LITTLE BUGS
AND THE GREAT
CORAL CRUNCHING SPONGE

By

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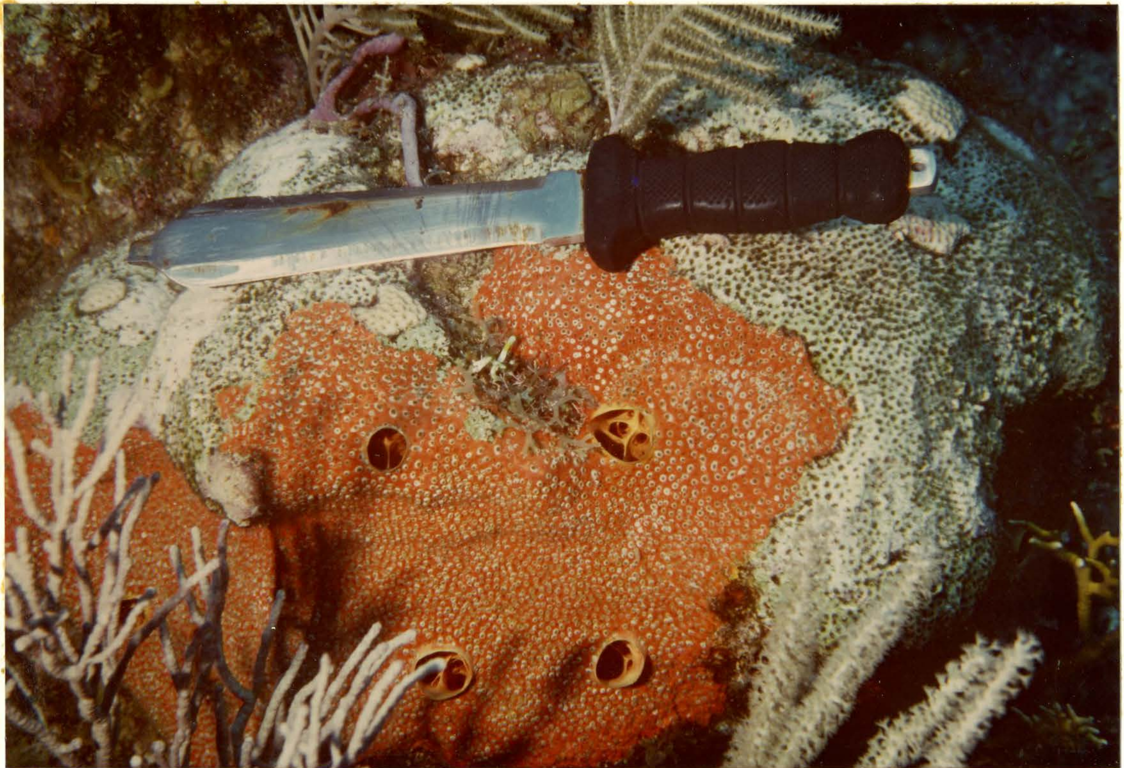

Plate 1. Cliona delitrix infesting dead Montastrea annularis substrate.

ABSTRACT

A 4.6-fold increase in the biomass of Cliona delitrix infesting Montastrea cavernosa substrate occurred in a portion of the Grand Cayman fringing reef affected by the discharge of untreated fecal sewage. It is suggested that the 6.3-fold increase in bacteria biomass (both coliforms and natural marine bacterioplankton) is linked to the sponge proliferation at the polluted site.

Since demosponges normally obtain much of their nutritional needs from URPOC and only 1% from bacteria, the significance of the elevated bacteria count may be limited to its importance as a flag as an indicator of untreated sewage effluent.

At the polluted study site, Montastrea cavernosa exhibited a 45% reduction in the amount of substrate occupied by living polyps. The loss of this respiring coral biomass is probably not compensated for by the biomass increases of C. delitrix and of the microflora inhabiting the dead substrate. The increased C. delitrix biomass reflects a similar increase in the amount of M. cavernosa skeleton that has been eroded and reduced to silt-sized sediment. Thus, the discharge of untreated sewage into the reef environment can have a profound effect upon the trophic distribution of reef fauna, leading to a disturbance of the precarious balance between carbonate production and destruction on the reef.

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INTRODUCTION

Coral reef response to environmental stress

The physical environment of shallow marine coral reefs is relatively stable, being subject to little seasonal fluctuation in energy and nutrient input.This constancy of light, temperature and nutrient conditions has allowed the evolution of a highly diverse and complex biological community, characterized by a well developed trophic structure and a high degree of interaction between and specialization of its inhabitants (Odum and Odum, 1955; Johannes, 1975).Futuyma (1973) proposes that a community characterized by a diverse fauna having many coevolved species relationships can only sustain a high stability in a relatively constant environment; a large perturbation in one or more physical conditions will inevitably lead to a dramatic change in community structure.It is therefore probable that the highly specialized and interacting component species of a reef collectively can not tolerate environmental fluctuations to the same extent that the generalist species of a less stable environment can (Johannes and Betzer, 1975).In addition, a stress upon one species is likely to be propagated via disrupted food chains and symbiotic relationships to other species of different trophic levels, resulting in a concerted infringement upon or elimination of reef inhabitants (Futuyma, 1973).

Conversely, Connell (1978) proposes that the high diversity of coral

reefs can only be maintained in a nonequilibrium state. Disturbances at intermediate scales of intensity and frequency operate to prevent the competitive exclusion of species that are less efficient in utilizing the shared resources (light, space, CO_2 and food). Although having undergone much coevolution, most reef organisms including corals do show considerable overlap in their food and habitat requirements. It is suggested, however, that excessive natural disturbances and anthropogenic perturbations, primarily siltation and pollution, may cause an irreversible reduction in the species diversity of the reef. The detrimental impact of the latter force is attributed to the poor adaptiveness of reef fauna in general to man-induced stresses (Connell, 1978).

Organic pollution represents a stress of potentially wide ranging impact because of its immediate effect upon the lower levels of many complex food chains. Bacteria growth rates are thought to be nutrient limited (Rheinheimer p.111, 1980) and the response of microbial activity to nutrient loading might subsequently have a profound influence upon the faunal distributions at higher levels of the trophic pyramid.

The role of bacteria in the reef

Bacteria fulfill several essential roles in reef ecosystems. Loss of nutrients to the surrounding ocean waters is countered by the bacterial decomposition of dead organic matter and the subsequent remineralization of nutrients into forms that can be utilized by the primary producers and consumers of the reef. Other key metabolic activities of bacteria involve the conversion of inorganic materials into nutrients and the production of bacteria biomass. Bacterial enzyme substrates include almost all compounds in

dead plant and animal matter and all the organics lost by algae and zooplankton through extracellular excretion, moulting and diffusion (Wood p.144, 1967; Nienhuis, 1981).Bacterial regeneration and assimilation of nitrogen and phosphate is thought to be particularily vital because of the low, possibly limiting concentrations of these nutrients in tropical surface waters (Fenchel and Jorgensen, 1977; Nienhuis, 1981).The loss of particulate and dissolved refractory organics (sea humus) is partially compensated for by the bacterial decomposition of allochthonous organic material entering reef waters.The extent to which bacteria actually recycle nutrients in reef waters remains an open question because of the unquantified influences of other animal metabolisms (Wood, 1967; Johannes et al., 1968) and the variable state of nutrient flux across the reef (Andrews et al., 1982).

An equally fundamental role is the introduction of bacteria biomass into reef food chains.Although primary production by bacteria is not thought to be quantitatively important (Rheinheimer p.137, 1980), secondary production in reef waters has been suggested to approach or even exceed the primary production by phytoplankton (Sorokin, 1974).Bacteria production for an aerobic tropical aquatic community as a whole has been theoretically calculated to be approximately 25% of the primary production (Fenchel and Jorgensen, 1977).This is based on the premises that about 50% of annual production enters the detritus food chain and that about 50% of the detrital organics consumed by bacteria enter biosynthetic pathways.Sorokin (1973) estimates that bacteria production in reef sediments and lagoonal waters exceeds that of tropical sea sediments and open oceans waters by factors of 1000 and 10-20 respectively.

The symbiotic association of heterotrophic bacteria and cyanobacteria with certain reef denizens illustrates another nutritional capacity of

bacteria in the reef.Wilkinson (1978) comments on microbial populations inhabiting the tissues of several reef sponges.While the cyanobacteria presumably function in the same manner as zooxanthellae, the typically facultative aerobic bacteria may serve to metabolize amino acids and urea excreted by the host sponge.Waste removal can consequently be carried out during phases of inactive pumping, which allows the sponge to withstand temporarily disturbed habitats.

Bacteria as a food source

The biomass of sediment and planktonic bacteria represents a potential food resource for most filter and detritus feeding benthic animals (Sorokin, 1974; Nienhuis, 1981).Detritus feeders ingesting bottom sediment and organic debris are thought to utilize mainly the microbial content of the ingested matter (Newell, 1965).Certain species of sponges, sabellid polychaetes, colonial and solitary tunicates, oysters and corals have all been observed to filter bacterioplankton at various efficiencies (Sorokin, 1974).Sponges and sabellid polychaetes demonstrate highly efficient bacterial filtering mechanisms (Reisweig, 1971; Sorokin, 1974).Although normally consumers of phytoplankton, particulate organic matter (including the unresolvable fraction) and bacteria, sponges can satisfy most of their energy needs by bacteria assimilation alone (Sorokin, 1974).It is estimated that corals normally satisfy about 20% of their total energy demands by feeding on dissolved organic matter and bacterioplankton (Sorokin, 1981).

Bacterial multiplication promotes the aggregation of bacteria and organic debris.The aggregated biomass, about one third of the total bacteria biomass (Sorokin, 1974), thus becomes available to the normally algal

feeding coarse filterers: tunicates and molluscs. Carnivorous zooplankton, including mollusc veligers, are known to feed upon single and aggregated bacteria (Sorokin, 1974). Although assimilation capabilities vary widely, it is generally accepted that benthic filtering invertebrates do derive a substantial proportion of their energy and nutrient requirements from the protein rich bacteria biomass of reef waters (Sorokin, 1974). An undetermined contribution is made by the dissolved and particulate organic matter that is ingested along with the bacteria.

The effect of pollution upon microbial activity

What is the immediate effect of organic pollutants upon microbial abundance and metabolic activity? Rheinheimer (p.110, 1980) states that organic material, or rather the readily assimilated fraction of that material: proteins, sugars and organic acids: is often the limiting factor in bacteria abundance. Sorokin' s data (1973,1974) of heterotrophic bacteria abundances for the heavily polluted Kaneohe Bay reef waters in Hawaii and for waters of other nonpolluted Pacific atoll reefs unexpectedly do not reveal significant differences. The Kaneohe Bay pollutants are biologically purified domestic wastes, meaning that 95% of the coliform bacteria have been eliminated (Rheinheimer p.198, 1980). Assuming that Sorokin's method of direct microscopy enumeration is reliable, bacteria counts for reef water subject to an input of purified sewage consequently can not be considered a useful pollution indicator.

In dealing with the problem of unpurified fecal sewage, one can analyse the rate of decline of coliform bacteria as a function of the toxic toll of the marine salinity, temperature and the amount of sunlight, suppression by

the diverse natural marine bacterioplankton and dilution through sedimentation, tidal flushing and current activity (see Stewart et al., 1969; Rheinheimer p.195, 1980). Stewart et al. (1969) have determined a 90% mortality time of 1.5 hours for coliforms released into Florida waters in August. The decline of coliforms away from the source is coupled with the rise of a new, predominantly saprophytic marine microflora of mainly proteolytic and cellulose digesting organisms (Rheinheimer, 1980). It is this population that carries out the natural self purification, i.e. the degradation and remineralization of the organic pollutants entering the reef waters.

Regarding the effect of sewage upon microbial metabolism, the Kaneohe Bay waters were found to give the highest daily turnover rate for bacteria for the four Pacific reefs studied by Sorokin (1974). The higher rates of metabolic activity, biosynthesis and nutrient regeneration can be explained by the higher levels of particulate organic matter observed by Banner (1974). Debris particles adsorb much of the suspended organics and the tendency of bacteria to agglutinate to such particles means that a higher concentration of substrate becomes available for bacterial breakdown (Nienhuis, 1981). Sorokin's data indicate that the ratio of bacteria to phytoplankton production is lowest for the polluted waters. DiSalvo (1971) found that the waters of inner Kaneohe Bay were oxygen depleted and that the rate of sediment metabolism was reduced accordingly. Phytoplankton photosynthesis typically shows a positive response to moderate nutrient loading, as shown by the nitrogen and phosphate fertilization of a microatoll reef by Kinsey and Domm (1974). Extreme loading, however, is thought to cause the sediment oxygen consumption of poorly aerated waters to exceed the daytime production by phytoplankton. Periodic anaerobiosis ensues,

leading to the poisoning of phytoplankton and corals by hydrogen sulphide liberating anaerobic bacteria (DiSalvo, 1971; Sorokin, 1973).

Effect of pollution upon bacteria consumers

Since the potentially high production of bacteria in organically loaded waters is not observed, one might presume that abundances of bacteria consumers rise concomitantly with the introduction of pollutants.The zooplankton population of Kaneohe Bay waters exhibited a low diversity and rapid fluctuations in size, possibly as a result of an augmented heterotrophic nature and dependence upon an unstable bacteria population.Banner (1974) also noticed the growing dominance of filter and detritus feeders: sponges, holothurians, oysters, clams and tunicates: in sediments surrounding the sewage outfall.Johannes (1975) lists cases of elevated densities and ranges of sponges, holothurians and tubiculous polychaetes in the vicinities of sewage outfalls.

Brock and Smith (1982) noted that the hard substrate benthic communities of Kaneohe Bay had demonstrated a dramatic change in biomass in response to the elevated nutrient input.During the period of heavy sewage discharge, the macrofaunal biomass was observed to increase towards the source of the sewage.Heavily affected communities near the sewage outfall were dominated by filter and suspension feeders, while the hard substrate communities further away displayed a more equitable distribution of biomass among different feeding types and trophic levels, and a less heterotrophic nature overall.The diversion of the sewage flow in 1977 resulted in a rapid decline in the biomass of the stressed communities, suggesting that the macrofaunal biomass was highly responsive to this particulate food source.

Effect of pollution upon reef bioerosion

While Johannes (1975) suggests that the release of a moderate amount of treated sewage can enhance reef productivity without appreciably altering the community structure, the observations at Kaneohe Bay (Brock and Smith, 1982) indicate that a significant shift in the trophic distribution of reef fauna may occur during a period of prolonged sewage input.The resultant increase in both primary and secondary productivity of the reef waters is coupled with an increasingly heterotrophic hard substrate benthic community.

With regard to the activities of coral bioeroders, it has been suggested that the boring of endolithic algae is accelerated by nutrient loading (Risk and MacGeachy, 1978).Bacteria themselves may contribute to the breakdown of coral substrate by mineralizing the internal organic of the skeletons (DiSalvo, 1973). Some macrofaunal members of the hard substrate community contribute much more substantially than others to reef bioerosion.Risk and MacGeachy list as important eroding macroborers Cliona and Siphonodictyon sponges; species of eunicid, sabellid and spionid polychaetes; sipunculid worms and boring bivalves.All except the eunicids are suspension or filter feeding benthic animals.

Hein and Risk (1975) state that clionid sponges and spionid polychaetes were responsible for the average removal of 28% of the primary framework of massive coral skeletons.Clionid sponges are known to excavate up to 50% of the infested substrate (Rützler, 1975); 97-98% of this skeletal material forms silt-sized sediment (Rützler and Reiger, 1973).These sponge chips are known to make up anywhere from 2-3% to 30% of shallow marine sediments (Fütterer, 1974).

The fact that the rate of bioerosion approximates the rate of skeletogenesis in mature corals (Hein and Risk, 1975) means that a delicate balance is maintained between the activity of reef bioeroders and coral growth. Risk and MacGeachy (1978) predict that reef infauna, including clionid sponges, are more successful in utilizing sewage matter and associated bacteria than are corals. Consequently, sewage input may irreversibly shift the balance between reef growth and erosion by preventing the regeneration of corals and stimulating the reduction of coral skeletons into carbonate sediment. This study is an attempt to quantify the changes in the physical interaction between a common boring sponge and a dominant coral that are induced by the organic and bacterial loading of a shallow exposed reef.

MATERIALS AND METHODS

I. Study area

A fringing reef surrounds essentially all of Grand Cayman Island (Roberts et al., 1975).The chosen research areas were two approximately 50 m reef tracts: the study reef was located opposite the Cayman Turtle Farm on the northwest shore, and the control reef was located about 1 km further north.Both areas of the coast are characterized by a moderate to high energy shelf profile having two forereef terraces separated by a drop-off at about 10 metres depth (Roberts et al., 1975).The reef crest described by Roberts et al. (1975) is not well developed on this portion of the coast.The offshore margin of the shallow terrace is defined by a well-developed coral buttress, the steep seaward side of which descends about 5 m to the gently sloping sand plain of the deeper forereef terrace.Both terraces and buttress are intersected at high angles by narrow sediment floored grooves which serve to attenuate and dissect the southwestwardly trending currents.All coral and sponge observations and measurements were made within a 3-4 m wide linear tract along the buttress at a depth of 9-11 m.

The Cayman Turtle Farm houses eighteen 3000-litre tanks which hold a maximum of 300 turtles.When the farm is at maximum holding capacity, tank water having a concentration of 0.0112 g/l of untreated fecal matter is discharged into the waters over the reef at a rate of 162 m^3/hour (from data of Wood and Wood, 1981).On calm days, a visible plume was observed to spread out over a 50 m length of the reef.The more northward control site was deemed to be far enough removed to escape contamination, especially in view of the predominantly southwestwardly trending currents along this portion of

the shoreline. The shore barrier at both sites, an exposed and weathered Pleistocene reef flanked by beach sands, is thought to minimize the runoff and siliciclastic input from cleared inland areas. Sewage from houses along the coast is discharged into wells drilled deep into the bedrock.

II. Assessment of coral and sponge interaction

An overall preliminary survey of coral head density and volumes and of boring sponge diversity and abundance was made at each site. *Montastrea cavernosa*, a massive large-polyped coral, appeared to be the dominant coral species in the buttress and was frequently infested by *Cliona delitrix* at the turtle farm locality. The obvious discrepancy in the degree of association of these two species at the two sites as well as the quantitative importance of the coral species as a framework producing agent prompted an investigation of this coral-sponge relationship.

Shore-parallel transects, of lengths 45 and 10 metres for the turtle farm and control sites respectively, were run along the buttress and all heads of *M. cavernosa* within two metres of the transect line were tagged and photographed. Surface area of *Cliona delitrix* colonies infesting the heads was estimated to the nearest 10 cm^2 using a quadrat frame divided into 100 cm^2 squares. During a second transect of 20 metres length, run adjacent to the first control site transect, heads were counted and checked for *C. delitrix* infestation but not photographed or measured.

Twenty-four small *M. cavernosa* heads showing *C. delitrix* infestation were collected at the turtle farm site and later fixed in 10% formalin and air dried. Spicule mounts were made for ten different sponge specimens using the method outlined by Rützler (1978). The heads were examined before and

after slabbing for infestation by other sponge species, lithophagine bivalves and boring worms.

Hand sample surface area estimates of live polyp tissue, dead coral including cover by coralline and filamentous algae, and sponge papillae with and without the surrounding dead coral zone, were obtained by folding a plastic sheet onto the coral sample and tracing and measuring the area of plastic in contact with the appropriate area of the coral.A second set of measurements was obtained for two heads by a second individual and the maximum operator error was determined to be 11% of the larger measurement. A comparison of the total polyp area values obtained for all the hand samples using both the quadrat frame and plastic methods yielded an average relatve error associated with the former method of 10% (see Appendix 4).No assessment of the relative error associated with the method of using plastic covers could be made.

Coral head volumes of the hand samples were measured by water displacement.The total volume of a sponge infested region was estimated by slicing the coral into 0.4-1.0 cm thick slabs and measuring the cross-sectional areas of the infested portions of each slab.Areas of adjacent slabs were averaged and multiplied by slab thickness to give volume.Coral slabs were oriented perpendicular to the long axis of the sponge colony and to the surface of the infested coral in order to minimize the error inherent in the procedure.All surface area measurements of hand samples were obtained using a MMOP.

The method of volume estimation used for the large in situ coral heads involved tracing cross-sectional views from the photographs.Sections taken from different photographs of the same head and from opposite sides of the same head were averaged to produce a profile for each head.An axis of

rotation was chosen on the basis of the apparent symmetry of the head.The final curve, depicting the average shape of one side of the coral head, was assigned the parameters of either an ellipse, cylinder, parabola or cubic curve (or a combination of several) and volume was calculated using the appropriate integral.In the event of a hollowed out head, the volume was corrected according to the thickness of the veneer (measured in the field).The accuracy of this method was determined by applying it to two hand samples and comparing the results to the values obtained using the water displacement method.As the relative error associated with the water displacement method was 5% and the maximum difference between results of the two methods was 28% of the displacement value, the maximum relative error of the volume by photograph method is taken as 33%.

To calculate biomasses of polyp and sponge tissue, chunks of unbored and infested coral were weighed before and after digestion in 50% hydrogen peroxide (immersion for 2 weeks).Specific gravity measurements of both unbored and sponge infested coral were obtained using the method outlined by Bergman (1983).The weight ratio of spicules to spicules plus sponge biomass and coral skeleton was calculated by weighing the spicule residue of a preweighed fragment of sponge infested skeleton that was dissolved in a heated, dilute solution of HCl.

III. Assessment of organic and bacterial loading of reef waters

Water sampling was carried out at both sites, using 125ml polyethylene bottles and 1-l plastic bags, at depths of about 10 m in the vicinity of the buttress and about 0.5 m within a few metres from shore and in the middle of the plume at the one site.Salinity and temperature readings were taken from

the bagged surface water within one hour of sampling using a S-C-T meter (YSI Model 33).Half-litre portions of this water were fixed with 3% formaldehyde (final concentration) and were filtered through 0.4 μm preweighed Millepore filters.The filters were oven dried and reweighed after transport in order to obtain concentration levels of total suspended particulate matter.

The bottled samples were fixed and stained with acridine orange (1:30,000) immediately after transport from the collection site.After subsequent storage for four months at -5° C, the samples were filtered through 0.4 um Millepores and attempts were made to count bacteria from the filters using epifluorescence microscopy (see Dale, 1974).The method was abandoned, however, because of poor or absent fluorescence of the bacteria cells.Instead, volumes of 15, 30, 60 and 90 ml were filtered through Nucleopore filters and bacteria were counted from SEM micrographs of the filters taken at 3,000X magnification.

Bacteria were identified on the basis of size and shape; only discrete intact cell bodies larger than the 0.2 μm filter pores and having smooth, fairly symmetrical outlines were counted.The widths and lengths of dried coliform cells fall into the ranges 0.4-0.8 μm and 1.0-3.0 μm respectively (Luria, 1960).Cells of this size class are termed coliform-like since large natural marine rods can not be distinguished from true coliforms on the basis of size and shape alone.Most marine cocci and rods, however, are substantially smaller, having a greatest dimension of 0.3-0.8 μm (Reisweig, 1971).A range of 0.2-1.0 μm was chosen for this study.Subspherical bodies with diameters larger than 1.0 μm were interpreted to be either algae or artifacts of the drying procedure and were not included in the analysis.

Regarding the process of enumeration, eight fields of view were chosen

at evenly spaced intervals along two transects across the central portion of each filter. In this manner, 0.00949 mm^2 of each 1080 mm^2 of filter paper, corresponding to a water volume of 0.132 ul for each 15 ml sample, was scanned. Those fields of view bearing creases in the filter or having charging of bound material occur under the SEM were not photographed. Fields of view that were dominated by clay flake aggregations, disintegrating fecal matter or bands of mucus were also rejected, although the occurrence of these particulate fractions was noted for each filter.

The operator error affecting the bacteria counts was checked by having a second individual derive the total bacteria data for two filters. The two values differed by 8-10%. The precision of the single operator enumeration was determined by comparing results obtained by the same individual for two sets of eight micrographs from the same filter. Although the counts for individual size classes of bacteria differed by a maximum of 5%, the total bacteria counts differed by only 1%. This result suggests that a small margin of error exists in the discrimination between the different bacteria sizes but that the procedure does give a highly precise determination of total bacteria abundance. The accuracy of the procedure, however, was not checked by comparison with the results of other enumeration methods. It is thought that the method used here may produce underestimations of the actual abundances due to the distortion of cells during preparation and the concealment of cells in bacterial aggregates or adhering to clay flakes.

RESULTS

I. Species descriptions

1. Montastrea cavernosa

Although Lehman and Porter (1973) identify two coexisting polymorphic forms of Montastrea cavernosa with different polyp sizes, the corals at Grand Cayman are represented by the small-polyped form only. Corallites are elliptical in cross-section with internal diameters of .56 and .46 cm. Both dimensions are normally distributed. The ratio of corallite wall thickness to average internal diameter, which gives a relative indication of skeletal density (Highsmith, 1980), is 0.36. A nonsignificant correlation ($r=-0.320$, $N=19$) was found between maximum polyp diameter and coral head size, suggesting that a constant polyp size is attained early in colony development and subsequent growth is limited to budding rather than polyp enlargement. The large-polyped form was observed by Lehman and Porter to be an indiscrimant ingestor of suspended particulate matter. This form may arise as an ecophenotypic variation in waters of locally reduced zooplankton abundance; more study is needed to assess the nutritional and genetic controls upon growth form.

The overall shape of the coral heads commonly resembled an ellipsoid with an obliquely cut base. Hemispherical, cylindrical and paraboloid shapes were less frequently observed, although cylindrical shapes were typically displayed by the larger, mature specimens. The algal infestation of the flat tops of these heads suggests that the polyps inhabiting the upper surfaces had been killed at a relatively recent time, i.e. after the major growth of

the coral had taken place.

2. *Cliona* *delitrix*

The species name of the clionid sponge under investigation is Latin for "a destroyer". The sponge overgrows the surface of its substrate and excavates long cylindrical galleries that run perpendicular to the coral surface (Pang, 1973). The sponge can be identified by its red to red-orange colour underwater (see plate 1) and brownish colour after formalin fixation and drying. The discrete ostial and oscular papillae of young specimens fuse early in development. The surface papillae of mature specimens are sometimes dotted by the white zoanthid *Parazoanthus* *parasiticus* (Pang, 1973). The outline of the fused papillae is commonly an irregular ellipse although some irregular shapes, indicating various degrees of fusion of immature papillae or isolated colonies, were also observed. A narrow band of dead coral is commonly found around the sponge papillae.

The spicule mounts revealed the existence of tylostyles only (see plate 2). The tylostyles are typically straight, although about 10% are slightly curved; all bear subterminal knobs or poorly developed heads (see Pang, 1973). Tylostyle lengths and widths, as measured on SEM micrographs of spicules from one sponge colony, are 325 and 10.05 μm with ranges of 256-358 and 5.03-12.02 μm (N=25 and N=30 respectively). Pang reports length and width values of 279 and 8.9 μm for spicules in colonies found at depths of 22-34 m, 12-24 m deeper than the colonies used in this study. This size difference supports her hypothesis that differences in silica concentration with depth may influence spicule sizes.

Skeletal excavation by *C.* *delitrix* appears to be concentrated in the

axial regions of corallites (see plate 3). Excavational activity is most intense in immature colonies. At this stage, the sponge occupies relatively large open galleries which have a maximum dimension of 0.8-1.4 cm and are separated by thin, ragged walls (see plate 4). The depth at which the original pioneering filaments fuse and initiate lateral excavation of galleries appears to be 1-2 cm beneath the substrate surface (see graph 5). Sponge filaments occupying the axial regions of neighbouring corallites give rise to additional discrete ostial and oscular papillae.

Subsequent growth after papillary fusion involves the addition of smaller, ellipsoidal galleries with maximum diameters of 0.3-0.8 cm to the periphery of the colony and the enlargement of preexisting central galleries and oscular canals (see plate 3) .Pioneering filaments penetrate into unbored skeleton and either encounter advancing sponge lobes or expand to excavate additional peripheral galleries. Consequently, all gallery walls are pierced by many holes with a variety of diameters (see plate 5). Although the lateral growth of the colony may be quite extensive, the depth of infestation did not exceed 5.0 cm for any of the specimens examined (see graph 5). This depth limit may correspond to the maximum length of incurrent and excurrent canals through which current flow can be generated by choanocyte pumping in the terminal chambers. The expansion of surface tissue during colony enlargement proceeds by the peripheral addition of outlying, discrete oscular and ostial papillae to the continually growing central papillae. The average diameters of the elliptical oscules incorporated into the central papillae were measured to be 7.67 and 6.38 cm for dried and fixed specimens. The ostia under 2 mm in diameter were usually circular while the larger elliptical ones had average diameters of 2.16 and 1.84 mm.

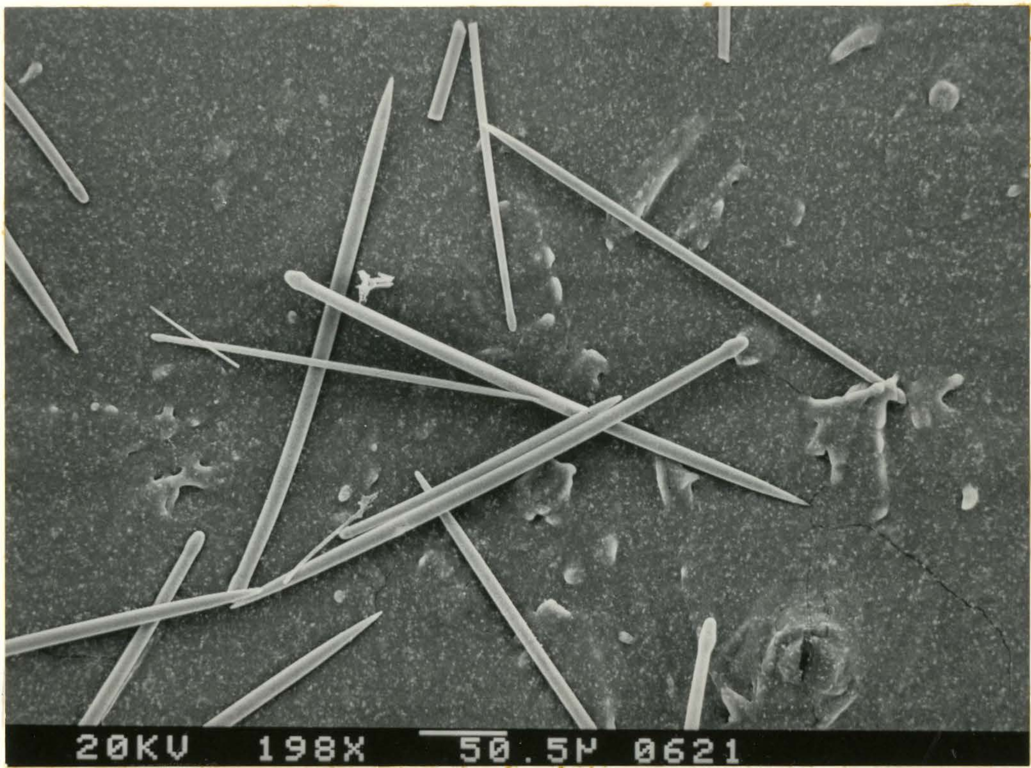
Subsurface lateral growth usually precedes the advance of the sponge

surface tissue.The outside edge of the surrounding dead coral zone almost always overlies the furthest extent of the subsurface colony growth.This suggests that the polyp killing agent is a product of the subsurface tissue of the sponge rather than of papillar tissue.Examination of the etched surface of the dead coral zone under the SEM did not reveal any sponge filaments to be penetrating into polyp tissue or into skeleton adjacent to polyp tissue.Instead, polyp death may be induced by the diffusion of a sponge produced toxin across the dead zone, similar to the toxin-mucus transfer mechanism effected by *Siphonodictyon* (Sullivan and Faulkner, 1983).

Plate 2. Tylostyles of *Cliona delitrix*

Plate 3. (left) Excavation of *M. cavernosa* skeleton by *C. delitrix*. Note that excavational activity is concentrated in the axial region of corallites.

Plate 4. (right) Sections through *C. delitrix* excavations made at an early stage of infestation. Note the large, open galleries separated by thin ragged walls.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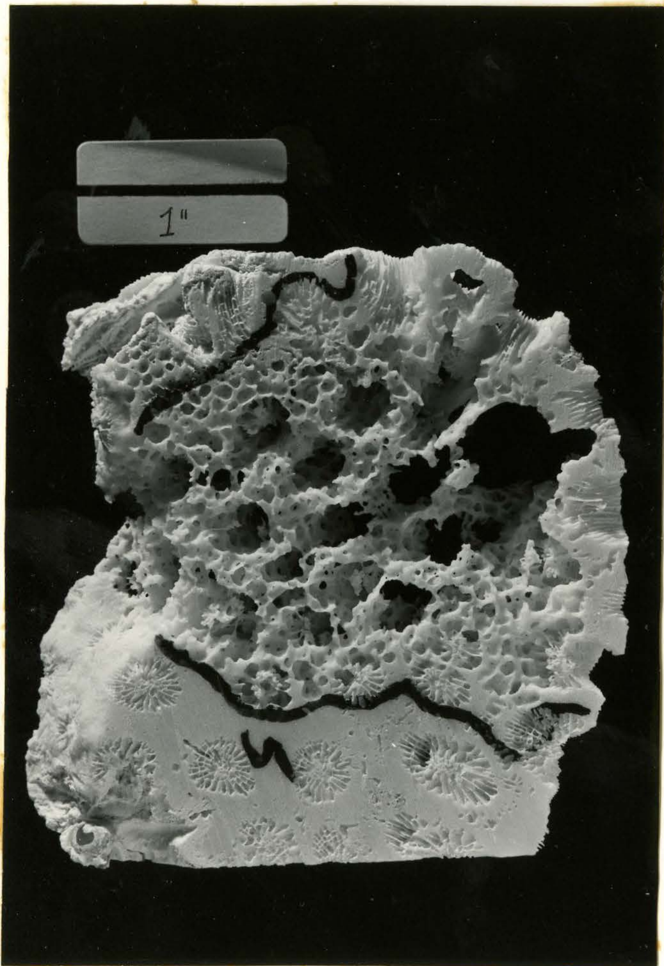
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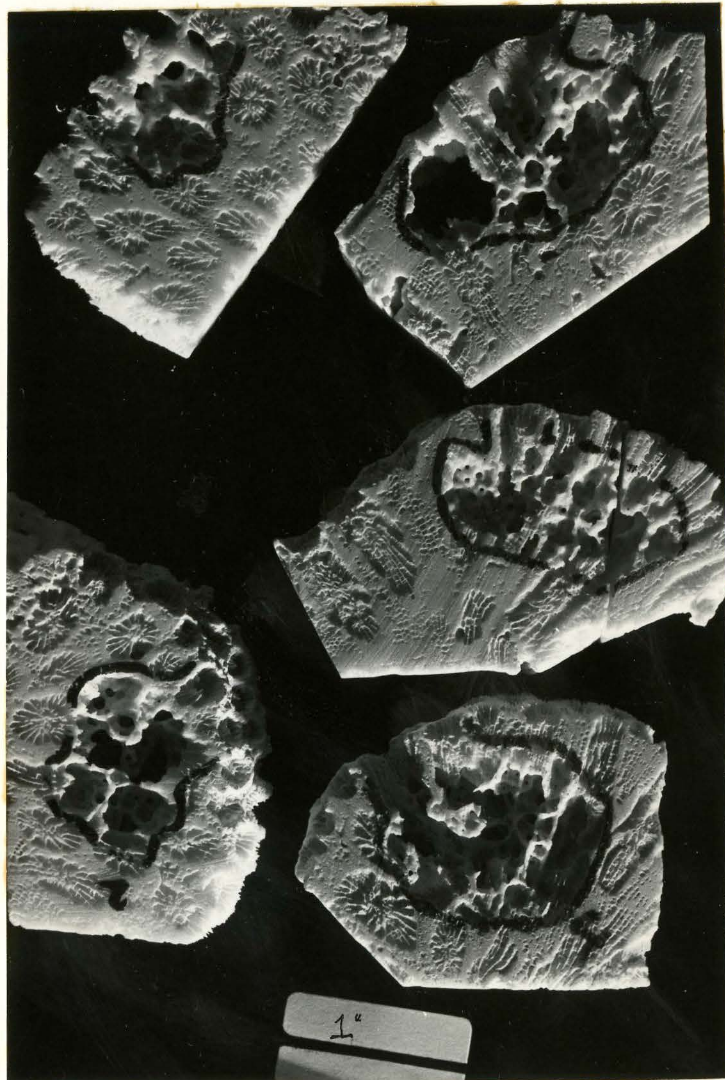
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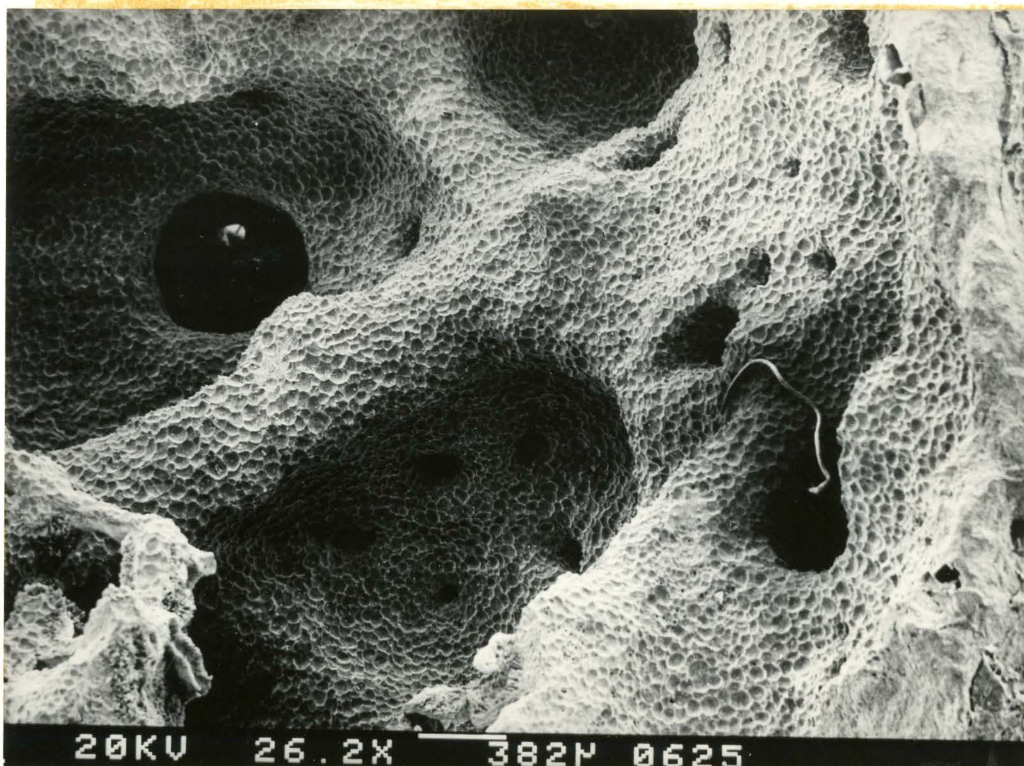
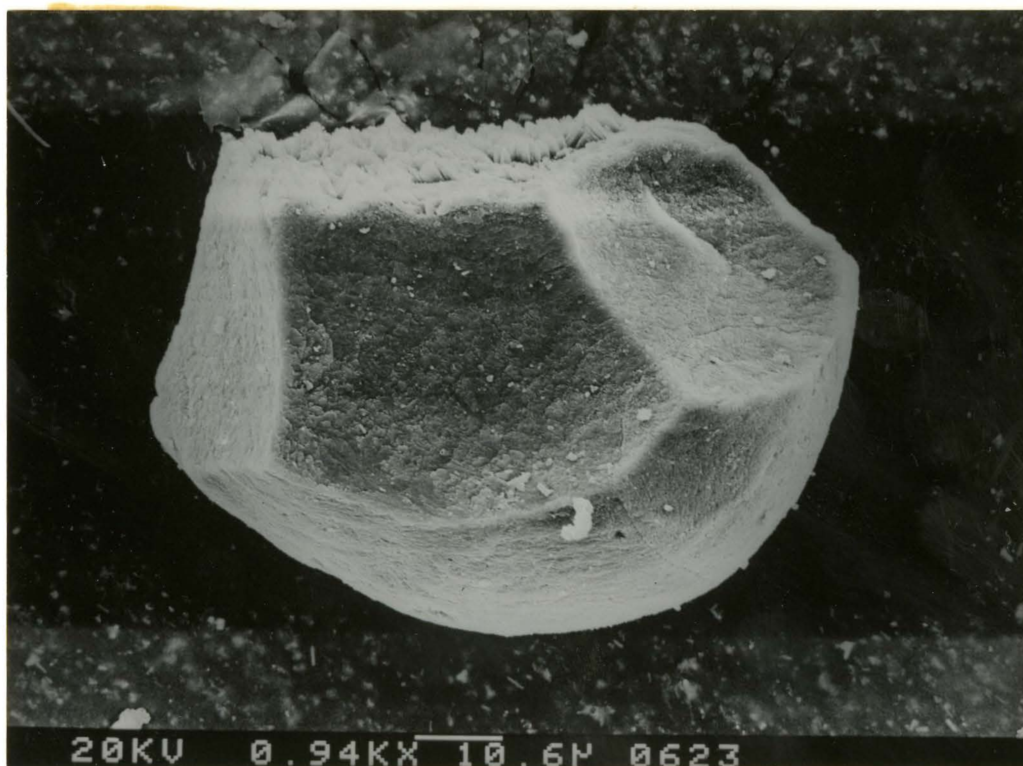
Plate 5. Close-up of skeletal surface excavated by C. delitrix. Note the scalloped surface and the holes with varying diameters. These tunnels were excavated by pioneering filaments and are eventually occupied by sponge lobes passing between chambers.

Plate 6. A sponge chip, one of the many silt-sized particles that are removed by C. delitrix in the excavation of the scalloped skeletal surfaces shown in plate 5.



20KV 26.2X 382P 0625



20KV 0.94KX 10.6P 0623

II. Comparison of reefs

Montastrea cavernosa and *annularis* dominated the shallow buttress zone at both sites. The distributions of coral heads, however, differed noticeably: at the control site, heads were smaller and more distantly spaced, leaving a greater amount of algal bound coral shingle exposed on the reef floor. The heads at the study site exhibited a substantially higher proportion of dead coral surface. The visual comparison of the reefs suggested that sponge diversity and abundance was greater at the turtle farm site than at the control. Besides *Cliona delitrix*, *C. caribbaea* and *Siphonodictyon corallophagum* were more frequently observed at the study site.

Sponge colony data

In order to perform a quantitative study of the relative extents of infestation and coral excavation, it was necessary to derive a regression equation to convert the in situ sponge surface area measurements into estimates of total sponge colony volume. The measurements made on the coral hand samples were used for this purpose (see Appendix 1: table 1). The following equations relating sponge colony volume and various aspects of surface area were obtained by regression analysis:

1. $S.V. = (D.C.A.)^{.983}$ $T = 25.13$, $N = 28$, $R^2 = .9590$

2. $S.V. = (S.A.)^{1.30}$ $T = 23.21$, $N = 26$, $R^2 = .9556$

2a. $\ln (S.V.) = 1.45 + 0.868 \ln (S.A.)$ $N = 26$, $R^2 = .858$

3. $S.V. = 2.72(S.A.)$ $T = 25.79$, $N = 26$, $R^2 = .9638$

where S.V. refers to the volume of infested coral (including pore and tissue space) occupied by one sponge colony; S.A. to the area of papillar tissue for that colony and D.C.A. to the area of sponge papilla plus the dead coral zone surrounding the colony (see graphs 1,2,3). Equation 3. suggests that the ratio of sponge colony volume to papilla area is constant throughout the growth of the sponge, assuming that the samples encompass the full size range of C. delitrix colonies (see graph 4). This implies that either the overall shape of the colony changes as the sponge excavates deeper into the substrate or that lateral expansion of the sponge occurs at a constant depth of excavation. It is likely that both factors are involved: the original vertical excavations of the corallite axial regions become more spherical at the stage of papillary fusion and most subsequent colony expansion is directed laterally (see plates 3,4). The anomalously high S.V./S.A. values in graph 4 represent immature colonies which have not yet undergone papillary fusion. Using the Y-intercept of Equation 2a, one can predict that a sponge colony having a papillae area of 1 cm^2 should occupy approximately 4 cm^3 of coral skeleton. This figure is an approximate indication of the volume excavated by a sponge in its initial penetration of a corallite.

Any one of Equations 1, 2 and 3 would provide a very accurate way of estimating sponge colony volume. Equation 1 was chosen, however, because of the closer approximation of quadrat measured sponge areas to the areas of papillae plus dead coral perimeter than to the areas of sponge papillae alone for the 26 sponge colonies in the hand specimens. Although a total of

29 colonies were counted after slicing up the coral samples, only 26 visibly discrete fused and unfused colonies had been previously identified and measured by the quadrat frame method (see Appendix 2: table 2). Regression analysis of the grouped data produced the equations:

4. D.C.A. = 1.20(EST.A) $R^2 = .97$

5. S.A. = 0.582(EST.A.) $R^2 = .72$

where D.C.A. and S.A. are areas obtained using plastic sheets to cover the corals and EST.A. are sponge areas estimated using a quadrat frame.The underestimation of D.C.A. implied by the slope of the first equation may be the product of using a planar measuring tool on the highly curved, often irregular surfaces of the small coral samples.If this is the case, the error involved in measuring the surfaces of the larger in situ heads should be significantly less.

The use of Equation 1. to predict the total volume of sponge colonies observed in the heads at the two sites requires the assumption that each discrete sponge mass and dead coral perimeter corresponds to only one sponge colony.This was not always the case for the colonies in the hand samples.Although total colony volume for such cases will be overestimated by the regression equation, it is likely the error involved is relatively insignificant due to the infrequent occurrence of neighbouring colonies that share the same dead coral perimeter and their inevitable fusing with later growth.The summation of sponge areas for each of the in situ coral heads produces a similar source of error.The overestimation of the total volume of the individual sponge colonies per head is negligible because of the

strongly linear relationship between papillae area and sponge volume.

Specific gravity data

The specific gravity of Montastrea cavernosa skeleton in the absence of any macroboring is 1.67 g/cm^3 (S.E.=0.032, N=40). Skeletal samples taken from a single head of Porites asteroides yielded a value of 1.31 g/cm^3 (S.E.=0.0417, N=7). The average densities of M. cavernosa and P. asteroides derived by Highsmith (1981) using a Hg displacement method are 1.60 and 1.48 g/cm^3 respectively. The average specific gravities of C. delitrix infested skeletons of the two corals are 0.79 g/cm^3 (S.E.=0.025, N=23) and 0.70 g/cm^3 (S.E.=0.447, N=5). A comparison between the two species reveals that while specific gravity of the substrate differs significantly (P<5%), the specific gravity of sponge infested skeleton does not. Highsmith (1981) noted that total percentage excavation by macroborers was positively correlated with coral density although it was not shown whether sponge excavation per unit volume of sponge infested coral is similarily correlated. The results presented here suggest that excavational activity per unit volume of infested skeleton is more intense in denser skeletons. Excavation by C. delitrix removes 53% of the M. cavernosa skeleton while only 47% of the P. asteroides skeleton is removed.

Biomass data

The concentration of organic material in the interior of M. cavernosa skelton is 3.86 mg per g of skeleton (S.E.=0.536, N=25). The chief constituent of this skeletal organic matter is presumably boring algal

filaments.The biomass of M. cavernosa polyp tissue, measured in 2 cm thick surface fragments and corrected for algal filament biomass, is 33.4 mg per cm^2 of coral surface (S.E.=4.62, N=12).Sponge biomass, including spicule mass, is 52.0 mg per g of coral skeleton (S.E.=3.20, N=22).A spicule mass to biomass ratio of 0.009, however, indicates a negligible mass contribution by spicules.

Cliona delitrix infestation

In assessing the effects of C. delitrix infestation at the two sites, it was decided that only the coral heads of the photographic study would be considered (see Appendix 2). The hand samples collected at the study site are excluded as they were selectively chosen to obtain sponge colony area and volume data for regression analysis.Similar sized heads at the control site may have been overlooked during the photographic survey because of their relatively insignificant contribution to the total coral volume.It was found that inclusion of the turtle farm hand samples generated less than a 2-3% increase in the area and volume data for the study site. The turtle farm coral volume and sponge biomass totals then only slightly underestimate the true values.

Regarding the relative abundances of M. cavernosa and C. delitrix at the two coral buttresses, all densities are calculated per unit area of reef.As the transect widths reflect the approximate widths of the buttresses, the calculated densities pertain only to a small region of the overall forereef slope; most of the forereef terraces are sand covered and devoid of reef corals.While suitable for comparative purposes in this study, the density values obtained for the two species may not reflect their typical densities

on more homogeneous forereef slopes.

The 58 heads of Montastrea cavernosa counted in the 45 by 4 m tract along the coral buttress of the study site produce a substrate density of 14.79 ± 4.89 kg per m^2 of reef while the 19 heads in the 10 by 4 m tract at the control site produce a density of 11.79 ± 3.89 kg per m^2 (see Appendix 5 for error calculations).A two tailed T-test revealed a significant difference in coral head size between the two sample areas ($P<5\%$).The average volumes of heads at the study and control site are 2.75 and 1.49 litres respectively.Both size distributions are strongly skewed towards small heads (see histograms 1,2).

Although none of the 19 heads encountered in the first control site transect bore any sponge infestation, a combination of the results for the two transects gives an infestation rate of 10% of all heads.The turtle farm heads, on the other hand, exhibited a minimum infestation rate of 70%.See Appendix 2 for predicted sizes of sponge colonies inhabiting the corals.Summation of the skeletal mass removed from the infested heads produced a total loss of 86.57 ± 8.51 g of coral per m^2 of reef for the turtle farm buttress.The turtle farm coral heads support a minimum sponge biomass of 4.02 ± 0.40 g per m^2 of reef.Although sponge area measurements were not obtained for the control site colonies, one can make a prediction of the sponge biomass residing in the 6 infested heads observed in the two transects.Assuming that the average sponge biomass per infested coral head is similar for both sites, a conversion factor can be calculated from the ratio of numbers of infested heads per unit area for the two sites:

$$\frac{\text{turtle farm: } 41 \text{ infested heads}/180\ m^2}{\text{control: } 6 \text{ infested heads}/120\ m^2} = 4.6$$

The density of sponge biomass at the control site is estimated to be 0.22x that at the control site or 0.87 g/m^2.The predicted value of excavated skeletal material is 18.83 g/m^2.

In order to assess the damage inflicted upon the coral biomass, a regression equation was derived to convert coral volume into exposed coral surface area:

6. $C.V. = (E.C.A.)^{1.23}$ $T = 75.07,\ N = 24,\ R^2 = 0.9959$

where E.C.A. is the area of all exposed surfaces other than around the base, i.e. all area that was at one time occupied by polyps (see Appendix 1: tables 3,4 and graph 6).The strength of this equation implies that the shapes of M. cavernosa heads on average adhere to a fixed volume to polyp surface area relationship.It will be assumed that the relationship holds for the larger in situ heads although, as already mentioned, some diversity in shapes was observed.

Coral surface area fractions of reef area are 0.12 and 0.11 for the study and control sites respectively.As none of the 19 control heads bore noticeable amounts of dead substrate, the biomass density of living polyp tissue can be calculated directly from the coral substrate density; the final value is 36.34$\pm$9.81 g of polyp tissue per m^2 of reef.Conversely, the corals of the study site bore extensive areas of dead substrate that supported either encrusting or filamentous algal growths.One quarter of the total potential polyp area of the hand samples was found to be occupied by C. delitrix infestations, 55% was occupied by living polyps and 20% was dead substrate (see Appendix 1: table 4).Applying the last of these percentages to the predicted total surface area of the in situ corals gives a biomass

density for the turtle farm corals of 22.10±5.97 g per m^2 of reef which is equal to 61% of the control site value.The dead coral substrate of the in situ turtle farm heads was visually estimated as a percentage of total surfaces and 29% having more than half of their exposed surfaces covered by dead coral (see histogram 3).

A detailed examination of the hand samples collected at the study locality revealed the frequent presence of other macroborers.Spionid and eunicid polychaetes borings were commonly observed, although never at an appreciable density in any one coral head.Lithophagine bivalve infestation was another frequent but not quantitatively important macroborer.Many samples contained Siphonodictyon galleries and excavations belonging to Cliona species other than C. delitrix.Very rarely were the other sponge excavations filled with sponge tissue, implying that most excavations had been abandoned prior to sampling.Tabulation of the results of infestation by the different macroborers did not reveal any trends among their relative abundances.

Levels of S.P.M. and bacterial loading

See tables 1,2 for the S.P.M. values.The means for the deep water concentrations of total suspended particulate material for the two sites are not significantly different (P<5%).The significant difference between the means for the grouped deep and shallow water values implies that the only real difference in S.P.M. levels exists between waters of different depths and/or distances from shore: suspended particulate matter is 1.7x more plentiful in the shallow waters near the shore than in waters passing over the coral buttress.

The bacteria counts are presented in table 3. Several important points emerge from a comparison of the tabulated values. Cocci are more abundant than rods in all samples. Cocci, rods and coliforms are all more abundant in the turtle farm waters than in the control waters. The numbers of coliform-like bacteria and cocci are of similar magnitudes in the turtle farm waters while the cocci outnumber the coliform types by a factor of 5 in the control waters. Finally, the shallow water bacteria abundances outnumber those of the corresponding deep water sites, this difference being more pronounced at the control locality.

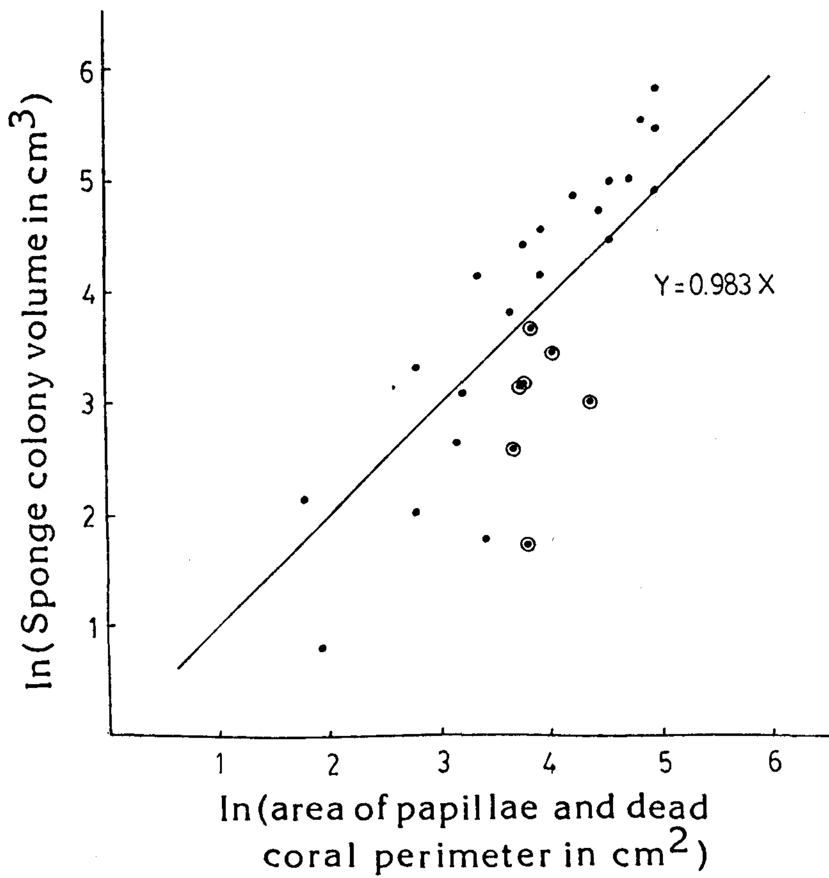
The SEM survey of the Nucleopore filters revealed some interesting features. The pores of the study site filters were frequently obliterated by bacterial scum, and fields of view were sometimes dominated by coliform bacteria aggregated to coral mucus strands and by fecal pellets in various stages of decay (see plates 7,8)..This patchiness of material was less frequently encountered on the control filters. No unarmoured cells and very few armoured cells were identified on any of the filters.

Temperature and salinity readings

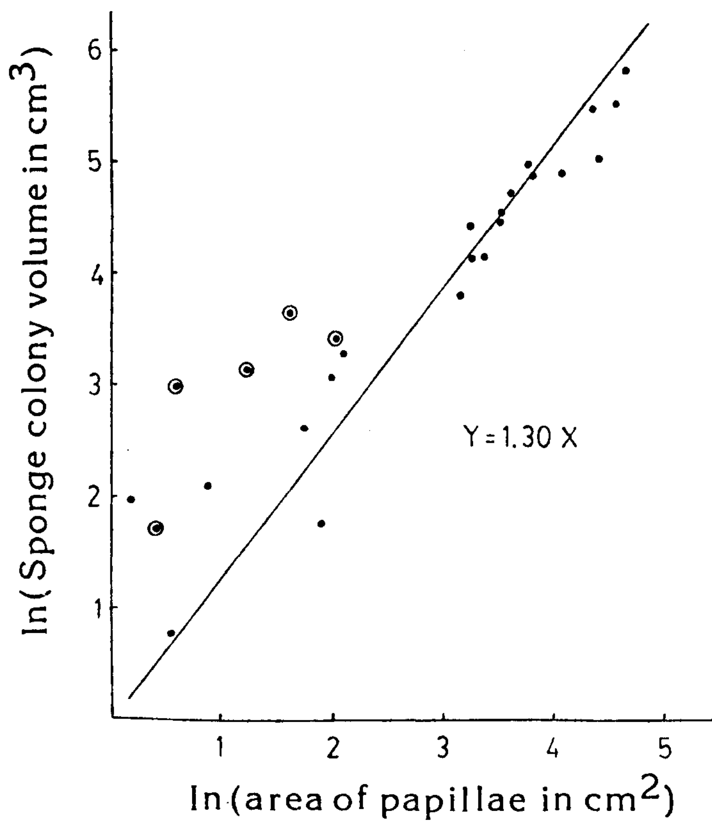
All sampling was done in the first two weeks of June. The temperature of surface water sampled at both sites was found to be 29°C. The water temperature average and range for June to October are 30°C and 26.5-31.5°C (Wood and Wood, 1981). The salinites of the deep and shallow waters opposite the turtle farm were 34.5 and 34.0 ppt respectively. A value of 35.0 ppt was obtained for both sampling depths at the control site.

Graph 1. In (sponge colony volume) versus In (area of papillae and dead coral perimeter) - constrained to pass through the origin, i.e. at area equal to 1 cm^2, volume of colony is set to equal 1 cm^3. ● indicates sponge colonies that have not undergone papillary fusion.

Graph 2. In (sponge colony volume) versus In (area of papillae) - constrained to pass through the origin. ● indicates sponge colonies that have not undergone papillary fusion.



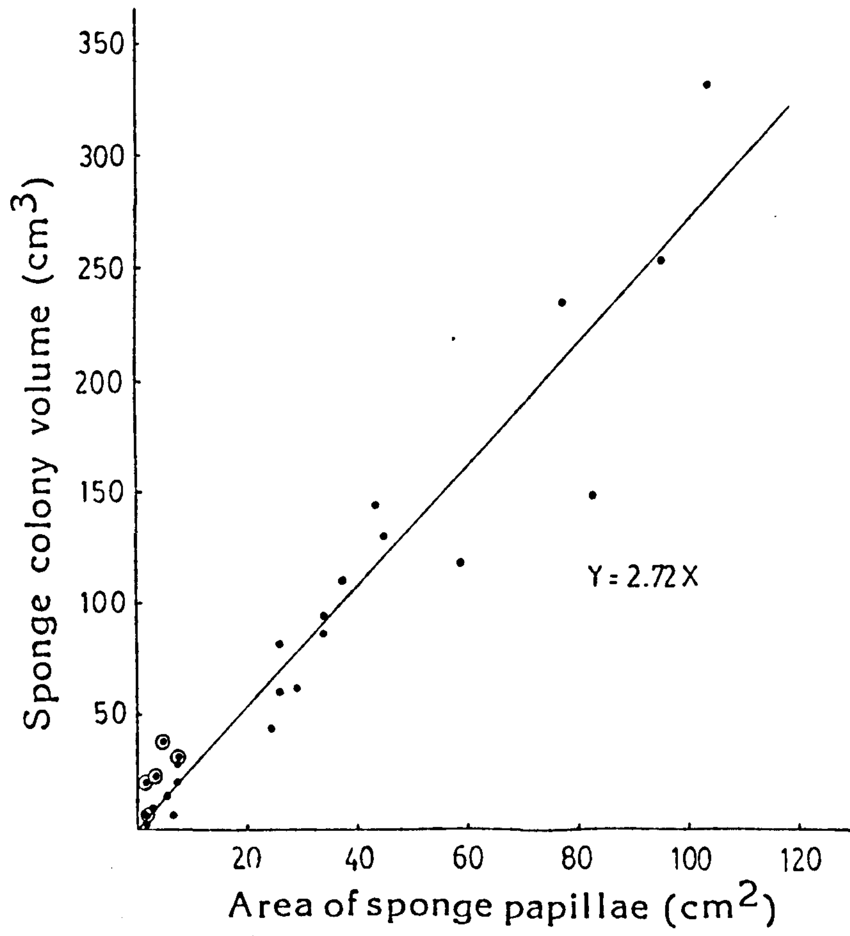
ln(Sponge colony volume in cm3)
Y=0.983 X
ln(area of papillae and dead coral perimeter in cm2)

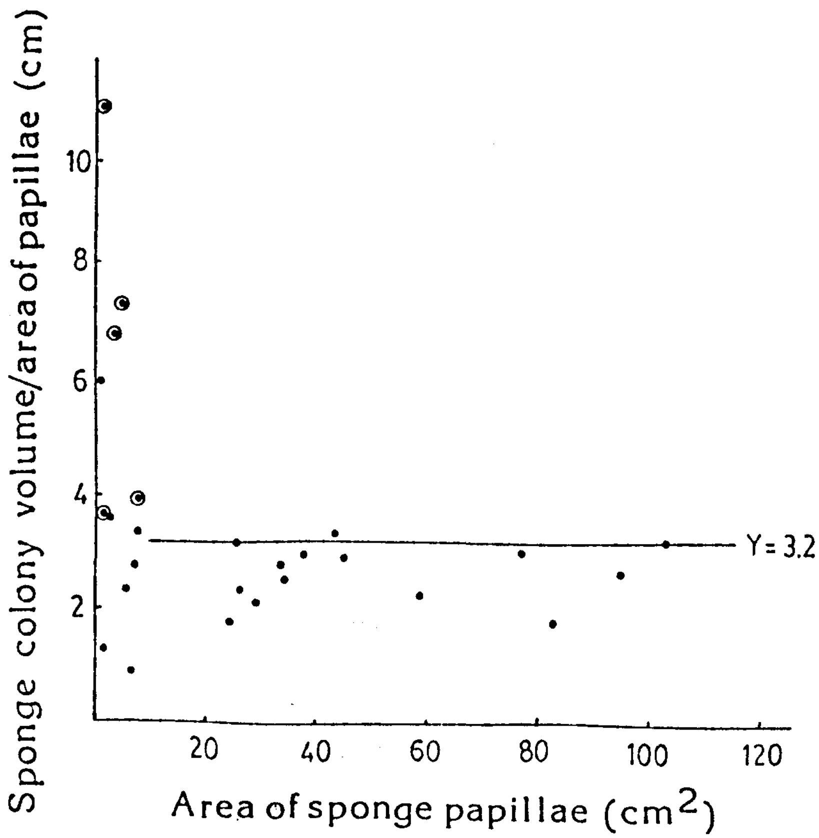


ln(Sponge colony volume in cm3)
Y=1.30 X
ln(area of papillae in cm2)

Graph 3. Sponge colony volume versus area of sponge papillae. ● indicates colonies that have not undergone papillary fusion.

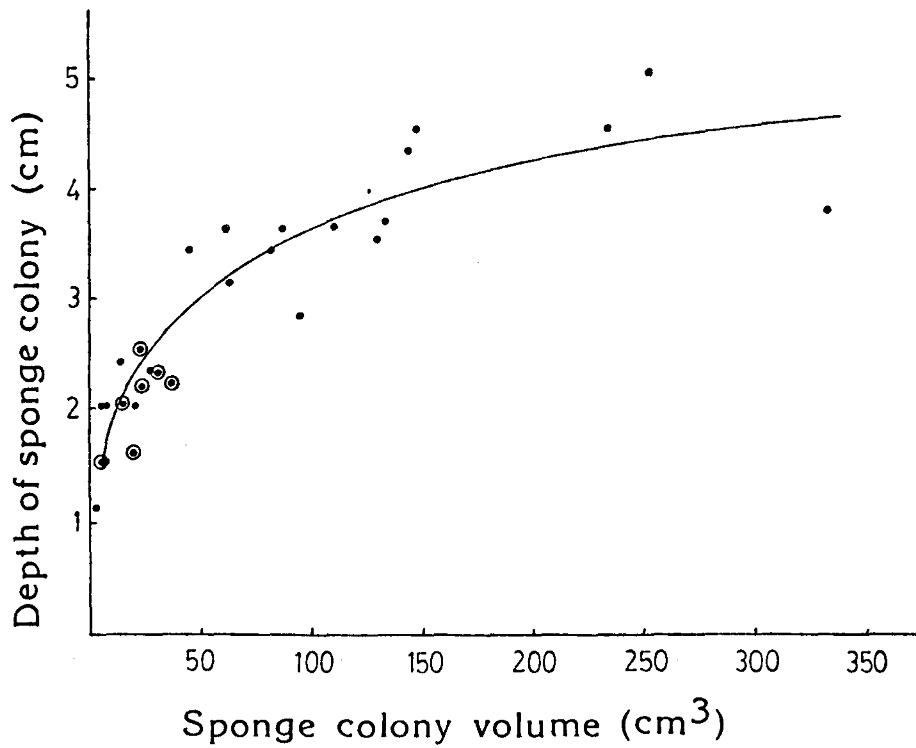
Graph 4. Ratio of sponge colony volume to papillae area versus area of papillae. ● indicates colonies that have not undergone papillary fusion.


Sponge colony volume (cm3)
Area of sponge papillae (cm2)
Y = 2.72 X
350
300
250
200
150
100
50
20
40
60
80
100
120

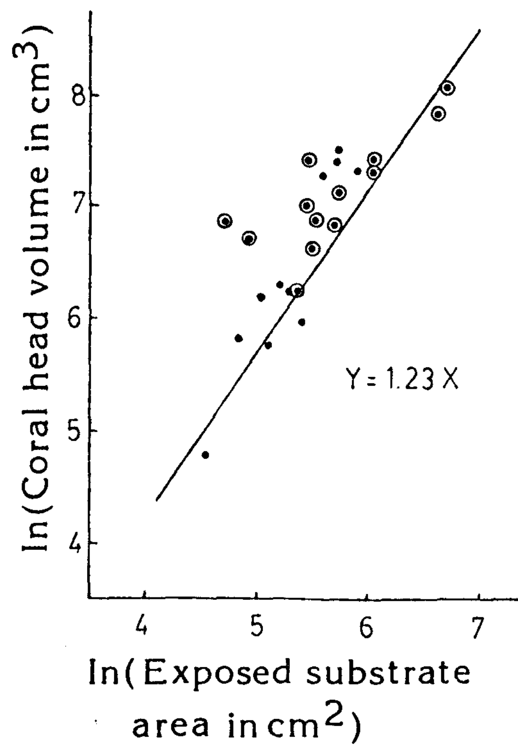

Sponge colony volume/area of papillae (cm)
Area of sponge papillae (cm2)
Y = 3.2
10
8
6
4
2
20
40
60
80
100
120

Graph 5. Maximum depth of excavation beneath coral surface versus volume of sponge colony. ● indicate colonies that have not undergone papillary fusion.

Graph 6. Coral sample volume versus area of exposed coral substrate, i.e. all substrate that was at one time occupied by polyps. ● indicates that coral sample was fragmented and did not represent an entire coral head.



Depth of sponge colony (cm)
5
4
3
2
1
50
100
150
200
250
300
350
Sponge colony volume (cm3)



ln(Coral head volume in cm3)
8
7
6
5
4
Y = 1.23 X
4
5
6
7
ln(Exposed substrate area in cm2)

Histograms 1,2. Volumes of in situ coral heads at the turtle farm and control sites.

Histogram 3. Percentages of total area of exposed substrate per head that is occupied by dead coral for the coral heads at the turtle farm site.

Table 1. Levels of Suspended particulate material (S.P.M.)

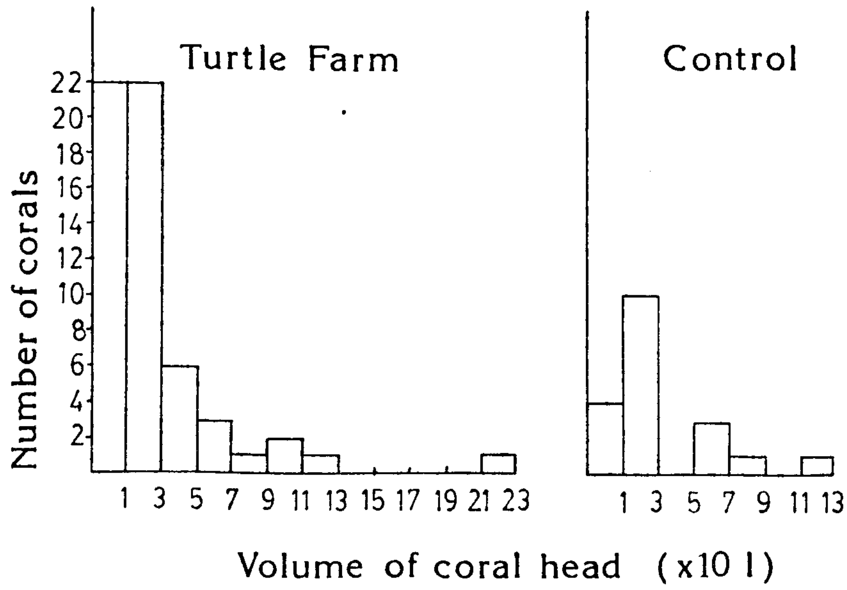
	Control deep	Control shallow	level of significance
	mean=0.90 (s.d.=0.566, N=2)	mean=1.42 (s.d.=0.635, N=6)	NS
	Turtle deep	**Turtle shallow**	
	mean=0.82 (s.d.=0.368, N=2)	mean=1.59 (s.d.=0.478, N=6)	NS
level of significance	NS	NS	

Table 2. Grouped S.P.M. data

Control(deep & shallow)	Turtle(deep & shallow)	level of significance
mean=1.29 (s.d.=0.626, N=8)	mean=1.40 (s.d.=0.557, N=8)	NS
Deep(control & turtle)	**Shallow(control & turtle)**	
mean=0.86 (s.d.=0.392, N=4)	mean=1.50 (s.d.=0.543, N=12)	P<5%

All S.P.M. concentrations in 10^{-2} g/l

All significance tests: two-tailed; pooled variance; NS at 5%


Turtle Farm
Control
Number of corals
22
20
18
16
14
12
10
8
6
4
2
1 3 5 7 9 11 13 15 17 19 21 23
1 3 5 7 9 11 13
Volume of coral head (x10 l)

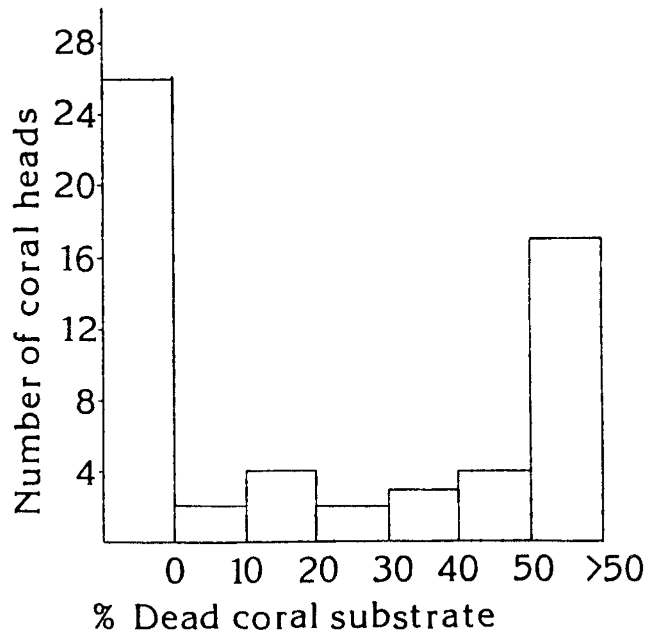
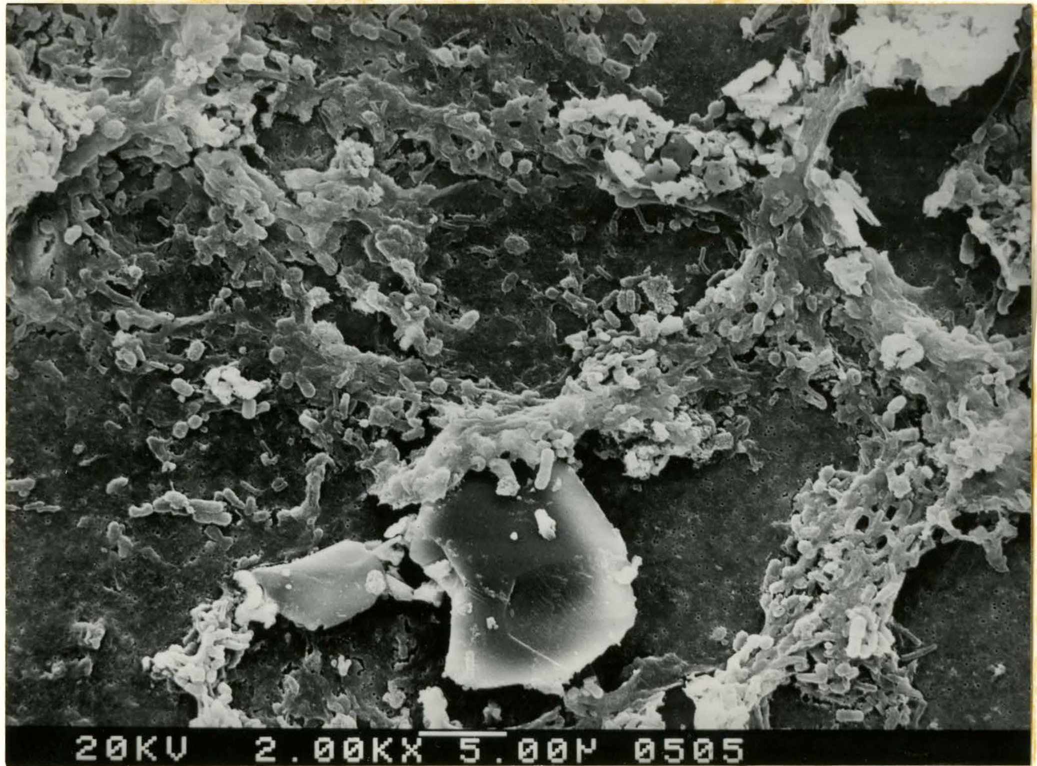
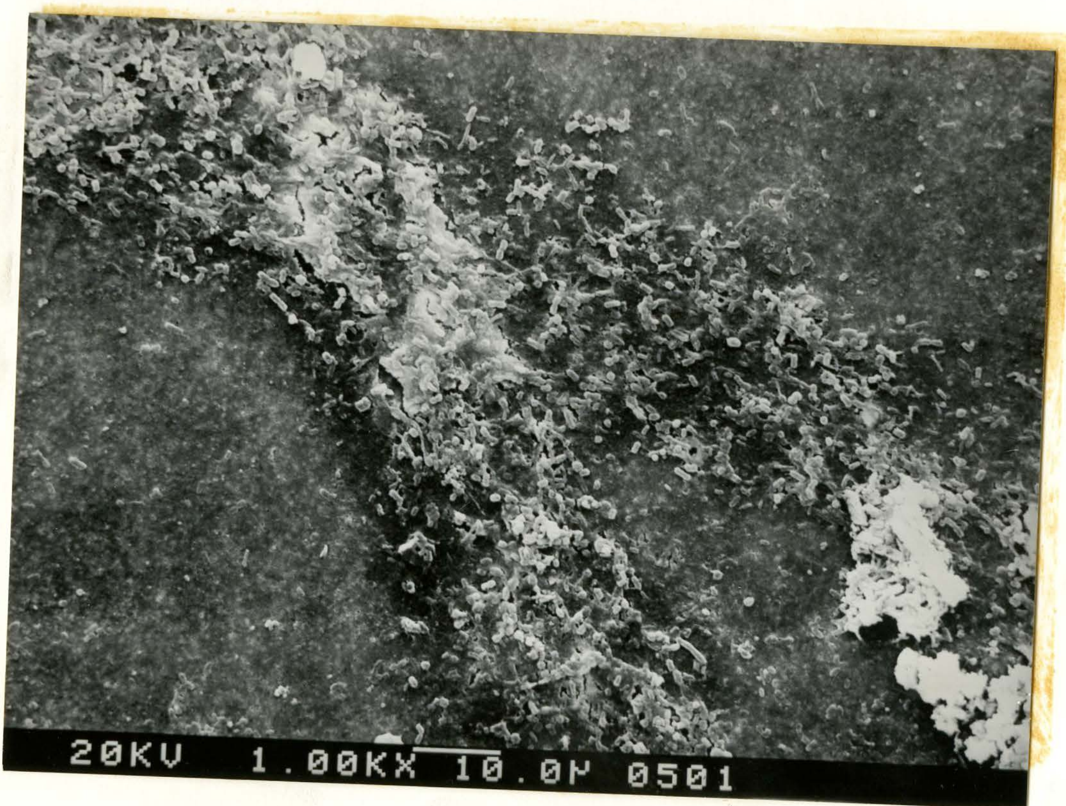

Number of coral heads
28
24
20
16
12
8
4
0 10 20 30 40 50 >50
% Dead coral substrate

Plate 7. Micrograph of Nucleopore filter showing bacteria (mostly coliforms), fiber and clay particles and bacterial slime within a disintegrating fecal pellet.

Plate 8. Micrograph of Nucleopore filter showing the density of coliform bacteria bound to a coral mucus strand.


20KV 2.00KX 5.00µ 0505


20KV 1.00KX 10.0µ 0501

DISCUSSION

I. Significance of the organic pollution

With regard to the extent of the organic loading of the turtle farm waters, it is difficult to account for the nonsignificance of S.P.M. differences between the two sites. The turtle farm plume previously described is being maintained by a daily influx of 22 kg of undigested fecal material providing that the farm is operating at half the maximum holding capacity of turtles. The particulate concentration of sewage effluent is 5.60 mg/l. An unknown proportion of this fecal matter is expected to either dissolve during disintegration of the pellets or settle upon entry into the slower moving coastal waters. Assuming that the rate of sewage influx equals the rate of diffusion/transport away from the plume, then 3.90 mg/l are required to be lost through these processes in order to account for the 1.70 mg/l difference in surface water concentrations at the two sites.

An alternative explanation, however, appears more plausible. The extreme clumping of particulate matter that produces the marked plume opposite the sewage source indicates a considerable patchiness in the distribution of the suspended material. The high variances of S.P.M. values from both sites, however, imply that the number and size of water samples were not large enough to estimate accurately S.P.M. levels or to detect a difference between the two sites.

Regarding the bacteria distributions, it is well documented that the smaller forms comprise the majority of natural marine bacterioplankton (ZoBell, 1963). It is significant, however, that bacteria of the coliform size range represent substantial fractions (17% and 6%) of the shallow and

deep water bacteria populations at the control site. Whether these cells are actually fecal coliforms or are exceptionally large natural marine bacteria is not known. One can conclude that the 8.5 and 10 fold increases in abundance of this size class observed in the shallow and deep waters of the study site are a direct result of the influx of untreated sewage into these waters.

It is interesting though, that the discrepancy between coliform abundances between the two sites is greater for the deep water samples. One would expect that the sedimentation of the dead and dying coliform cells would tend to produce an unproportionally low deep water "coliform" abundance for the turtle farm waters. Most of the turtle farm "coliforms", however, enter the ocean water in fecal pellets or as aggregates. As SEM fields of view dominated by such densely packed bacteria were avoided during the enumeration procedure, it is likely that the shallow count for the sewage laden study site waters was underestimated. Subsequent transport to waters over the coral reef buttress would allow disintegration of the pellets and the release of these aggregated bacteria, meaning that a more accurate bacteria count is obtained for the deep water samples.

To what extent are the reef waters of the study site enriched in bacteria? The concentration of bacteria of the deep water at the control locality is $4.46 \cdot 10^5$ cells/ml; 80% of these are small cocci and rods. This value does not differ substantially from abundances reported for other reef waters: 1.14 and $0.40 \cdot 10^5$ cells/ml for bay and outer reef waters of Jamaican reefs (Reisweig, 1971); 4.90, 28.30, 6.20 and $7.40 \cdot 10^5$ cells/ml for Pacific atoll reefs (Sorokin, 1974). Variance is expected because of the different sampling and enumeration methods used, seasonal and daily differences in times of sampling and the varying influence of tides, currents, climate and

biotic factors inherent to each reef. The deep water concentration of turtle farm bacteria, which is $1.53 \cdot 10^6$ cells/ml (split evenly between coliforms, and the smaller cocci and rods), exceeds the control value by a factor of 3.4 and is higher than all except one the values reported for the unpolluted reefs.

In converting bacteria cell counts into biomass, separate conversion factors are needed for the coliform and natural marine bacteria fractions due to the significant volume difference between the two size classes. ZoBell (1963) gives a dry weight of $4 \cdot 10^{-11}$ mg for an average marine bacteria cell of volume 0.2 μm^3. Using Luria's data (1960) for E. coli, a coliform cell of dried volume 1 μm^3 has a calculated mass of $2.2 \cdot 10^{-10}$ mg. The organic carbon content of each type of cell is approximately half the dry weight. The bacteria biomass of the deep water control and study sites are 3.16 and $20.05 \cdot 10^{-2}$ mg/l (see table 4 for other data). Coliform-like bacteria contribute 85% of the latter biomass as opposed to 53% of the former. In summary, a ten -fold increase in coliform biomass coupled with a two-fold increase in cocci and rod biomass has produced a six-fold difference in total bacteria biomass between the two deep water sites.

In order to assess quantitatively the response of C. delitrix growth to the organic and bacterial loading of reef waters, one must first consider the normal dietary habits exhibited by sponges in unpolluted reef waters. Reisweig (1971) has shown that the same bimodal pattern of particle retension is demonstrated by three morphologically dissimilar species of demospongia. Particles of diameter greater than 2-5 μm and less than 50 μm, the diameter of the dermal pores of the inhalant surfaces, are captured by amoebocytes lining the inhalant surfaces. Smaller elements are retained by the collars of the choanocytes. Reisweig (1971) estimates that the average

percentage retension of total particulate organic matter in normal sea water is about 45%. Four fifths of what is retained and presumably assimilated belongs to the class of non-discrete unresolvable particulate organic matter (URPOC). The 0.1 μm slits of the choanocyte collar, however, limit the efficiency of URPOC retension to about 35%.

The organic carbon reserve in the microscopically resolvable particulate elements of normal reef water is substantially smaller but this material is retained by the sponges at a much higher efficiency. The unarmoured cells, mainly naked flagellates, contribute about 16% of the total dietary particulate material while armoured cells: diatoms, dinoflagellates and coccolithophores: contribute about 2.5% and bacteria only 0.9%. The bacteria, however, are retained by all three species at the highest efficiency (98%). Reisweig maintains that this retension efficiency is representative of the entire phylum because of the apparently uniform function of choanocytes in all sponges. Bacteria and URPOC together then comprise over 81% of the total POC diet of the typical demosponge (Reisweig, 1971).

Although it is known that the fraction of total S.P.M. contributed by bacteria biomass is at most a few percent (see table 4), it can not be determined what contributions to the organic fraction of total S.P.M. are made by unarmoured cells, URPOC and resolvable organic debris. Reisweig (1971) found that URPOC comprised 87% of the total particulate organic of Jamaican reef waters. What effect the introduction of decaying fecal debris will have upon URPOC levels depends on the activity of the decomposing bacteria. It is predicted that the turtle farm waters are enriched in URPOC, although whether the degree of enrichment is proportional to the bacteria biomass increase remains an open question.

The ratios of bacteria biomass, suspended in a one metre thick boundary

layer, to sponge biomass within the reef are 4.99 and $3.63 \cdot 10^{-2}$ for the study and control sites respectively. It is proposed that the 6.3 fold increase in bacteria biomass at least partially accounts for the predicted 4.6 fold increase in sponge tissue density observed at the polluted reef. If most or all of this suspended bacteria biomass can be and is utilized by the actively filtering C. delitrix biomass, then it is likely that the bacteria play a larger role in satisfying the dietary needs of the sponge population in the polluted environment than of the control population. It may be that with the predicted increase in URPOC in the polluted waters, close to 100% of the sponge's total dietary carbon is being supplied by URPOC and bacteria.

An undetermined proportion of the coliform biomass, however, is not going to be available to C. delitrix because of continual decomposition and sedimentation of dead suspended cells as well as their consumption by other filter and suspension feeders. The actual increase in available bacteria biomass in the polluted waters may be closer to the 4.6 fold increase predicted for the sponge biomass, i.e. the ratios of available bacteria biomass to sponge biomass for the two sites are more similar than the ratios given above. In any case, the observed rise in sponge biomass at the polluted reef is positively related to the elevation of suspended bacteria in waters passing over the reef.

II. Reef Metabolism

Odum and Odum (1955) calculate the mean animal biomass of several species of Pacific corals to be 25.0 mg/cm^2, which is of similar magnitude to the animal plus zooxanthellae biomass for M. cavernosa, 33.4 mg/cm^2. The

densities of Montastrea cavernosa substrate, 0.12 and 0.11 m^2/m^2 of reef, compare to values obtained for the dominant corals at 7 m depth on the Bermuda Platform: 0.38 and 0.17 m^2/m^2 for Diploria strigosa and D. labyrintha respectively (Johannes et al., 1970).

The fact that only 55% of the available M. cavernosa at the study site is inhabited by living polyps means that rates of oxygen and food consumption by this coral per unit area of reef are only 60% of the corresponding rates in effect at the control site. The 0.024 m^2 of dead coral substrate per m^2 of the turtle farm buttress, however, also represents an important oxygen consuming agent. DiSalvo (1971) gives a minimum respiration rate for the microflora inhabiting dead coral substrates of 240 mg O_2/m^2 hour. Johannes et al. (1970) provide a mean respiration rate of 400 mg O_2/m^2 of coral substrate hour for four species of coral. Using these figures, one derives values for total rates of oxygen consumption by living and dead coral substrate of 32 and 44 mg O_2/m^2 of reef hour for the study and control site reefs respectively. The respiration of corals in polluted waters may be depressed further by the periodic anaerobiosis of the bottom layer at times of heavy loading. The possible stimulatory effects of an increased availability of food, i.e. elevated levels of dissolved organics and bacteria and possibly zooplankton in the polluted waters, upon coral respiration and growth rates, however, should not be overlooked.

Regarding the metabolic activities of the Cliona delitrix community, Reisweig (1974) has shown that another generalist sponge, Mycale sp., exhibits a high pumping efficiency and metabolic rate. The eurytopic nature and potential for rapid colonisation of these two opportunistic sponges suggests a similarity of competitive strategies and metabolic rates. Both sponges do have low tissue densities that allow the colonies to function in

turbid conditions (Reisweig, 1971). _Mycale_ was found to have a year round pumping rate of 3 cm^3 water/s g of dry tissue and an average respiration rate of 0.787 mg O_2/g dry tissue hour (from Reisweig's data, 1974). If the latter rate can be applied to _C. delitrix_, the sponge populations at the study and control site would consume oxygen at average rates of 3.16 and 0.685 mg O_2/m^2 hour. It can similarily be predicted that the sponge standing crop of the turtle farm site would filter a volume of water equivalent to a one metre thick boundary layer over the reef in a period of 23 hours. The corresponding period for the control site is 4.5 days. Using a 98% retension efficiency, the maximum potential rates of assimilation of bacteria biomass are calculated to be 205 and 7 mg/m^2 of reef day.

There is an obvious discrepancy between the relative differences of the two maximum potential assimilation rates and of the two normal oxygen consumption rates. Some of this discrepancy is explained by the fact that sedimentation and competing filter feeders prevent _C. delitrix_ from capturing all the suspended bacteria biomass. The unporportionally high maximum potential assimilation rate for the turtle farm site, however, does imply that sponges living here have a much greater potential for growth than those sponges at the control.

The summation of sponge and coral substrate respiration rates results in net respiration rates for the coral-sponge association of 35 and 45 mg O_2/m^2 of coral buttress hour at the study and control sites respectively. The reduction in area of living coral substrate appears to be primarily responsible for the lower rate in effect at the turtle farm. This shift towards a depressed level of respiration is contrary to the pollution induced trend toward heterotrophy of the hard substrate benthic community that was observed by Brock and Smith (1981). This study, however, has focused

upon a single coral sponge association and does not take into account the rise of other nonbioerosive filter feeders. It is expected that other such animals have increased in abundance and that the heterotrophic aspect of the overall reef is augmented in response to the artificially elevated levels of available organic material.

III. Reef destruction

Rützler (1975) has shown for two clionid sponges that the boring rate, measured as the increase in mg $CaCO_3$ removed per cm^2 of sponge papillae with time, levels off at a value of 700 mg/cm^2 after twelve months of growth. The graph of the ratio of sponge colony volume/papillae area versus papillae area for Cliona delitrix (graph 4) levels off at 3.2 cm, which corresponds to a value of 2.82 g $CaCO_3$ removed per cm^2 papillae area. Obviously, the intensity of burrowing is much higher in mature specimens of C. delitrix than in the C. lampa colonies examined by Rützler. Although the age of the C. delitrix colonies is not known, it is significant that the ratio of 3.2 cm is attained by sponges of relatively small surface area (25 cm). As it appears that the burrowing activity per unit area of sponge remains constant after papillary fusion, the actual burrowing rate of Cliona delitrix depends upon the growth rate of the sponge. Unless C. delitrix grows substantially slower than C. lampa, it is likely that the mean burrowing rate of the former sponge easily surpasses the maximum burrowing rate of 700 mg $CaCO_3/cm^2$ papillae year that is reported by Rüztler.

Rüztler (1975) found that the total biomass density of boring sponges in coral substrates at 8-10 m depths on the Bermuda Platform was 4.3 g dry weight per m^2 of substrate area. The density of the species of maximum

abundance, Cliona vermifera, was 3.1 g/m^2; all others were below 0.1g/m^2. The control site biomass density for Cliona delitrix, expressed relative to the area of M. cavernosa substrate, is estimated to be 7.91 g/m^2. This is comparable to values given by Rützler for Cliona caribbaea growing in coral substrates at shallower depths on the Bermuda Platform. The corresponding value for Cliona delitrix at the study site is 33.5 g sponge tissue/m^2 of M. cavernosa substrate, far in excess of any values reported by Rützler.

The implications of this elevated sponge biomass density for modern coastal carbonate buildups are vital. If 2.5% of the removed carbonate is dissolved during excavation (Rützler and Reiger, 1973), then the C. delitrix crops have reduced 0.57 and 0.16 % of the available M. cavernosa substrate at the study and control sites to silt-sized sediment (see plate 6). If the sediments are deposited on portions of the terraces of equal area to the coral buttresses, the sediment densities for the two sites would be 84.4 and 18.4 g/m^2 respectively. In summary, the 4.6-fold increase in sponge biomass density that was induced by organic loading of the reef environment reflects the increase in the bioerosive activity of this sponge species.

The significance of these figures should be considered in the light of two important contraints. First of all, the figures represent the amount of sediment removed by the present standing crop of C. delitrix colonies. It is not possible to infer rates of sediment production as the history of sewage input rates for the past ten years and the rate at which sponge proliferation responds to organic loading are unknown. This study simply suggests that the bacteria loaded waters support a higher standing crop of one dominant boring sponge and that a higher percentage of the available coral substrate is eroded as a consequence.

The second important constraint is that no attempt was made to assess

the response of coral growth and skeletogenesis to the sewage influx. Although the proportion of dead coral substrate appears to be related to sewage loading, it is not known whether the coral polyps are being killed at a faster rate than the production of new coral substrate. Another unquantified relationship regarding coral growth is the balance between the possible enhancement of zooxanthellae photosynthesis by nutrient loading and the reduction of calcification rates induced by the elevated turbidity of the water (Stoddart, 1969; Bak, 1974).

Subsidiary effects of the pollution, for example the spreading of Black Band disease (Taylor; Rutzler et al., 1983) about areas of injured or stressed coral and H_2S poisoning during periodic anaerobiosis of the bottom layer, may also have played a role in the death of the coral. Evidence of such agents: black filamentous mats adjacent to white, exposed coral substrate and black iron sulphide coatings on the substrate: were not observed at either site. The higher average head size of the turtle farm corals suggests that coral recruitment may have been inhibited by the sewage (although the exclusion of coral hand samples does the bias the data to a small extent). Consequently. the potential imbalance between carbonate production and destruction on the reef can not be assessed without knowing the rates and influences of the various processes mentioned above.

SUMMARY

This study has shown that the magnitude of bioerosion caused by a particular filter feeding macroborer is positively related to the degree of organic pollution affecting the reef. Although it was not determined whether the elevation of sponge biomass at the polluted reef can be directly attributed to the greater bacteria abundance, the similarity of the bacteria to sponge biomass ratios for the two sites suggests a positive relationship between these two component members of the reef community. Judging by the dietary dependence upon URPOC of demosponges living in unpolluted environments, however, the sponge proliferation at the turtle farm site is more probably attributable to an elevated concentration of URPOC in the polluted waters. The activity of decomposing bacteria presumably reduces much of the incoming fecal matter into dissolved and quasi-particulate organics, thus making it available for choanocyte capture and assimilation by the filtering demosponge population. In any event, elevated abundances of bacteria (both "coliforms" and the smaller natural marine microflora) serve as a flag for the discharge of unpurified fecal sewage into reef waters, if not actually contributing to the proliferation of the hard substrate filter and suspension feeders.

The enhanced mortality of the coral polyps that is encountered at the polluted reef results in a net reduction in the levels of oxygen consumption and respiration by the sponge-coral association under investigation. The strength of this analysis, however, is limited by the questionable application of respiration and pumping rates for *Mycale* spp. to *Cliona delitrix.* Furthermore, an examination of biomass changes for all reef inhabitants, particularily the other resident filter and suspension feeders,

must be carried out in order to determine the extent to which the heterotrophic nature of the benthic community is affected by sewage input.

The organic loading of the turtle farm reef correlates with a 4.6-fold increase in the amount of Montastrea cavernosa that is eroded by Cliona delitrix and reduced to silt-sized sediment.Unless countered by an accelerated rate of coral growth, the enhanced sponge bioerosion reflects a marked shift away from the dynamic balance maintained between reef growth and destruction.

The question of the irreversibility of this shift may be answered by looking at the rates of trophic changes that are induced by the organic loading.The rate at which sponge colony growth and proliferation responds to a change in the levels of URPOC or bacterioplankton is of primary importance.Some consideration must also be given to how different species of coral respond to loading with particulate organics.Polyp mortality may be enhanced by an elevated abundance of pathogenic agents in the polluted environment.The potentially detrimental effects of turdibity and organic pollutants upon coral spat settling and development may hinder the process of coral recruitment on the reef.Rates of coral skeletogenesis may either be augmented or depressed depending upon the net effects of increased turbidity and nutrient levels and the nutritional dependence of the coral species upon zooxanthellae.Further study must be done in order to assess the dynamics of the trophic response that is demonstrated by a reef community stressed by organic loading.

APPENDIX 1. Hand Sample Data

Table 1. Volume and area data for individual sponge colonies

Sponge colony number	Sponge colony volume (cm^3)	Complete/ Incomplete sponge colony	Sponge colony depth (cm)	Area of sponge papillae (cm^2)	Area of papillae & dead coral (cm^2)	Papillary fusion
1a	87.11	C	3.6	34.07	92.61	Y
1b	8.75	C	2.0	2.42	5.92	Y
2	7.15	C	2.0	1.19	15.58	Y
3	20.01	I	1.6	1.81	78.58	N
4	21.30	C	2.0	7.38	24.31	Y
5a	5.82	I	1.5	6.52	30.11	Y
5b	2.18	C	1.1	1.71	6.88	Y
6a	13.08	I	2.0	*	37.92	N
6b	23.25	I	2.5	*	42.69	N
7a	13.62	C	2.4	5.76	22.98	Y
7b	23.19	I	2.2	3.38	42.93	N
8	62.65	C	3.1	29.04	49.85	Y
9	130.12	I	3.5	44.63	68.98	Y
10	44.26	C	3.4	24.30	38.00	Y
11	37.54	C	2.2	5.04	45.45	N
12	*	I	*	8.37	111.05	Y
13	253.15	C	5.0	95.32	128.78	Y
14	61.36	I	3.6	26.03	28.49	Y
15	143.85	C	4.3	43.22	92.45	Y
16	132.84	C	3.6	58.79	84.74	Y
17	233.51	I	4.5	76.90	144.06	Y
18	30.65	I	2.3	7.75	54.55	N
19	148.15	C	4.5	82.35	111.13	Y
20	5.52	C	1.5	1.50	42.81	N
21	82.34	C	3.4	25.82	42.12	Y
22	94.94	C	2.8	33.81	50.42	Y
23	109.90	C	3.6	37.26	86.75	Y
24a	333.04	C	3.8	103.46	141.17	Y
24b	27.01	C	2.3	7.98	16.26	Y

Sponge colony volumes: mean=77.01, s.d.=84.2, N=28
Sponge papillae areas: mean=28.73, s.d.=30.6, N=27
Areas of papillae plus
dead coral perimeter: mean=59.92, s.d.=39.8, N=29

Table 2. Area data for grouped sponge colonies*

Area of sponge papillae (cm^2)	Area of papillae & dead coral perimeter (cm^2)	Estimated area of of sponge mass (cm^2)
34.07	92.61	80
2.42	5.92	15
1.19	15.58	20
1.81	78.58	75
7.38	24.31	20
8.23	36.99	35
*	80.61	65
9.14	65.91	65
29.04	49.85	40
44.63	68.98	80
24.30	38.00	25
5.05	45.45	35
8.37	111.05	95
95.32	128.78	75
26.03	28.49	26
43.22	92.45	90
58.79	84.74	65
76.90	144.06	102
7.75	54.55	40
82.35	111.13	80
1.50	42.81	35
25.82	42.12	40
33.18	50.42	30
37.26	86.75	90
103.46	141.17	115
7.98	16.26	10

Areas of sponge papillae: mean=31.03, s.d.=30.7, N=25
Areas of papillae & dead coral perimeter: mean=66.83, s.d.=38.9, N=26
Estimated area of sponge mass: mean=55.69, s.d.=30.4, N=26

* grouping of colonies that share a common dead coral perimeter.

Table 3. Volume data for coral hand samples

Coral sample #	Volume of coral sample (cm^3)	Complete/In-complete coral head	Total volume of sponge colonies per sample (cm^3)
1	1633	I	95.86
2	534	C	7.15
3	469	C	20.01
4	118	C	21.30
5	1120	I	8.00
6	759	I	36.33
7	1445	C	36.81
8	924	I	62.65
9	3208	I	130.12
10	1245	I	44.26
11	331	C	37.54
12	1570	C	*
13	1824	C	253.15
14	501	I	61.36
15	1664	I	143.85
16	821	I	132.84
17	497	C	223.51
18	315	C	30.65
19	380	C	148.15
20	975	I	5.52
21	948	I	82.34
22	1505	C	94.94
23	1459	I	109.90
24	2550	I	360.05

Volumes of coral samples: mean=1116.5, s.d.=744, N=24
Sponge colony volumes per coral sample: mean=93.31, s.d.=88.8, N=23

Table 4. Area data for coral hand samples

Coral sample number	Total exposed area (cm^2)	Area of sponge and dead coral perimeter (cm^2)	Area of living polyp cover (cm^2)	Area of dead coral substrate (cm^2)
1	424.48	98.53	325.95	0
2	185.40	15.58	151.01	18.81
3	155.57	78.58	76.01	0.98
4	95.01	24.31	70.70	0
5	240.61	36.99	203.62	0
6	247.25	80.61	166.64	0
7	274.67	65.91	208.76	0
8	302.75	49.85	241.85	11.05
9	824.58	68.98	345.99	409.61
10	313.88	38.00	113.65	162.23
11	127.42	45.45	55.48	26.49
12	313.13	111.05	202.08	0
13	312.86	128.78	181.44	2.64
14	217.62	28.49	28.15	160.98
15	237.63	92.45	126.96	18.22
16	136.05	84.74	51.31	0
17	202.96	144.06	51.16	7.74
18	163.86	54.55	76.23	33.08
19	226.66	111.13	111.71	3.38
20	251.83	42.81	145.56	63.46
21	112.98	42.12	68.29	2.57
22	368.58	50.42	262.05	56.11
23	430.02	86.75	133.72	209.55
24	756.97	157.43	420.84	178.70

Total exposed area: mean=288.45, s.d.=179
Area of sponge and dead coral: mean=72.40, s.d.=38.4
Area of living polyps: mean=159.13, s.d.=103
Area of dead coral substrate: mean=56.92, s.d.=99.6

APPENDIX 2: In situ coral head data

Table 1. Area and volume data for Turtle Farm corals

Coral head volume (cm^3)	Total exposed area of head (cm^2)	Total area of sponge papillae (cm^2)	Total volume of sponge colonies per head (cm^3)
9139	1660	578	519
100544	11666	2640	2309
10604	1874	0	0
17485	2814	380	344
91185	10775	180	165
13714	2310	485	437
6538	1265	30	28
8502	1566	280	254
13450	2273	430	388
5914	1166	105	97
43689	5924	905	806
37863	5274	330	299
20942	3258	1090	968
21127	3282	1080	959
7037	1343	750	670
4555	943	370	335
6698	1290	700	626
3795	813	0	0
16987	2748	90	83
23628	3594	700	626
61389	7811	360	326
17356	2797	165	151
43008	5849	780	670
7405	1399	280	254
14681	2441	1700	1498
24319	3679	800	714
8449	1558	0	0
29077	4255	0	0
3120	693	300	272
7823	1463	195	178
65712	8256	320	290
7245	1375	200	183
3428	748	0	0
119441	13419	95	88
37787	5265	0	0
48950	6498	0	0
13929	2339	0	0
24851	3745	430	388
7881	1472	0	0
6052	1188	360	326
5265	1061	0	0
7427	1403	0	0
2567	591	60	56
26005	3885	40	38
2963	665	110	102

Table 1. Continued

Coral head Volume (cm^3)	Total exposed area of head (cm^2)	Total area of sponge papillae (cm^2)	Total volume of sponge colonies per head (cm^3)
23079	3526	205	187
14282	2387	0	0
2355	551	850	760
20852	3247	350	317
81818	9866	0	0
3484	758	0	0
14254	2383	260	237
23948	3634	70	65
215437	21677	0	0
10198	1815	330	299
26095	3896	0	0
56685	7321	0	0
41052	5632	350	317

Coral head volumes: mean=27467, s.d.=35928, N=58
Areas of exposed coral: mean=3730.7, s.d.=3780
Areas of sponge papillae: mean=481.29, s.d.=491, N=41 infested heads
Total volume of sponge colonies per head: mean=430.56, s.d.= 430

Table 2. Area and volume data for Control corals

Coral head Volume (cm^3)	Total exposed area of head (cm^2)	Total area of sponge papillae (cm^2)
698	205	0
278	97	0
9215	1672	0
8510	1567	0
7614	1431	0
41302	5660	0
7261	1377	0
11201	1959	0
8630	1585	0
63425	8021	0
28970	4242	0
13816	2323	0
1591	401	0
5005	1018	0
6580	1271	0
27247	4036	0
4910	1002	0
28048	4132	0
7954	1483	0

Coral head volumes: mean=14856, s.d.=16196, N=19
Areas of exposed coral: mean=2288.5, s.d.=2044

APPENDIX 3. S.P.M. Data

Concentrations of S.P.M. (X10 mg/l)

	Control deep	Control shallow	Turtle deep	Turtle shallow
	0.50	0.40	0.56	1.40
	1.30	1.60	1.08	0.74
		1.00		2.06
		1.50		1.96
		2.16		1.68
		1.88		1.72
mean	0.90	1.42	0.82	1.59
s.d.	0.566	0.635	0.368	0.478

APPENDIX 4. Bacteria Concentration Data

All filters: summation of data from 8 fields of view at 3000X magnification.
Concentrations in cells/ml.

Filter	Volume(ml)	Cocci	Rods	Coliforms	Total
TS1	15	$1.67 \cdot 10^6$	$4.02 \cdot 10^4$	$1.91 \cdot 10^6$	$3.62 \cdot 10^6$
TS2	30	$3.52 \cdot 10^5$	$3.41 \cdot 10^4$	$3.79 \cdot 10^5$	$7.65 \cdot 10^5$
TD1	15	$6.89 \cdot 10^5$	$4.55 \cdot 10^4$	$6.06 \cdot 10^4$	$7.95 \cdot 10^5$
TD2	30	$7.46 \cdot 10^5$	$1.14 \cdot 10^4$	$1.13 \cdot 10^6$	$1.89 \cdot 10^6$
CS1	30	$6.52 \cdot 10^5$	$7.58 \cdot 10^3$	$1.25 \cdot 10^5$	$7.84 \cdot 10^5$
CS2	60	$4.56 \cdot 10^5$	$9.47 \cdot 10^3$	$9.47 \cdot 10^4$	$5.61 \cdot 10^5$
CD1	30	$6.63 \cdot 10^5$	$7.58 \cdot 10^3$	$1.14 \cdot 10^5$	$7.84 \cdot 10^5$
CD2	60	$3.03 \cdot 10^5$	$7.58 \cdot 10^3$	$5.49 \cdot 10^4$	$3.66 \cdot 10^5$
CD3	90	$2.99 \cdot 10^5$	$7.58 \cdot 10^3$	$7.95 \cdot 10^4$	$3.86 \cdot 10^5$
TS2E	30	$3.71 \cdot 10^5$	$3.03 \cdot 10^4$	$3.60 \cdot 10^5$	$7.61 \cdot 10^5$

TS: Turtle farm shallow (E: extra set of 8 fields of view for operator error determination)
TD: Turtle farm deep
CS: Control shallow
CD: Control deep

APPENDIX 5. Accuracy and Precision Determinations

Hand samples:

1. Precision of surface area measurements with plastic sheets:

   maximum relative error between measurements by two individuals
   = 11% of larger sample (3 samples used)

2. Accuracy of volume measurement by water displacement:

   error of three weighings involved in procedure = 3 X ($\pm$5g) = $\pm$15g
   error of water volume = $\pm$45g
   therefore: error of each volume = $\pm$60g
   average coral volume = 1116.5g
   therefore: average relative error = $\pm$5% (24 samples used)

In situ coral heads:

1. Accuracy of sponge area estimations:

   average of $\frac{\text{estimate by quadrat method}}{\text{actual D.C.A. value (plastic method)}} = 0.91$
   therefore: average relative error = $\pm$10% (24 samples used)

2. Accuracy of sponge colony volume measurements:

   average relative error of sponge area estimations = $\pm$10%
   use regression equation 1. S.V. = $(\text{D.C.A.})^{0.983}$
   therefore: average relative error of colony volume = (.983)($\pm$10%)
   = $\pm$9.8%

3. Accuracy of coral volume measurements from photographs:

   maximum relative error between volumes by photograph method and volume by displacement method = $\pm$28% of displacement volume
   average relative error of displacement method = $\pm$5%
   therefore: maximum relative error of photograph method = $\pm$(28+5)%
   = $\pm$33% (2 samples used)

4. Accuracy of total exposed surface area per coral head:

   maximum relative error of volumes by photograph method = $\pm$33%
   use regression equation 6. C.S.A. = $(\text{C.V.})^{0.81}$
   therefore: relative error of exposed surface area = (0.81)($\pm$33%)
   = $\pm$27%

APPENDIX 5. Continued

Bacteria Counts:

1. Precision (operator error) of total bacteria counts:

   maximum relative error between counts for filter (8 fields of view) derived by two individuals =10 % of larger value (filters TD2 and CD3 used)

2. Accuracy of total bacteria counts:

   relative error of counts obtained for two sets of 8 fields of view photographed from filter TS2 = 1% of the larger value. (relative error obtained for different size classes of bacteria = 5.1% for cocci and coliforms; 11% for rods.)

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