<td>21.5014</td>
<td>8.74</td>
<td>1.80</td>
</tr>
<tr>
<td>D2</td>
<td>90L</td>
<td>10</td>
<td>117.4812</td>
<td>30.8894</td>
<td>8.80</td>
<td>2.74</td>
</tr>
<tr>
<td>D4</td>
<td>2</td>
<td>12</td>
<td>133.3355</td>
<td>16.0332</td>
<td>5.58</td>
<td>0.89</td>
</tr>
<tr>
<td>D3</td>
<td>60L</td>
<td>15</td>
<td>110.4418</td>
<td>45.3295</td>
<td>8.86</td>
<td>4.02</td>
</tr>
<tr>
<td>D6</td>
<td>3</td>
<td>7</td>
<td>87.2262</td>
<td>15.8903</td>
<td>6.68</td>
<td>1.06</td>
</tr>
<tr>
<td>D5</td>
<td>310L</td>
<td>8</td>
<td>89.6003</td>
<td>17.7485</td>
<td>6.65</td>
<td>1.18</td>
</tr>
<tr>
<td>D8</td>
<td>4</td>
<td>20</td>
<td>131.3559</td>
<td>14.0903</td>
<td>3.27</td>
<td>0.46</td>
</tr>
<tr>
<td>D7</td>
<td>330L</td>
<td>15</td>
<td>51.4059</td>
<td>13.9723</td>
<td>3.71</td>
<td>0.51</td>
</tr>
<tr>
<td>D10</td>
<td>5</td>
<td>15</td>
<td>102.4591</td>
<td>6.9302</td>
<td>6.24</td>
<td>0.43</td>
</tr>
<tr>
<td>D9</td>
<td>70W</td>
<td>18</td>
<td>62.4921</td>
<td>16.0271</td>
<td>2.82</td>
<td>0.45</td>
</tr>
<tr>
<td>D11</td>
<td>6</td>
<td>13</td>
<td>86.3658</td>
<td>18.3690</td>
<td>3.30</td>
<td>0.61</td>
</tr>
<tr>
<td>D12</td>
<td>280L</td>
<td>14</td>
<td>132.2278</td>
<td>34.3912</td>
<td>2.80</td>
<td>0.96</td>
</tr>
<tr>
<td>D14</td>
<td>7</td>
<td>14</td>
<td>122.6932</td>
<td>26.8408</td>
<td>3.13</td>
<td>0.84</td>
</tr>
<tr>
<td>D13</td>
<td>330L</td>
<td>13</td>
<td>100.3708</td>
<td>33.4128</td>
<td>2.25</td>
<td>0.75</td>
</tr>
<tr>
<td>D15</td>
<td>8</td>
<td>15</td>
<td>85.3817</td>
<td>21.5228</td>
<td>2.89</td>
<td>0.68</td>
</tr>
<tr>
<td>D16</td>
<td>330L</td>
<td>20</td>
<td>50.6364</td>
<td>40.0382</td>
<td>2.77</td>
<td>1.11</td>
</tr>
<tr>
<td>D18</td>
<td>9</td>
<td>11</td>
<td>122.0219</td>
<td>22.1144</td>
<td>2.68</td>
<td>0.59</td>
</tr>
<tr>
<td>D17</td>
<td>270L</td>
<td>14</td>
<td>90.3420</td>
<td>47.1553</td>
<td>1.70</td>
<td>0.80</td>
</tr>
<tr>
<td>D19</td>
<td>DDR</td>
<td>12</td>
<td>71.6930</td>
<td>5.4860</td>
<td>4.13</td>
<td>0.23</td>
</tr>
<tr>
<td>D20</td>
<td>60W</td>
<td>14</td>
<td>89.2145</td>
<td>24.6191</td>
<td>2.71</td>
<td>2.71</td>
</tr>
</tbody>
</table>
Figure 20. Histogram showing the distribution of the fractions within the sediment. Blackened areas show the %Chips found within the silt fraction. Plotted above is a cumulative graph of the fractions in the sediment.
Figure 21. Cumulative plot showing the windward-leeward distribution of sediment. $W =$ windward, $L =$ leeward.
Trends across the reef (i.e., front - back) are not clearly defined, although three peaks do appear on the leeward side (Fig. 22). The first peak occurs on bommie Fred, just behind the reef crest. Although plague abundance is low (Chapter 3), the abundance of other clionids in this area is relatively high. This may be, to some extent, the result of transport of chips across the reef crest. The maximum peak at bommie 2 corresponds to a high abundance of plague on the windward side of this bommie (Chapter 3). This suggests some transport of sediment windward-leeward around the bommie. The third peak, occurring on the leeward side of DDR bommie, is possibly due to transport of sediment off the sandspit. Windward samples across the reef show a general trend to decrease in the number of sponge chips from the reef-front to back-reef. This corresponds to a general decrease in plague across the reef (Chapter 3). The small peaks are most probably due to sediment movement from the lee side of one bommie to the windward side of the next bommie. This would suggest sediment transport within the lagoonal system. Andrews and Mueller (1983) found evidence of a similar system operating at Britomart Reef, Great Barrier Reef, using nutrient monitoring. Thus the generalization of Fuetterer (1974) is not applicable to Davies Reef, and similar conditions appear to exist at Britomart Reef.
Figure 22. Moving averages plot showing the windward-leeward %Chips across Davies Reef Lagoon. $W =$ windward, $L =$ leeward.
Chapter 7 -- Conclusions

Plague is more abundant on the windward sides of lagoonal bommies on Davies Reef. This sponge extends laterally about 1 cm yr\(^{-1}\), bores to a relatively constant depth of around 1.3 cm, and removes substrate at a rate of approximately 1 gm cm\(^{-2}\) yr\(^{-1}\) with an average biomass of 9.8%. Plague continues to bore until about 37% of the substrate has been removed. The contribution of the boring sponges to the lagoonal sediment on Davies Reef is approximately 1.2% with a greater %abundance of sponge chips on the leeward sides of the bommies.

The above results suggest a number of processes affecting both sponge and chip distribution:

a) abundance of *Cliona viridis* is related to substrate availability and water energy (i.e., %abundance is greater on the windward side of bommies.

b) sponge chip distribution supports the hypothesis of Andrews and Mueller (1983) of water cycling around bommies.

c) amount of substrate removed is proportional to the original density of the substrate.

None of the parameters measured in this study appeared to affect the %biomass. In areas of increased substrate availability, however, the sponge boring rate may increase thereby decreasing the sponge biomass within the gallery; if substrate were limited,
boring rate would decrease and hence biomass increase. One of the factors controlling biomass may be the boring rate. Further studies of this sort are required.

Much work is required both in sorting out the taxonomy of the group, and the factors controlling the distribution and boring rates. Studies in situ monitoring a number of parameters over a period of time are required. Transplant studies would then be useful in determining the effect(s) of changing one or more of these factors on growth and boring rate over time.

Once there is a clear understanding of the processes affecting this group of organisms in modern carbonates, we will then be in a better position to interpret both Pleistocene reefs and ancient records of sponge borings. Bioerosion plays a major role in determining the morphology and porosity of reefs preserved in the fossil record; sponges are particularly important contributors to reef derived lagoonal sediments.
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