Internal bioerosion of *in situ* living and dead corals on the Great Barrier Reef

Thesis submitted by
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DECLARATION

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Abstract

This thesis reports on a series of sampling and experimental studies aimed at quantifying the extent of internal bioerosion by four major groups of boring organisms in *in situ* coral substrates. Additional objectives of the study were to investigate the patterns of variability of internal bioerosion and overall skeletal degradation across common coral substrates and a number of spatial scales within a single habitat. The response of internal bioeroders to availability of dead coral substrate, such as following an *Acanthaster planci* outbreak, was also addressed.

Internal bioerosion and external degradation were studied in living and dead corals of three species of *Acropora* (*A.hyacinthus, A.gemmifera* and *A.cuneata*) using a manipulative field experiment over a 21 month period. Coral colonies were killed *in situ* to simulate local episode of coral predation. In addition, living colonies of the same species were sampled and intenral bioerosion was quantified. The extent of internal bioerosion in living colonies was generally small, but differed strongly among the three coral species. *A.cuneata* was excavated up to ten times more than the other two species. The major source of difference among the species was the presence of the live-coral boring bivalve, *Lithophaga lessepsiana,* in colonies of *A.cuneata*. The majority of the remaining variation across the three species was explained, to different extent for each boring group, by inter-specific differences in the amount of exposed skeleton. This was found to be species-specific and, in the case of *A.hyacinthus*, to differ also between the two locations. Variation in the extent of excavation was high at small spatial scales for all coral species and all boring taxa. Sponges (*Cliothosa hancocki* in particular) were by far the most destructive borers in living colonies of the three species, together with the bivalve *L.lessepsiana*, which bored exclusively in living portions of *A.cuneata*. Worms, mostly polychaetes, although numerically more abundant, accounted for little of the total bioerosion in living corals.

Colonies of the three species of *Acropora* were killed and left *in situ* for 21 months. Changes in colony size and rugosity over the period of exposure were examined using photographic monitoring. Both colony size and rugosity decreased significantly over time following death. The decrease in both size and rugosity varied considerably among the three coral species with very rapid skeletal degradation occurring soon after death in plate colonies of *A.hyacinthus*. The rates of external degradation in *A.hyacinthus* were not costant through time and were higher soon after death. In contrast, *A.cuneata* experienced no significant variation

in size, while *A.gemmifera* decreased in size at a relatively uniform rate. In *A.hyacinthus,* the position of the colonies with regard to location, resulted in different rates of external degradation but this pattern decreased with time. At the study sites, external erosion of colonies of *A.hyacinthus* killed and left standing on the reef surface contributed a total of 0.41 to 1.19 kg of $CaCO_3$ per m^2 per year (when assuming a 100% cover of *A.hyacinthus*).

Following the 21 month period of exposure to borers, the colonies were collected and analysed for the extent and nature of internal bioerosion. This differed greatly among the three coral species. The difference in the extent of bioerosion by worms was entirely explained by the extent of colony surface area available for settlement in the three coral species. On the contrary, availability of surface area did not explain the considerable difference in the extent of bioerosion by sponges in the three species. It is suggested that newly available substrates on the reef surface are readily excavated by boring sponges which are already present in adjacent substrates. Furthermore, it appears that the occurrence of large bivalve borings in colonies of *A.cuneata* might have determined a larger extent of excavation by sponges in this species. Bioerosion by bivalves was larger at South East exposed sites but no effect of location was detected for any other individual groups of borers. *A.cuneata* had a greater extent of total bioerosion by all taxa at the front sites, which is explained by the cumulative effect of sponges and bivalves. As was the case in the living colonies, the majority of the variability encountered was due to variation at small spatial scales (within-site variation for all groups and within-colony variation for worms and bivalves in *A.hyacinthus* and *A.gemmifera*). However, a small proportion of variability was explained at the spatial scale of site (hundreds of meters) for both worms and sponges. Total bioerosion was not correlated to any of the colony parameters considered. However, when bioerosion was considered for each group separately, there was a high correlation between colony surface area and bioerosion by worms, while bioerosion by sponges and bivalves correlated with colony volume.

The comparison between bioerosion in living and dead coral colonies of the same species over a period of 21 months following death showed that the volume removed by internal bioeroders from dead colonies per unit of colony surface area, was significantly higher than the volume of skeleton excavated from living colonies. The average amount of $CaCO_3$ reworked by internal bioeroders per m^2 per year varied from a minimum of 0.23 g x m^{-2} x y^{-1} for barnacles to a maximum of 766.1 g x m^{-2} x y^{-1} for sponges. The reworking by borers of $CaCO_3$ in dead coral

colonies varied up to 4-5 times among the coral species. This suggests that coral community composition and the dynamics of mortality of individual species may affect the overall reef bioerosion. Rates of excavation also varied between locations, with the SE more exposed sites experiencing higher rates of $CaCO_3$ loss via excavation by sponges and bivalves. In all coral species considered, sponges were the group that excavated the most of the $CaCO_3$ per unit of surface area and time.

In order to investigate the effect of massive coral mortality on rates of internal bioerosion, a sampling study was conducted at two reefs which had been severely affected by *Acanthaster planci,* and at two reefs which had not experienced outbreaks in the last 20 years. Internal bioerosion was quantified for all reefs from dead *Porites* substrates. These were dated for the year of death of the living tissue using fluorescent bands occurring in the skeleton of these corals. The time elapsed since death was assumed to be the time of exposure to boring organisms. Bioerosion rates in *Porites* were not linear over time, but decreased with time after death of the substrate. Rates of bioerosion among reefs were not different although there were differences among sites within reefs. The major borers were worms, mostly sipunculans at all reefs, although sponges were locally abundant (i.e. Green Island). Sponges, when present, tended to be far more destructive than the other groups.

No effect of outbreaks of *Acanthaster planci* was detected. The volume excavated per unit of time did not appear to either increase nor decrease as a result of severe episodes of coral mass mortality. This suggests that following an outbreak the production of carbonate by-products via excavation of dead corals may increase proportionally to the increase in dead coral cover. The majority of variation in rates of bioerosion was due to the duration of exposure of the substrate to borers. Bioerosion rates were highly variable at small spatial scales also (centimeters to meters), suggesting that processes occurring at small spatial scales, such as recruitment of borers, are most important in determining spatial patterns of internal bioerosion in *Porites* substrates. The instantaneous rates of bioerosion in dead *Porites* ranged between 8±4 to 626±170 g $CaCO_3$ m^{-2} y^{-1}.

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1.1 Introduction

This thesis examines the process of internal bioerosion by large boring invertebrates in coral reef substrates. Little is known at present of the dynamics of internal bioerosion within *in situ* coral substrates. A major difficulty faced by scientists investigating boring organisms on coral reefs, arises from the large variety of substrates excavated and the diversity of organisms involved in the process (Hutchings 1983 and 1986). Reef substrates are heterogeneous, which poses considerable problems for establishing sampling protocols appropriate for investigating the extent and patterns of distribution of internal bioerosion. Consequently, many quantitative estimates of bioerosion have been characterised by high levels of variation which make interpretation of ecological patterns unclear. In response to this problem, much recent research on bioerosion has focused on the use of artificial coral substrates (usually coral blocks placed on a suspended grid). Artificial substrates have the advantage of providing replicable units and thereby allow for controlled experiments (Hutchings 1986). However, in order to assess the importance of bioerosion in the ecology and morphology of coral reefs, a thorough understanding of the distribution and extent of bioerosion in *in situ* substrates is essential. The overall goal of the research described in this thesis was therefore to examine how internal bioerosion in live and dead *in situ* colonies varies among coral species and spatial scales and which factors may influence the process. A more specific objective was to address the question of the fate of *in situ* coral skeletons following widespread coral mortality, such as that resulting from outbreaks of Crown-of-Thorns starfish (COTS).

1.2 Significance

Reef bioerosion has a fundamental role in determining the structure and morphology of modern and ancient coral reefs (see Davies 1983 and Hutchings 1986 for review). Coral reefs are considered to be the result of two antagonistic forces which act simultaneously on the reef framework: constructive processes, in the form of calcium carbonate deposition mainly by corals and coralline algae, and destructive processes which result

from biological and physical erosion of the reef surface (Scoffin *et al.* 1980; Davies 1983). Hubbard *et al.* (1990) recently highlighted the importance of destructive processes in determining the reef fabric of modern and ancient coral reefs. Schroeder and Zankl (1974) showed that the detrital material resulting from processes of reef degradation forms the majority of the reef interiors in modern and fossil reefs. It has been suggested that our perception of reef morphological development overemphasises the relative importance of constructional processes (Hubbard *et al.* 1990). This has resulted in a good understanding of the processes of coral zonation and calcium carbonate deposition across a reef system (Done 1983; Kinsey 1977; Davies 1983). However, we know very little about their destructive counterparts (Hutchings 1986).

Living and dead standing coral skeletons are major components of the framework on which many reef organisms and processes depend. Processes affecting their structural integrity and the rates at which they are reworked, include both physical erosion and external (grazers) and internal (borers) bioerosion. The fate of standing coral skeletons depends primarily on the intensity of these processes, their relative importance and interactions, and the occurrence of episodic highly destructive events, such as storms and cyclones (Scoffin 1992; MacIntyre 1984). After a cyclone or a violent storm and in areas of exceptionally high wave energy, physical erosion including both mechanical breakdown and abrasion, may temporarily and locally exceed bioerosion (Spencer 1985). This will result in a reduction of the structural complexity of the reef framework, and the detrital compartments of the reef (rubble and sediments) will predominate at a local scale. However, in situations of low disturbance, eg. during periods between cyclonic events, the processes of biological destruction of reef substrates dominate over physical erosion (Scoffin *et al.* 1980; Spencer 1985).

The process of reef bioerosion depends on the ecology of bioeroding organisms. The temporal and spatial distribution of bioeroders on the reef surface and their responses to ecological gradients will determine patterns of bioerosion at a reef scale. In this respect external and internal bioeroders differ substantially. External bioeroders are vagile, while the majority of boring organisms are colonial or non-colonial sessile organisms and, therefore, are likely to respond differently to environmental conditions. The two

groups also differ with regard to the impact they have on the reef surface. It has been suggested that external bioeroders, and excavator scarids in particular, decrease the topographical complexity of the reef surface by preferentially excavating convex substrates (Bellwood and Choat 1990). In contrast, boring organisms are believed to increase rugosity by creating holes and perforations in the reef framework, which may provide microhabitats for non-boring cryptic organisms (Moran and Reaka 1988). Thus, biological destruction has diverse implications for the ecology and morphology of coral reefs which warrant further investigation. A knowledge of the relative importance of destructive processes for *in situ* reef substrates is essential to assess the ecological and geological significance of bioerosion.

In the Pacific, heavy outbreaks of the Crown-of-Thorns starfish, *Acanthaster planci* (COT), are important disturbance events which are likely to shift the construction-destruction balance on coral reefs. Following an outbreak, a reef experiences a dramatic increase in cover of dead coral colonies (up to 90 %, Moran *et al.* 1985). As both internal and external bioerosion act primarily on dead corals, it is reasonable to expect that heavy outbreaks may result in a shift in the overall rates of biological destruction. A number of authors have highlighted the potential increase in bioerosion following COT outbreaks (Sano *et al.* 1984; Hutchings 1986; Glynn 1988), however no previous study has directly addressed this question.

1.3 Rationale

This study incorporates both manipulative and sampling approaches to the investigation of reef bioerosion in order to examine how the process varies among coral species and spatial scales. I chose to focus the experimental component of the study on the reef crest habitat at a number of spatial scales and to make use of live and dead, *in situ* coral colonies belonging to three common species. In this component of the study, I also addressed questions of the effects of *Acanthaster planci* predation on the process of internal bioerosion by simulating predation on a local scale on three species of *Acropora* corals. In the second component of the study, which involved a large-scale sampling programme, I examined the process on reefs with a known history of heavy

COTS outbreaks and on reefs which have no recorded outbreaks. Below, I provide the rationale for these choices.

1.3.1 Reef crest - justification for the experimental site and design

The experimental component of the study was confined to a single reef habitat on one reef with experimental units replicated at a variety of spatial scales (within colonies to among sites). Due to time and resource constraints it was unfeasible to perform the experiment on more than one habitat or reef, while addressing issues of spatial variability at multiple spatial scales.

The distribution of organisms on coral reefs is highly variable and many processes, such as coral zonation, community structure and recruitment, operate at small to medium spatial scales (Carleton and Sammarco 1987; Green *et al.* 1987; Fisk and Harriot 1990; Done *et al.* 1991; Nelson 1994). The necessity to investigate reef processes at multiple spatial and temporal scales has been recently emphasised (Andrew and Mapstone 1987; Jackson 1991 and 1992). Previous studies have attempted to address habitat-related patterns in internal bioerosion (Davies and Hutchings 1983; Hutchings and Bamber 1985; Kiene 1988), however no previous study has investigated the process at multiple spatial scales within a habitat.

While concentrating on one habitat on one reef implies that the experiment could not provide unequivocal information on large-scale patterns, the priority of this study was to gain an insight of the small to medium scale patterns in the process (within colonies and between sites). The present study, therefore, implements hierarchical experimental and sampling designs which include spatial scales ranging from centimetres to hundreds of meters within a reef to inter-reef comparisons. The importance of identifying the scale at which bioerosion varies most is twofold: firstly, hypotheses on the mechanisms that underlie the distribution of different borers and how they may interact in coral community dynamics may be generated; secondly, it constitutes an essential prerequisite for efficiently allocating resources for future research.

The choice of focussing the experimental study on the reef crest and reef front habitats was based on three considerations. Firstly, the exposed side of the reef is the structurally most dynamic area of a coral reef (Davies 1983). The high rates of calcium carbonate deposition (Kinsey 1977) suggest rapid turnover of coral colonies and assemblages and rapid reworking of the reef framework. Recent studies on coral community dynamics indicate that the reef crest is an area of high species diversity and high growth and mortality rates, ie. it is a very dynamic environment (Nelson 1994). Previous experimental studies on the Great Barrier Reef suggested that windward, exposed sites may host a more diverse bioeroding infauna than sheltered sites (Davies and Hutchings 1983). Secondly, the reef crest and front are the habitats which are commonly the most impacted by COTS outbreaks. Thirdly, as I used *in situ* coral colonies (see below), the high coral cover on the reef crest provided large numbers of similar sized colonies which allowed for suitable replication of experimental units.

1.3.2 In situ *coral substrates - realistic model for studying bioerosion*

The use of *in situ* coral colonies ensures that the results are directly relevant to substrates that occur naturally on the reef area under study. In this study bioerosion is examined in both living corals colonies and in the skeletons of corals that have been dead for a known period of time. These two categories of substrate are important structural components of the reef framework which are likely to differ in the extent to which they are excavated by internal bioeroders. A thorough understanding of how bioerosion operates within naturally occurring substrates will guide us in the interpretation of results obtained from studies which use artificial substrates, such as coral blocks layed on grids. This will provide the quantitative basis necessary to link bioerosion with the dynamics of coral communities and the potential impacts of natural and anthropogenic disturbances on reef systems.

1.3.3 Implications of COTS predation on reef bioerosion

Bioerosion is a process that affects predominantly the skeletons of dead coral colonies (Highsmith 1981). On the Great Barrier Reef, severe outbreaks of the Crown-of-Thorns starfish result in large expanses of dead coral colonies standing on the reef surface. In situations of widespread coral mortality the amount of substrate available to internal

bioeroders increases dramatically. The consequences on local and reefwide rates of bioerosion may be expected to be large. However, they have not been addressed directly prior to this study. An understanding of the fate of coral colonies standing on the reef surface is required to address such questions. The use of coral colonies killed *in situ*, as in this study, simulates a situation of local predation by COTS and allows us to examine the fate of coral skeletons after the death of the living tissue. Three coral species are chosen for the experimental study which are known to be preferred preys by COTS (De'ath and Moran 1992).

The effect of Crown-of-Thorns on bioerosion is addressed in a broader spatial and temporal scale by comparing bioerosion in dead corals among individual reefs that have a documented history of heavy starfish outbreaks with reefs which have historically low COTS population densities. The two components of this study provide the spatial and temporal context necessary to more fully interpret the importance of such episodes in the ecology and development of coral reefs on the Great Barrier Reef.

1.4 Background

The term "bioerosion" was introduced by Nuemann, during a study of coastal erosion in Bermuda. He defined it as "the destruction and removal of consolidated mineral or lithic substrate by the direct action of organisms" (Neumann 1966). Applied to a coral reef system, bioerosion artificially groups a number of biological processes that result in the alteration and destruction of the reef surface and includes taxa from several invertebrate phyla and one class of vertebrates. It is conventional to separate two major categories of bioerosion: internal bioerosion produced by boring organisms (sponges, polychaetes, sipunculans, barnacles and others), and external bioerosion produced by grazers and scrapers (eg. echinoids and scarids). A further distinction is made within borers, based on the size of individual borings: microborers, such as algae, bacteria and fungi, which produce microscopic excavations; and macroborers, which produce macroscopic borings and include several groups of invertebrates, the most important being sponges, bivalves, polychaetes, sipunculans and barnacles. This study is primarily

concerned with bioerosion by macroborers and their impact on intact scleractinian corals on the reef surface.

The importance of the process of bioerosion was recognised early in the history of coral reef science:

"....*A proper understanding of the relationships between those organisms that build and help to protect reefs, and those that aid, directly or indirectly, in their destruction is essential in the proper understanding of the whole.*" (Otter 1937).

However, quantitative research of the process of reef bioerosion is relatively young. Pioneering work in the Barbados established the importance of bioerosive processes on the reef and the relative significance of different agents of bioerosion (Stearn and Scoffin 1977; Scoffin et al. 1980). They calculated rates of calcification, boring and grazing for various carbonate substrates on an individual reef. They established that external bioerosion by echinoids (*Diadema antillarum* at densities of 23 ind. m^{-2}) and internal bioerosion by sponges were the most important destructive processes on the reef. The results of these studies on calcification, sedimentation and biological and physical erosion were combined to provide the $CaCO_3$ budget of a fringing reef system. In this model, reef bioerosion exceeded growth by about 26 metric tons of $CaCO_3$ every year (Stearn and Scoffin 1977). In a subsequent re-evaluation of the study, which accounted for substrate re-cementation and a lower estimate of *Diadema* grazing rates, the reef calcification rates slightly exceeded destruction rates (206 ± 10 tons $CaCO_3$ per year versus 123 ± 7 tons $CaCO_3$ per year respectively; Scoffin *et al.* 1980). The study showed that for the Northern Bellairs Reef, calcification and erosion were occurring at very similar rates. Despite the extrapolations on which this study was based, it provided a quantitative basis for the construction-destruction balance theory of coral reefs. The process of reef development had previously been equated to the process of calcium carbonate fixation (Smith and Kinsey 1976). After the study in Barbados, it became clear that the reef structure was the result of the interaction between coral and algae calcification and bioerosion. In addition, Scoffin *et al.* (1980) first highlighted the

problems in obtaining representative quantitative data for such a complex and diverse process.

1.3.1 Impacts of bioeroders on coral reef substrates

The mechanisms by which bioeroders destroy the reef substrates are diverse. They are usually divided into chemical ($CaCO_3$ is dissolved) and mechanical (the substrate is degraded to rubble or coarse to silt sediment), although in most cases a combination of the two occurs (Hutchings 1986).

Early studies concerned with boring reef organisms provided thorough descriptions of the many individual species, their mechanism of penetration and the boreholes that they produce (sponges: Cobb 1969; Pang 1973a; Rützler 1974; Thomas 1979; polychaetes: Blake and Evans 1973; Zottoli and Carriker 1974; sipunculans: Rice 1969; bivalves: Ansell and Nair 1969; Appukuttan 1972; Wilson 1979). As a result, and strongly in contrast with the dearth of information on the life history and ecology of individual boring taxa, extensive and detailed descriptions of boreholes are available in the literature. This allows the identification of many internal bioeroders from their borings, and it has been widely used in studies where bioerosion has been estimated from sections of the substrate.

Sponges penetrate calcium carbonate by the means of specialised cells which send filopodia into the substrate from which they isolate small, characteristically shaped "chips" (Rützler and Rieger 1973; Pomponi 1977, 1980). These are expelled into the environment through a system of exhalant canals. This mode of excavation also results in the characteristic scalloped appearance of the walls of boring sponges excavations. The filopodia are aided in the excavation by enzymatic secretions (carbonate anhydrase). Rutzler and Rieger (1973) showed that only the 2-3% of the eroded calcium carbonate is dissolved by *Cliona lampa*, the most abundant and destructive boring species in the Caribbean (Rützler 1974). Most of the calcium carbonate is reworked into silt size sediments in the form of identifiable "chips". Futterer (1974) calculated that the "chips" produced by boring sponges accounted for up to the 30% of the silt size sediments in the lagoon at Fanning Island, where sedimentation rates are also very high (Futterer 1974).

Boring bivalves display a variety of mechanisms to excavate the substrate. Some Pholodidae mechanically penetrate the coral rock through rotatory movements of their shells (Yonge 1963). Other bivalves like *Lithophaga* spp. use both chemical and mechanical means (Soliman 1969). Lithophaginae display an interesting evolutionary trend associated with an increasing substrate specialisation, from dead coral substrates to live corals and species-specificity of coral host (Morton and Scott 1980). While species found in dead coral substrates bore by both mechanical and chemical means, some species that live in living corals use mainly chemical means for inhibiting calcium deposition by the coral at the aperture of their borehole. This trend is accompanied by considerable modifications in shell thickness, muscular apparatus and glandular system (Morton and Scott 1980). In terms of bioerosion and its calcium by-products, live and dead coral *Lithophaga* spp. seem to have different impacts on the reef.

Mechanisms of boring for most polychaetes and sipunculans are not clear. Some species of both taxa possess structures, like teeth and hooks, which they use to mechanically excavate into the substrate. However there is experimental evidence that at least some species of polychaetes (Haigler 1969) and sipunculans (Williams and Margolis 1974) chemically dissolve calcium carbonate. Other groups of internal bioeroders, such as chitons (although depending on the species, they may be regarded as external bioeroders also) or barnacles, use mostly mechanical mechanisms of excavation, which result in the production of coarse to fine sediments (Warme 1975).

External bioeroders mechanically excavate the substrate. Scarids have developed a powerful buccal apparatus to bite/scrape off coral substrates. However, not all species of scarids contribute to the destruction of the substrate they graze on. Recently, Bellwood and Choat (1990) have identified two functional groups of species, of which only the 'excavator' ones are capable of considerable bioerosion. The products of their feeding activity include both what they ingest and what they accidentally break off while feeding. The pieces of substrate ingested are reworked into fine sediments (Frydl and Stearn 1978), but a portion of it is dissolved (Smith and Paulson 1975). This means that bioerosion by scarids results in the dissolution of calcium, production of fine sediments and coarse sediments to rubble. However, most studies have focused on the ingested material and the quantification of fine

sediment produced (Frydl and Stearn 1978) and their role in rubble production has not been quantified.

Echinoids are not known to dissolve calcium carbonate (Hutchings 1986). They excavate the substrate using both the complex of exoskeletal plates that surrounds their mouth and spines. They bioerode while grazing on the surface of the substrate but for many species their ability to erode provide them also with shelter during periods of feeding inactivity. Hunter (1977) found that 50-80% of the sediment produced by *Diadema antillarum* is silt size, with the remaining portion being fine to coarse sediment.

Reef bioerosion is executed by a variety of organisms and results in a diverse range of carbonate products. Depending on their mechanism, and largely on their biology and ecology, bioeroding organisms will have various impacts on both the ecological and the geological structure of the reef. Although for most species the modality of penetration into the carbonate substrate is not clear, what is known strongly suggests that only a small portion of the calcium carbonate eroded is dissolved. The most of the substrate is reworked into either rubble or coarse to fine sediments. The ultimate fate of these carbonate by-products will depend on various and complex factors including local hydrological regimes. This has been the object of increasing attention of reef geologists (see Davies 1983 for a review). In contrast, the main concern of ecologists investigating bioerosion has been to establish the rates at which bioeroders excavate the substrate and what factors determine or affect their spatial and temporal distribution on the reef surface.

1.3.2 Spatial and temporal patterns of internal bioerosion. What do we know?

The study of reef internal bioerosion in the field is characterised by considerable difficulties. This is mainly due to the cryptic nature of internal bioeroders, to the enormous variety of substrates on the reef framework that are excavated by bioeroders, and to the need for determining the time of exposure to borers for any individual substrate (for both calculating rates and for stratifying the samples).

Internal bioeroders are by definition endolithic. Sampling involves collecting and breaking, or sectioning, many replicated samples. To obtain data on the abundance of

borers and on the extent of excavation is time consuming, which is one reason why much more is known of the distribution and community structure of epibenthic or nektonic reef organisms. A more important obstacle in the investigation of reef internal bioeroders, is the large heterogeneity of substrates that are bioeroded on a reef. Hutchings (1983) recognises several problems in the sampling of reef cryptic biota, which are due to substrate heterogeneity. In particular, the problem of choosing replicates among very heterogeneous substrates, how to standardise data on endolithic organisms among different samples and how to extract the infauna. A direct consequence of the large variety of substrates is that in any attempt to estimate the abundance and distribution of boring organisms, a stratification of sampling, based on the substrate features that are likely to affect bioerosion, requires focussing on few, easily identifiable and abundant substrates. This has important implications for our ability to describe in full the process of bioerosion over the range of substrates found on a coral reef. It also explains why many studies on reef bioerosion have used living corals as study substrates, as they can be easily identified for sampling (Hein and Risk 1975; MacGeachy and Stearn 1976; Stearn and Scoffin 1977; Sammarco and Risk 1990). However, internal bioerosion in living corals is restricted and excavation is small (Highsmith 1981a; Highsmith *et al.* 1983; Peyrot-Clausade *et al.* 1992), which makes them less desirable than dead coral substrates for studying bioerosion.

As a consequence of the difficulties associated with the study of reef cryptic organisms, many works on internal bioerosion have been descriptive, based on qualitative data, or on quantitative data collected with sampling designs and techniques which do not allow for a satisfactory stratification of the samples. A number of factors that may contribute to inter-substrate variations in the extent of bioerosion have been singled out by previous studies. The presence of living coral tissue is known to inhibit the excavation activity of borers (MacGeachy and Stearn 1976; Hutchings and Weate 1977; Scoffin *et al.* 1980; Highsmith 1981a). The extent of encrusting organisms, in particular coralline algae (MacGeachy 1977; Bak 1976; Smyth 1989), the structural complexity of the substrate (Peyrot-Clausade and Brunel 1990), and the skeletal density (White 1980; Highsmith 1981b) have all been suggested as affecting the extent of excavation, although evidence was not conclusive (especially in White 1980 and Peyrot-Clausade

and Brunel 1990). The duration of exposure of the substrate to bioerosive agents is responsible for changes in both the extent of bioerosion and the taxonomic composition of the boring communities (Hutchings and Bamber 1985; Peyrot-Clausade *et al.* 1992). It appears that the development of boring communities in newly available substrates follows a succession, with the pioneers microborers being followed by polychaetes and with sponges, bivalves and sipunculans appearing later (after 6-9 months, Davies and Hutchings 1983: Hutchings and Bamber 1985; Kiene 1985). Davies and Hutchings (1983) showed that during the initial stages after a substrate becomes available, there are large fluctuations in the numbers of borers. Moreover, these fluctuations are exacerbated by large inter-year variations in recruitment of some non-colonial borers (Hutchings 1985; Hutchings *et al.* 1992). As a result, reef substrates exposed for varying and unknown times to borers, may display high levels of unexplainable variability. Therefore, sampling substrates that have been exposed to borers for a known duration is highly desirable, if not necessary, in studies of internal bioerosion.

Recent studies on the Great Barrier Reef (GBR) have shifted the emphasis of research on reef bioerosion towards an experimental and manipulative approach, in order to identify spatial and temporal patterns of the process (Davies and Hutchings 1983; Hutchings *et al* 1992; Kiene 1988). Davies and Hutchings (1983) started a long term experiment using blocks cut from *Porites* skeletons and laid at different times in different reef zones. Results from this experiment have been reported at various intervals by Hutchings (1985), Hutchings and Bamber (1985), Kiene (1985), Hutchings *et al.* (1992) and Kiene and Hutchings (1992). The main purpose of the study was to estimate the rates of bioerosion and the composition of boring communities over time across five habitats. After 3.5 years of exposure of the substrates, Kiene (1985) reported higher rates of bioerosion on the reef slope than the reef flat and lagoon, and differences among the agents responsible for the erosion in the different reef zones. This pattern differed from the one observed by Davies and Hutchings (1983) after only 18 months of exposure, when they had found that blocks on a patch reef in the lagoon and on the reef flat had experienced higher rates of bioerosion by polychaetes than the reef slope. Kiene and Hutchings (1992), reporting the long term results of this experiment (7-9 years of exposure), which included additional blocks in two leeward habitats, found higher rates of bioerosion in the deeper leeward habitat, but the patterns

among the other habitats varied between blocks laid for 7 and 9 years. They concluded that their experiment highlights the variability of bioerosion on reefs. Although this may indeed reflect high levels of natural variability in the distribution of borers across a reef, it may also be due to the experimental design implemented. In particular, a low number of samples had been examined after each period of exposure ($n \leq 3$ in most cases; Davies and Hutchings 1983; Hutchings and Bamber 1985; Kiene and Hutchings 1992) and samples were not replicated within habitats. However, the methodological approach they used has the considerable advantages of standardising the substrate inherent features, controlling for time and duration of exposure and potentially allowing for rigorous design and high number of replicates.

The high levels of variability encountered during that experiment highlight the need for carefully designed sampling and experimental programmes, capable of partitioning variability associated with the process of bioerosion on reef substrates. The distribution of borers across small spatial scales which occur within a single habitat, remains largely uninvestigated. The only study that implemented a hierarchical design to look at multi-scale spatial effects, was carried out on the GBR, and investigated internal bioerosion in living colonies of *Porites* species at the leeward side of five reefs (Sammarco and Risk 1990). Results from the study indicated high variation at small spatial scales, and suggested a cross-shelf pattern in the distribution of major groups of borers (Sammarco and Risk 1990), although confirmation of such pattern would require a study which includes replication of each cross-shelf position.

In spite of the generally acknowledged significance of internal bioerosion for coral reefs at many levels (impact on other reef organisms, geomorphology, palaeoecology, potential impacts in high nutrients conditions etc.), and despite research on bioerosion has been conducted for few decades, our understanding of the process is poor. In particular the generalisations that we can make in regards to bioerosion are few, because unequivocal and representative results on the major factors affecting spatial and temporal patterns in the distribution of borers are yet to be obtained.

1.5 Thesis contents

The structure of the study is schematically represented in Figure 1.1. The study consisted of a field experiment and sampling exercises which aimed at i) quantifying the extent and rates of internal bioerosion in different reef substrates *in situ*; ii) determining the effect of spatial scales and type of substrate on the process and iii) describing the distribution and impact of the different boring agents. The research has two components: the first consists of studies of internal bioerosion in *in situ* colonies of three common coral species (*Acropora hyacinthus, A.gemmifera* and *A.cuneata*). I quantified the extent and short term rates of bioerosion by each of five major groups of borers in living colonies and dead colonies that had been exposed for a known duration to bioeorders. These studies were carried out at the same sites on the reef crest of a single reef in the northern Great Barrier Reef (GBR). The results from these studies, which included both sampling exercises and experimental manipulation, are described in Chapters 2, 3 and 4.

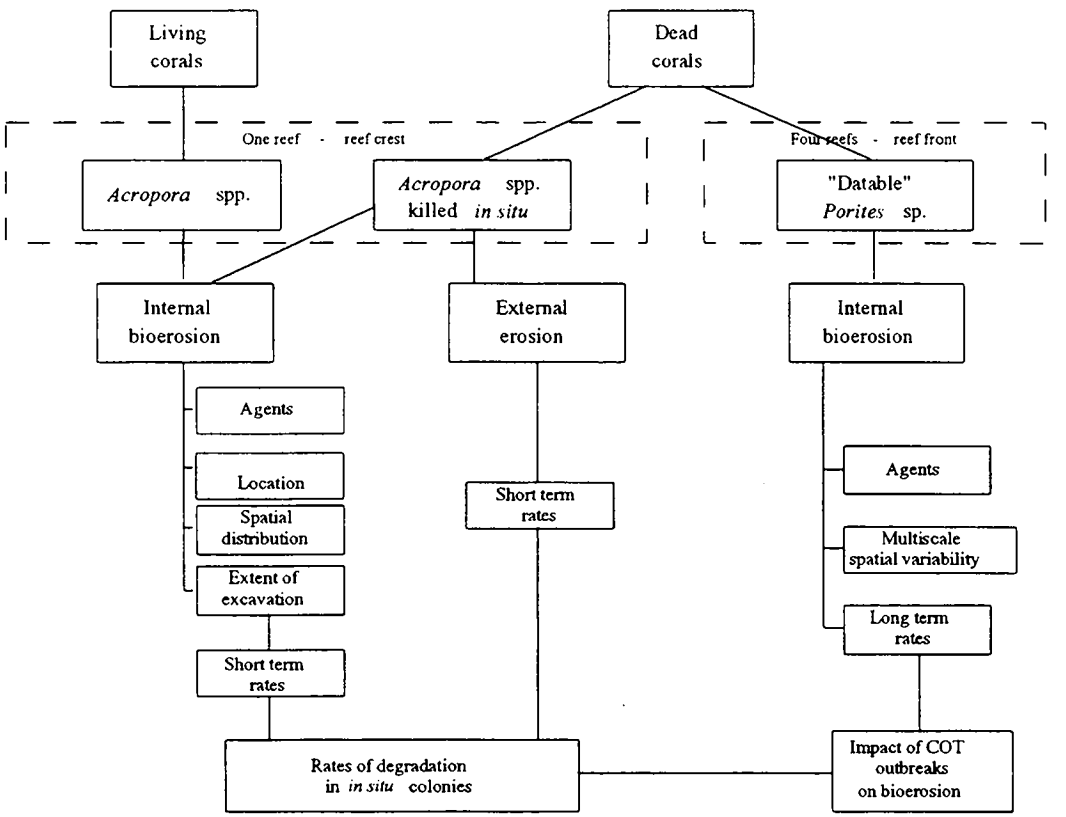


***Figure 1.1**: Schematic representation of the components of the study and their relationship to the impact of Crown of Thorns outbreaks on internal bioerosion on the Great Barrier Reef.*

The second component was a sampling exercise which visited four different reefs in the central and northern GBR. The major aim was to obtain estimates of medium to long term rates of internal bioerosion for one type of dead coral substrate (namely, large dead *Porites* surfaces), in order to study the variability of the process over different spatial scales (within site, between sites and between reefs). The length of exposure of the substrates to borers was estimated during the study, and varied between 1.5 and ~100 years. An additional aim of the study was to examine the effect of the sudden and massive availability of dead coral substrates, which follows *Acanthaster planci* outbreaks, on bioerosion. The reefs sampled included two reefs that had experienced heavy *A.planci* outbreaks and two reefs that are considered pristine with respect to the outbreaks. This study is described in Chapter 5.

Chapter 2

Patterns of internal bioerosion in living colonies of three coral species

2.1 Introduction

This study investigates the extent of internal bioerosion in living colonies of three species of acroporid corals. The objectives were 1) to investigate species-specific patterns of bioerosion in living coral colonies and 2) to provide quantitative estimates of calcium carbonate removed by the major bioeroding agents. Patterns of bioerosion in living corals were investigated both in terms of the relationships between bioerosion by different taxa and colony volume, rugosity, extent of skeleton not covered by living tissue (=dead surface area); and as patterns of bioerosion within one reef habitat due to coral species and spatial variation at multiple scales.

The three coral species chosen for this study, *Acropora hyacinthus*, *A.gemmifera* and *A.cuneata*, are common throughout the GBR (Veron 1986), and were the most common species at the study sites (V. Nelson, unpublished data). They occur in high energy environments, i.e. reef crest (Done 1982), are fast growing, often dominant and, particularly in the case of *A.hyacinthus*, are often the first species to recolonise areas following disturbance (Veron and Wallace 1984). No information is currently available on the extent to which colonies of these species are affected by boring organisms.

Bioerosion in living corals has been the subject of a diverse range of studies (Hein and Risk 1975; MacGeachy and Stearn 1976; Highsmith 1981a; Highsmith *et al.* 1983). A common and significant finding of these studies was that, due to the inability of most bioeroders to settle onto corals, the extent of excavation in living colonies depends primarily on the presence of patches of skeleton not covered by living tissue (Pang 1973b; MacGeachy and Stearn 1976; Highsmith 1981a). Exposed portions of dead skeleton in living colonies occur at the base of corals with stalked morphology (plate, digitate and submassive corals) or may result from partial mortality. Colonies within species and among different species are likely to differ substantially in the extent of dead surface area (Highsmith 1981a). As a consequence, to correctly compare bioerosion of colonies within or among treatments, differences in the extent of dead surface area must be taken into account. This can be achieved by standardising estimates of bioerosion per unit of dead surface area. This study focuses on the

relationship between bioerosion in living colonies and the extent of dead surface area among three coral species and, in particular, the effect of standardisation by the extent of dead surface area on the total variation in bioerosion of living colonies.

Previous works on bioerosion in living corals have highlighted the significance of high levels of excavation by borers occurring at the base of the colonies (Tunnicliffe 1981 and 1982; Highsmith 1981a; Highsmith *et al.* 1983). Internal bioerosion considerably affects the stability of coral colonies standing on the reef surface, as boreholes decrease the amount of bending strength necessary to break the colony (Tunnicliffe 1979; Schuhmacher and Plewka 1981; Scott and Risk 1988). In particular, borings of *Lithophaga* bivalves further decrease the coral's mechanical resistance by acting as stress concentrating points in the skeleton (Scott and Risk 1988). This considerable impact of borers on living corals is likely to affect coral population dynamics through two mechanisms, namely increased mortality and increased fragmentation. Species with high fragment survival rates are likely to benefit from borers excavating basal portions of the skeleton (Tunnicliffe 1982; Highsmith 1980b; Highsmith 1982). More information on the inter- and intra-specific variation in the extent of internal bioerosion of coral colonies is required in order to establish the potential adaptive susceptibility of corals to borers to enhance fragmentation rates.

This chapter examines spatial patterns of internal bioerosion and the effect of coral species on the extent of excavation of living colonies. Previous work on the GBR that has investigated spatial distribution of bioerosion in living colonies on a number of scales involved sampling of *Porites* colonies on various sites on five reefs (Sammarco and Risk 1990). Intra-colonies variation in skeletal excavation was found to be higher than variation across larger spatial scales. The present study extends the investigation of spatial patterns of bioerosion in live corals to three species of abundant *Acropora* corals.

2.2 Methods

2.2.1 Materials

The species chosen for this study were *Acropora hyacinthus, A.gemmifera* and *A.cuneata*. *A.hyacinthus* consists of small, sometimes anastomosing branches, which form a tabulate structure supported on a stalk. *A.hyacinthus* is one of the most abundant coral species in the Pacific (Veron 1986) and is a dominant feature of the front and back reef slopes of the GBR, where it forms large tabulate structures up to few meters in diameter. It affects both abundance and species composition of the surrounding coral fauna due to shading effect (Sheppard 1981; Stimson 1985). In contrast to tabulate species occurring in the Atlantic, the stalk and the underside of *A.hyacinthus* are covered with living tissue, the dead portions being restricted to the very base of the stalk and to areas of partial mortality. The diameter of the stalk and the thickness of the Tabulate portion appear to increase with age. These characters were considered, in addition to the overall colony size, when choosing the samples for collection (Table 2.1). Entire colonies were collected.

A.gemmifera has a digitate morphology. It consists of a wide basal stalk supporting short, thick conical branches which occasionally ramify. It is a common species on the reef crest of middle shelf reefs of the GBR and it was one of the most abundant species at the study sites (Nelson pers. com.). The thickness and length of the branches vary among colonies and this variation is related to the energy of the environment in which they are found (Veron and Wallace 1984). The characters considered during collection of *A.gemmifera* were colony size, stalk thickness and the degree of ramification of the branches. Entire colonies were collected.

A.cuneata has a blade-like or columnar morphology. Colony morphology varies widely, but it is characterised by a massive or semi-massive, branchless growth form with large prominent corallites (Veron and Wallace 1984). *A.cuneata* is distinguished from the similar species *A.palifera* when they co-occur within habitats (Ayre *et al.* 1991). Colonies with smaller, cylindrical corallites and darker colour morph (*A.cuneata*) rather than those with spherical corallites (*A.palifera*; Veron and Wallace 1984) were

consistently selected. In *A.cuneata* it is often difficult to distinguish individual colonies, due to partial mortality. The samples collected for this species consisted of a blade or column which either represented a single colony or was separated from other columns of the colony by large expanses of dead coral.

Care was taken to sample similar aged colonies within each species. Therefore some age related features, as well as size, were measured in the field prior to collection. The means and standard errors of these parameters are reported in Table 2.1. For all species, healthy colonies with no sign of partial mortality were chosen.

	A.hyacinthus stalk diameter (cm)	*A.hyacinthus* plate diameter (cm)	*A.gemmifera* stalk diameter (cm)	*A.gemmifera* colony diameter (cm)	*A.cuneata* colony height (cm)
LH	6.6	26.26	7.58	17.82	11.96
	0.23	1.35	0.31	0.97	0.56
SI	5.66	24.66	7.16	15.78	11.74
	0.20	1.06	0.17	0.84	0.24
NR	6.26	25.12	6.98	17.38	12.4
	0.27	1.10	0.44	0.84	0.35
WM	6.18	26.24	7.34	18.22	11.22
	0.26	0.59	0.30	0.75	0.62

Table 2.1: Means and Standard Errors (n=5) of the measurements taken on the samples of living colonies collected from the four sites in February 1991.

2.2.2 Sampling sites and sampling design

The study was undertaken on the reef crest habitat at Lizard Island on the northern Great Barrier Reef. The complex of islands formed by Lizard Island, Palfrey Island and South Island is surrounded by a fringing reef the width of which varies (Figure 2.1). The three islands enclose a shallow lagoon. The present study was limited to the crest of the fringing reef. Depending on the width, the fringing reef is generally characterised by well defined zones. Both the reef crest and the slope are characterised by relatively high coral cover (Nelson 1992). The depth of the reef crest and reef flat of the fringing reef is approximately 30 to 100 cm at low tide and 150 to 300 cm at high tide and large portions of the reef crest are exposed during the spring low tides. The reef slope rapidly falls to a depth of 5 (NE sites) to 15 m (SE sites) where it meets a sandy bottom scattered with small coral aggregations and occasional large patch reefs. Behind the reef flat a rubble deposit usually occurs. Only in a few places a branching *Acropora* zone is developed. The reef is limited at the back by the steep granitic shore of the islands.

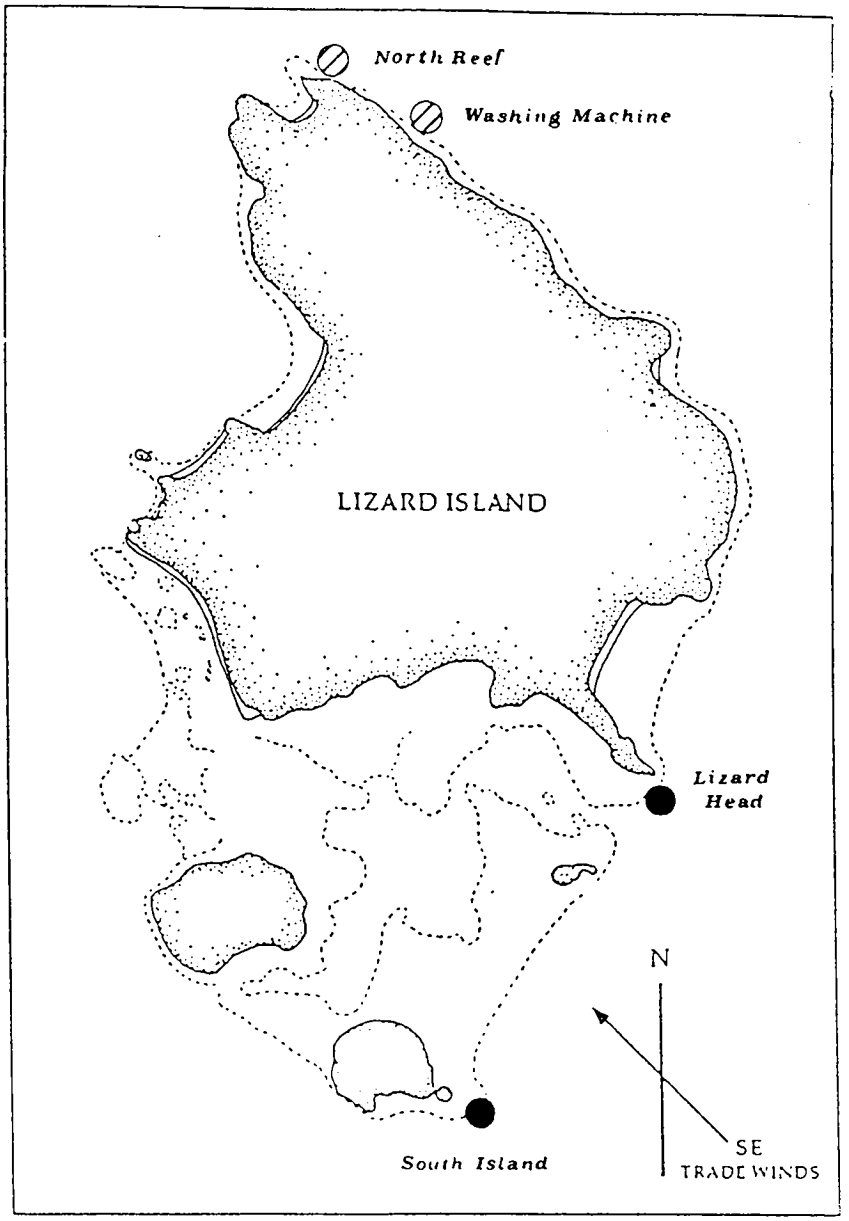


Figure 2.1: Map of Lizard Island with the four sites. South East sites are Lizard Head and South Island and North East sites are North reef and Washing Machine.

I chose two locations within the reef crest habitat which differed in the exposure to the prevailing winds (Figure 2.1). The reef crest at the south-east (SE) location is perpendicular to the direction of the trade winds, which average 15-20 knots for approximately 9 months of the year while the north-east (NE) location is tangential to the direction of the trade winds. The two locations differ slightly with regard to depth, with only the NE sites being totally exposed during spring low tides. Location is intended in this study as a spatial factor within the reef crest habitat. However, as the two locations differ clearly in the extent of exposure to the trade winds, they are treated as levels of a fixed factor. The author is aware that interpretation of the effect of 'location' in this study has to account for both spatial and exposure factors.

The sampling design followed a three-way mixed model nested ANOVA. Location and coral species were fixed factors and sites were nested within location. Within each location, two sites were chosen, Lizard Head (LH) and South Island (SI) at the SE, and North Reef (NR) and Washing Machine (WM) at the NE (Figure 2.1). The two sites within a location were at least 400 m apart, approximately 30 m long, 5 m wide and ran parallel to the reef crest. The extremes of each site were marked with a steel rod hammered in the substrate. On two occasions samples of living colonies of the three species were collected at each site. Five samples per species per site were collected in November 1990 and an additional three colonies of each species per site were collected in November 1992.

2.2.3 Sample processing

. The colonies were collected using hammer and chisel. They were put in a plastic bag before being removed from the substrate and for most colonies tapping at the side of the stalk was sufficient to detach the whole colony. Following collection the samples were stored in 6% formalin and seawater and then processed. Colonies were set in square blocks of casting plaster to facilitate cutting with a diamond blade (4.5 mm) rock saw. A laterally sliding table allowed colonies to be shifted sideways to obtain parallel slices. The minimum shift allowed by the table was one millimetre. Each colony was cut into parallel, 5 mm thick slices, perpendicular to the long axis. This was the minimum

feasible thickness, as thinner slices tended to break during the cutting process or subsequent handling.

The slices from each colony were dried, cleaned of plaster, laid on coded transparencies and xeroxed. Each xerox image was compared to the corresponding slice to ensure correct identification of the boreholes and the boreholes were assigned to one of five categories (see below). A digitiser was used to calculate a) the area of the boreholes on the cut surfaces, b) the total area of the slice; c) the portion of the perimeter of the slice covered by living tissue and d) the portions of perimeter not covered by living tissue (Figures 2.2 to 2.4). The accuracy of the digitiser, as indicated by the manufacturer, was ± 0.25 mm. The total time necessary to process a colony, including cutting and digitising, was approximately 45-60 minutes.

The estimate of colony volume and colony surface area was used to estimate an index of rugosity for each colony. Rugosity is defined as the surface area to volume ratio of the colony. It will be at a minimum for a colony shape approximating a sphere, and increase with the degree of branching of the colony. Thus, the rugosity index provides a measure of the structural complexity of a colony. The effect of structural complexity on the composition of the boring community is investigated for living corals in this chapter and for dead coral colonies in Chapter 3.

Skeletal density in each species was estimated by using the formula density = weight/volume. Fragments from 10 colonies for each species were collected on the reef crest. After bleaching, in order to remove the living tissue, and drying, each fragment was weighed and its volume estimated by water displacement. The bulk densities of the margins of *A.hyacinthus*, the branch tips of *A.gemmifera* and the columns of *A.cuneata* were analysed with a one-way ANOVA and Tukey test for multiple comparisons. *A.hyacinthus* margins have a lower density than *A.cuneata* (Tukey test, $p<0.01$, 27 df) and *A.gemmifera* ($0.05<p<0.1$).

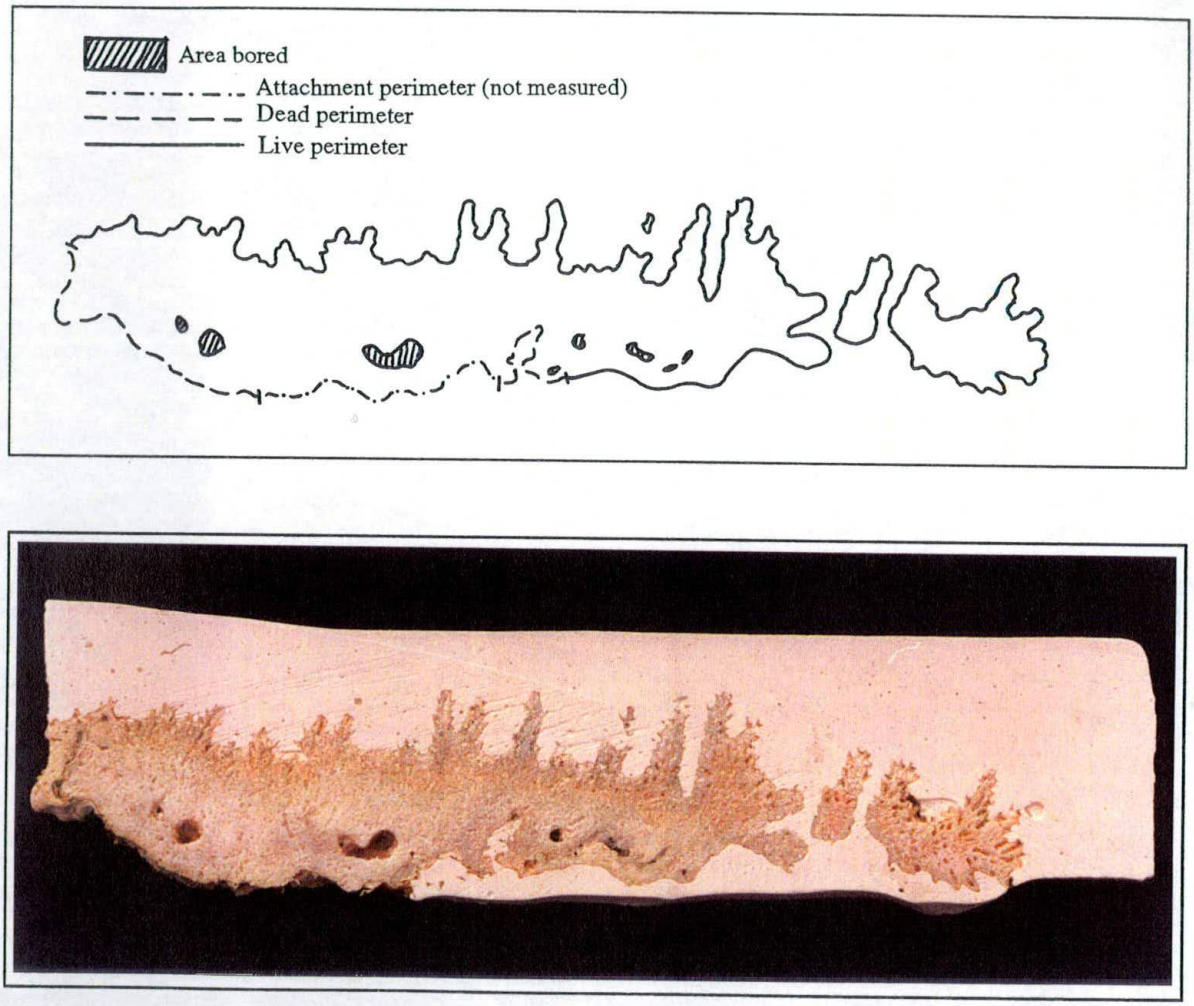
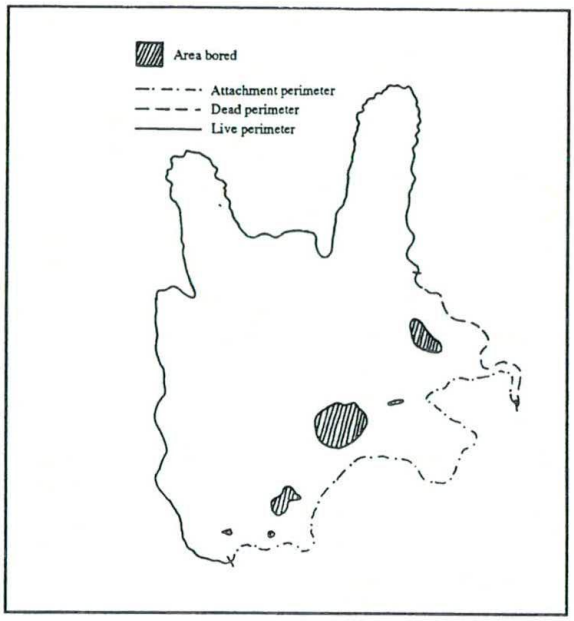


Figure 2.2: *Section of a living colony of* Acropora hyacinthus. *Top Diagram of the section showing the parameters being measured with a digitiser (living perimeter; dead perimeter; area of the boreholes; total area of the section). Bottom: photograph of the colony section represented in the diagram.*



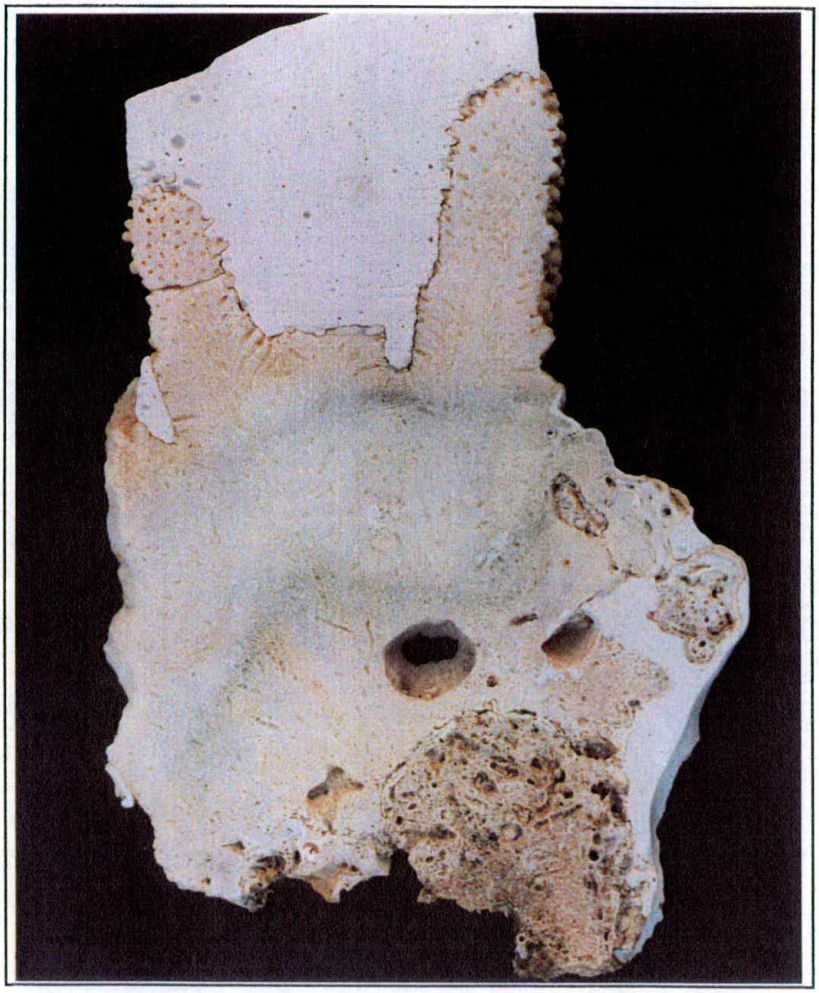


Figure 2.3: *Section of living colony of* Acropora gemmifera. *Top: diagram of the section indicating the parameters measured using a digitiser (live perimeter; dead perimeter, surface area of boreholes; surface area of the section). Bottom: photograph of the section represented in the diagram above.*

Figure 2.4:*Section of a living colony of* Acropora cuneata. *Left: photograph of the section. Right: diagram showing the parameters measured using a digitiser (living perimeter; area of boreholes; area of the section). There was no "dead perimeter" in this section. "Attachment" is the side of the section corresponding to where the colony was attached to the reef surface.*

2.2.4 Categories of borers and identification of the boreholes

Only macroborers were considered in this study. The definition of macroborers varies among authors. However, it usually refers to the taxonomic identity of the borer rather than to the actual size of the boring. Endolithic algae, fungi and bacteria are considered microborers, while boring invertebrates are considered macroborers. Davies and Hutchings (1983), when measuring bioerosion as the volume of animals extracted from the substrate, defined macroborers as animals of size > 1 cm. Kiene (1985) measured bioerosion in *Porites* substrates as the volume of the borehole produced by a boring organism, and defined macroborings as being > 0.5 mm in diameter. Due to the larger size of corallites in the species investigated in this study, and hence the possibility of mistaking transversally cut corallites for boreholes, the lower size limit of the boreholes considered was 1 mm in diameter.

The boreholes on the cut surface of the slices were identified as belonging to one of five major groups of boring organisms: sponges, WORMS*, bivalves, barnacles and OTHERS. This broad grouping includes a large number of species. For the purpose of the present study, further taxonomic identification of the borers encountered was made only in a few instances for dominant borers. The boreholes were assigned to the five categories on the basis of their shape and size (Warme 1975 and Bromley 1978) with identification often aided by the presence of the animals or fragments of them in the boreholes.

The group 'sponges' includes several species of boring sponges belonging to the family Clionidae. Other families known to have boring representatives were not encountered in the samples, although boring species of both Adociidae and Spirastrellidae occur in the area (unpublished data). Borings produced by sponges can vary widely with species, ranging from small (~1 mm or less) intercommunicating chambers to large (up to few cm) solitary chambers with inhalant and exhalant papillae opening at the surface of the substrate. The chambers are usually spherical or subspherical. In the case of solitary chambers, this feature allows them to be distinguished from boreholes produced by

* WORMS and OTHERS are in uppercase throughout the text, to denote that they arbitrarily group boring animals which may belong to different phyla (e.g. Anellidsand Sipunculans).

bivalves or worms (polychaetes or sipunculans). Often several closely grouped chambers form a string running parallel to and just beneath the surface of the substrate.

The group WORMS includes species of both polychaetes and sipunculans. Relatively little information is available on the boring representatives of these two taxa and the relative similarity of their borings make the identification of their excavations difficult and time consuming. In general, borings by sipunculans are larger in cross section however this varies considerably. Therefore it was decided to group the two taxa in one category. Boring produced by polychaetes and sipunculans have a circular, sometimes oval section and, generally, there is no lining deposited by the borer. In longitudinal section the borings can be straight or winding and sometimes U-shaped, as is the case for polychaetes of the family Spionidae (Bromley 1978). Longitudinal section of borings by sipunculans are usually narrower towards the opening on the surface than in the middle section, with the extremity opposite the opening on the surface usually being tapered (Warme 1975).

In this study the group 'bivalves' includes species of the genera *Lithophaga* (fam. Mytilidae) and *Gastrochaena* (fam. Gastrochaenidae). The borings of *Lithophaga* and *Gastrochaena* spp. are easily identified. They are circular to elliptical in cross section, elliptical in longitudinal section, usually very elongated, with the borings being longer than the shell of the animal. In some species of *Lithophaga,* the borehole bifurcates partially in proximity of the surface of the substrate , so that a typical eight-shaped opening is produced from which the syphonal apertures of the mantle protrude. This occurs in *Gastrochaena* spp also, but the bifurcation produces two separate openings. Some species of *Lithophaga* (i.e. *Lithophaga obesa*, Wilson 1979) and *Gastrochaena* spp. deposit an aragonitic lining on the walls of the borings which are thicker at the two extremities. However, no borings with lining were encountered in this study. *Lithophaga* spp. from the Great Barrier Reef have been well documented since the early scientific expeditions (Otter 1937). Wilson (1979) and Kleeman (1984) provide recent descriptions and reviews of species from living and dead coral substrates.

The group barnacles in this study includes species of the genus *Lithotrya* (Thoracica). The boreholes excavated by barnacles are usually easily recognised by the presence of longitudinal grooves in the walls of the borings (Seilacher 1969). Acrothoracican barnacles are very small (Warme 1975) and no identification was attempted in this study.

The group OTHERS includes all the remaining taxa of boring organisms. These were recorded only in few coral colonies and for this reason were grouped together. Representatives of this group include chitons and alpheid shrimps, usually identified by the presence of the animal. This group also allow to account for those boreholes of unknown origin.

2.2.6 Data analysis

Ungrouped data of all variables (colony volume, colony dead surface area, total colony surface area, total bioerosion, bioerosion by each taxonomic group) were tested for normality using D'Agostino's test (Table A1[*]). When the variables were moderately or strongly non-normal, log transformation minimised non-normality in all cases. Multivariate normality was tested graphically (McArdle, pers. comm.). Homoscedasticity was tested graphically for each grouped variable, by plotting the values of the residuals versus the expected values assuming a general linear model. Multivariate homogeneity of covariance matrices was tested with Levene's test.

The relationship between total bioerosion and colony volume, surface area and total area was investigated with partial correlation analysis. Canonical correlation and redundancy analyses were performed between bioerosion by individual taxa (Dependent Variables, DVs) and the set of colony variables (volume, surface area and rugosity index; Independent Variables IVs). Canonical correlation analysis was performed (procedure CANCORR, SAS) to examine the relationships between the two sets of variables and to assess the degree of correlation within DVs and IVs.

[*] Tables marked with A and a number are in Appendix A, at the end of the Thesis.

Uni- and multivariate data grouped by treatments (species, location, site) were analysed as follows:

- To ensure that samples from the two collections could be pooled for a single analysis, a 4-way, mixed model, nested ANOVA was performed on colony volume and total bioerosion, including the factor 'collection' as fixed and orthogonal to species and location.
- A 3-way, mixed model, nested ANOVA was performed on the extent of dead surface area to test for species, location and site effects.
- A 3-way, mixed model, nested ANOVA was performed on total bioerosion per unit of surface area, and total bioerosion minus bioerosion due to bivalves, to test for species, location and site effect. Significance level was α=0.05.
- Assumptions for Multivariate ANOVA on bioerosion by the five taxa were not met, as data were not multivariate normal and variance-covariance matrices were not homogeneous (Levene's test: Wilk's Lambda $F_{10,68}$=3.39, p=0.0012; Pillai Trace $F_{10,70}$=3.17 p=0.002). Pooled within-group correlations among the bioerosion variables were low (Table A2). Univariate ANOVAs were performed on data of bioerosion by the five groups. To control for inflation of Type I Error a Bonferroni corrected significance level of α=0.01 was used, which yielded an overall significance level of α=0.049.
- A Simple Correspondence Analysis was used to represent in a reduced space the relationships of bioerosion by the five taxa of borers and the treatments of the sampling units.

2.3 Results

2.3.1 Comparison between collections

Volume of the colonies of each species and at each site of the two locations, did not vary with time of collection (F_s=13.89, $F_{0.05;1,2}$=18.51; p=0.06; Φ=2.54, ν_1=1, ν_2=2; Table A3). No effect of time of collection on total bioerosion was detected (F_s=7.80, $F_{0.05;1,2}$=18.51; p=0.10; Φ=1.84, ν_1=1, ν_2=2; Table A4). Therefore data from the two sampling exercises were pooled into one data set.

2.3.2 Correlation between bioerosion and the extent of dead surface area, colony volume and colony surface area

Total bioerosion was significantly correlated to of dead surface area, but not to the colony volume or total surface area (Table 2.2). In *A.hyacinthus* and *A.gemmifera* total bioerosion was significantly correlated to the dead surface area, while the correlation was weak and non significant for *A.cuneata* (Table 2.3). Correlation coefficients for *A.hyacinthus* and *A.gemmifera* were not different ($Z=0.0712$, $Z_{0.05(2)}=1.960$; $\beta=0.97$).

	Dead Surface Area	Volume	Total Surface Area
Total bioerosion	**0.62**	0.07	-0.09
	(0.0001)	(0.51)	(0.37)

Table 2.2: Partial correlation coefficients between total bioerosion and colony dead surface area, volume and total surface area. Values in parenthesis are probability values for the coefficients to be equal to zero. Coefficient in bold and underlined are significant at $\alpha=0.05$.

	A.hyacinthus	*A.gemmifera*	*A.cuneata*
Partial correlation	**0.60**	**0.61**	0.38
	(0.0004)	**(0.0007)**	(0.054)
	n=33	**n=29**	n=28

Table 2.3: Partial correlation coefficients between total bioerosion and colony dead surface area, for the three coral species. Values in parenthesis are probability values for the coefficients to be equal to zero. Coefficient in bold and underlined are significant at $\alpha=0.05$. Sample sizes are given for each species.

Results from the canonical correlation analysis (Table 2.4) showed that the first two pairs of canonical variates were significantly different from zero with $p=0.0001$ and $p=0.002$ respectively. Correlations between the variables and the first pair of canonical variates indicated that the larger the extent of dead surface area (0.98) the greater the bioerosion by sponges (0.80), OTHERS (0.55) and, to a smaller extent, WORMS (0.39) and bivalves (0.49). The correlations among the variables and the second pair of canonical variates showed that colonies with large living surface area (0.86) were associated with low bioerosion by bivalves (-0.78). The first pair of canonical variates can be interpreted as representing the response of the main groups of borers to the availability of substrate suitable for settlement and/or further excavation of the substrate. The second pair of variates is likely to describe an association between bivalves and *A.cuneata*, which has low living surface area values compared to the other two species.

	1st canonical variate		2nd canonical variate		
	Correlation	Coefficient	Correlation	Coefficient	
Colony variables:					
Dead surface area	.98	.86	.10	.54	
Volume	.51	.31	.16	-.71	
Live surface area	-.32	-.24	.86	1.57	
Rug. index	-.57	.14	.49	-.59	
% of variance	.41		.25		tot=.66
Redundancy	.24		.07		tot=.31
Bioerosion variables:					
sponges	.80	.58	.09	.09	
WORMS	.39	.39	.28	.00	
bivalves	.49	.41	-.78	-.86	
barnacles	.30	.08	.26	.23	
OTHERS	.55	.27	.51	.50	
% of variance	.33		.20		tot=.53
Redundancy	.17		.05		tot=.22
Canonical correlation	.77		.53		

Table 2.4: Canonical correlation statistics between 4 colony variables and 5 bioerosion variables. Correlations between variables and canonical variates; standardized canonical coefficients; percent of variance; redundancies between colony and bioerosion variables; canonical correlations.

2.3.3 Extent of exposed skeleton and colony rugosity in the three species

Extent of dead surface area (ratio of dead to total colony surface area) differed significantly among the three coral species (F_s=72.92, $F_{0.05;2,4}$=6.94; p=0.0007; Table A5). The ratio was significantly the smallest in *A.hyacinthus* and the largest in *A.cuneata* (Tukey test, α=0.05 n=90). There was a large but not significant effect of location on the extent of dead surface area (F_s=14.15, $F_{0.05;1,2}$=18.51; p=0.06), which was due to *A.hyacinthus* showing a larger proportion of dead skeleton at the SE sites (Figure 2.5).

The colony rugosity index (colony surface area to volume ratio) differed among the three species (F_s=41.14; $F_{0.05;2,4}$=6.94, p=0.002; Table A6), in the following order *A.hyacinthus* > *A.gemmifera* > *A.cuneata*. *A.hyacinthus* had a significantly higher rugosity index than the other two species (Tukey test, α=0.05, df=78; Figure 2.6).

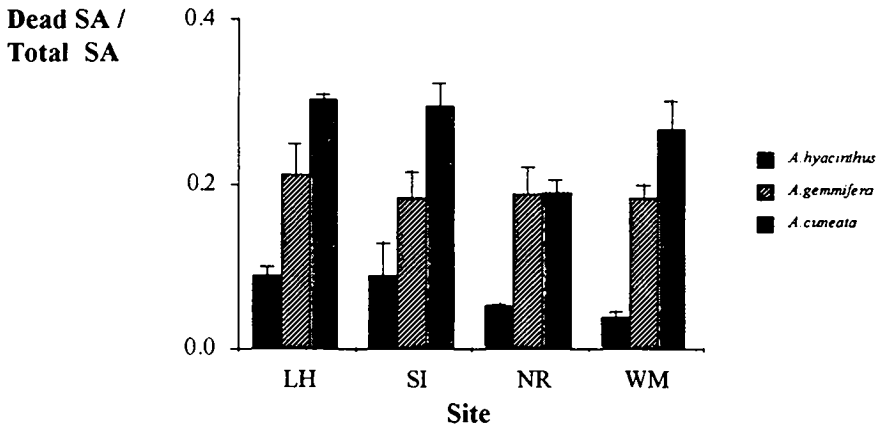


Figure 2.5: Ratio of dead surface area to total colony surface area (untransformed) for A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH),South Island (SI), North Reef (NR) and Washing Machine (WM). Error bars are Standard Errors.*

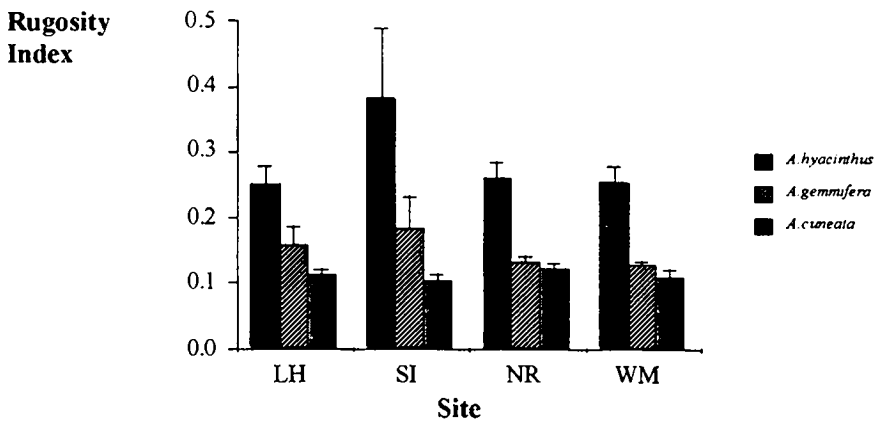


Figure 2.6: Rugosity index (untransformed) (ratio of total colony surfacearea to colony volume) for A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Error bars are Standard Errors.*

2.3.4 Excavation of living colonies by macroborers

All the boreholes observed and measured on the coral slices were located in the portion of the skeleton that lies underneath or in close proximity of the basal dead exposed area (Figures 2.2 to 2.4). The only exception consisted of borings excavated by one species of bivalves (*Lithophaga cf. lessepsiana*) which seemed capable to bore through the living tissue of the coral *A.cuneata*. Consequently, in *A.hyacinthus* and *A.gemmifera* the portion of the skeleton covered by living tissue had virtually no bioerosion, while *A.cuneata* was bored throughout the colony, with bivalves occurring mainly underneath the living tissue. Sponges, bivalves and worms were the major borers in living colonies of the three coral species. Colonies of *A.cuneata* were heavily bored by bivalves of the species *Lithophaga cf. lessepsiana* (Vaillant 1865) whose siphonal apertures were found among the living polyps of the coral. Sponges dominated bioerosion in the other two species, but occurred only in proximity to portions of dead coral skeleton. The species more commonly found were *Cliothosa hancocki*, *Cliona viridis* and *Cliona cf. jullieni*.

			Total	sponges	WORMS	bivalves	barnacles	OTHERS
A.cuneata								
SE Sites	LH	7	55.48	17.32	0.83	36.01	0.07	1.25
			17.12	*4.38*	*0.25*	*20.03*	*0.07*	*0.77*
	SI	6	58.31	20.03	1.05	36.01	0.43	0.79
			6.41	*6.95*	*0.36*	*7.47*	*0.43*	*0.44*
NE Sites	NR	8	52.1	20.39	0.61	29.64	0	1.46
			9.12	*7.78*	*0.19*	*6.61*	-	*0.78*
	WMII	7	45.14	22.26	0.71	21.67	0	0.49
			11.41	*10.56*	*0.25*	*5.57*	-	*0.34*
A.gemmifera								
SE Sites	LH	8	11.6	8.18	1.96	0.84	0	0.63
			2.79	*1.67*	*0.92*	*0.63*	-	*0.44*
	SI	8	15.36	12.39	1.41	0.97	0.14	0.43
			6.22	*5.94*	*0.36*	*0.41*	*0.09*	*0.16*
NE Sites	NR	7	10.82	7.65	1.46	0.05	0.19	1.48
			2.57	*2.43*	*0.22*	*0.05*	*0.09*	*0.71*
	WMII	6	11.86	9.73	0.98	0.24	0	0.91
			2.15	*2.21*	*0.1*	*0.15*	-	*0.36*
A.hyacinthus								
SE Sites	LH	8	4.07	2.46	0.57	0.29	0.06	0.7
			0.92	*0.91*	*0.13*	*0.16*	*0.04*	*0.22*
	SI	9	12.3	10.82	0.56	0.25	0	0.66
			6.96	*6.38*	*0.2*	*0.21*	-	*0.3*
NE Sites	NR	8	5.29	3.13	0.53	1.41	0.06	0.15
			1.5	*0.78*	*0.17*	*0.93*	-	*0.08*
	WMII	8	5.08	4.23	0.32	0.43	0	0.1
			2.39	*2.38*	*0.09*	*0.21*	-	*0.09*

Table 2.5: *Means, standard errors and sample sizes of volume (mm^3) per unit of surface area (cm^2) removed from each colony by the five groups of borers at the four sites.*

The total volume removed by borers in the three coral species ranged between 4.07 to 58.31 mm^3 per cm^2 of exposed dead surface area (Table 2.5). The group sponges was the most destructive, occurring in all colonies and removing from 3.13 up to 22.26 mm^3 of skeleton per cm^2 of dead exposed area. They were responsible for the largest proportion of total bioerosion (31.22 to 83.3%; Table 2.6) for all species but *A.cuneata,* where bivalves were more important. The volume of skeleton excavated by bivalves accounted to 0.05 mm^3 up to 36.01 mm^3 per cm^2 of exposed area. The largest volumes were excavated from colonies of *A.cuneata,* where bivalves accounted for up to 64.9% of the total bioerosion. Borers belonging to the group WORMS did remove little skeleton from all species (0.53 to 1.96 mm^3 per cm^2 of dead exposed area). Therefore they were responsible for only a small proportion of the total bioerosion, although at Lizard Head they accounted for the 14 and 16.9% in colonies of *A.hyacinthus* and in *A.gemmifera* respectively (Table 2.6). Barnacles were very rarely observed, being absent in all the samples from Wachine Machine II. Their excavation amounted only to a maximum of 0.43 mm^3 cm^{-2}, and they accounted for a maximum of 1.8% of the total bioerosion. Excavations possibly by alpheid shrimps were observed in colonies of *A.gemmifera* and *A.hyacinthus*. Individual excavations were large, and this explains the relatively high values of volume removed by the group OTHERS (0.1 to 1.48 mm^3 cm^{-2}), and the high variability within this group. Other excavations were included in this group because difficult to identify (possibly sponges).

		sponges	WORMS	bivalves	barnacles	OTHERS
A.cuneata						
SE Sites	LH	31.22	1.5	64.9	0.1	2.3
	SI	34.3	1.8	61.8	0.7	1.3
NE Sites	NR	39.1	1.2	56.9	-	2.8
	WMII	49.3	1.6	48	-	1.1
A.gemmifera						
SE Sites	LH	70.5	16.9	7.2	-	5.4
	SI	80.7	9.2	6.3	0.9	2.8
NE Sites	NR	70.7	13.5	0.5	1.8	13.7
	WMII	82	8.3	2	-	7.7
A.hyacinthus						
SE Sites	LH	60.4	14	7.1	1.5	17.2
	SI	88	4.5	2	-	5.4
NE Sites	NR	59.2	10	26.6	1.1	2.8
	WMII	83.3	6.3	8.5	-	2

Table 2.6: Percent of volume excavated by each group of borers, for the three species and the four sites.

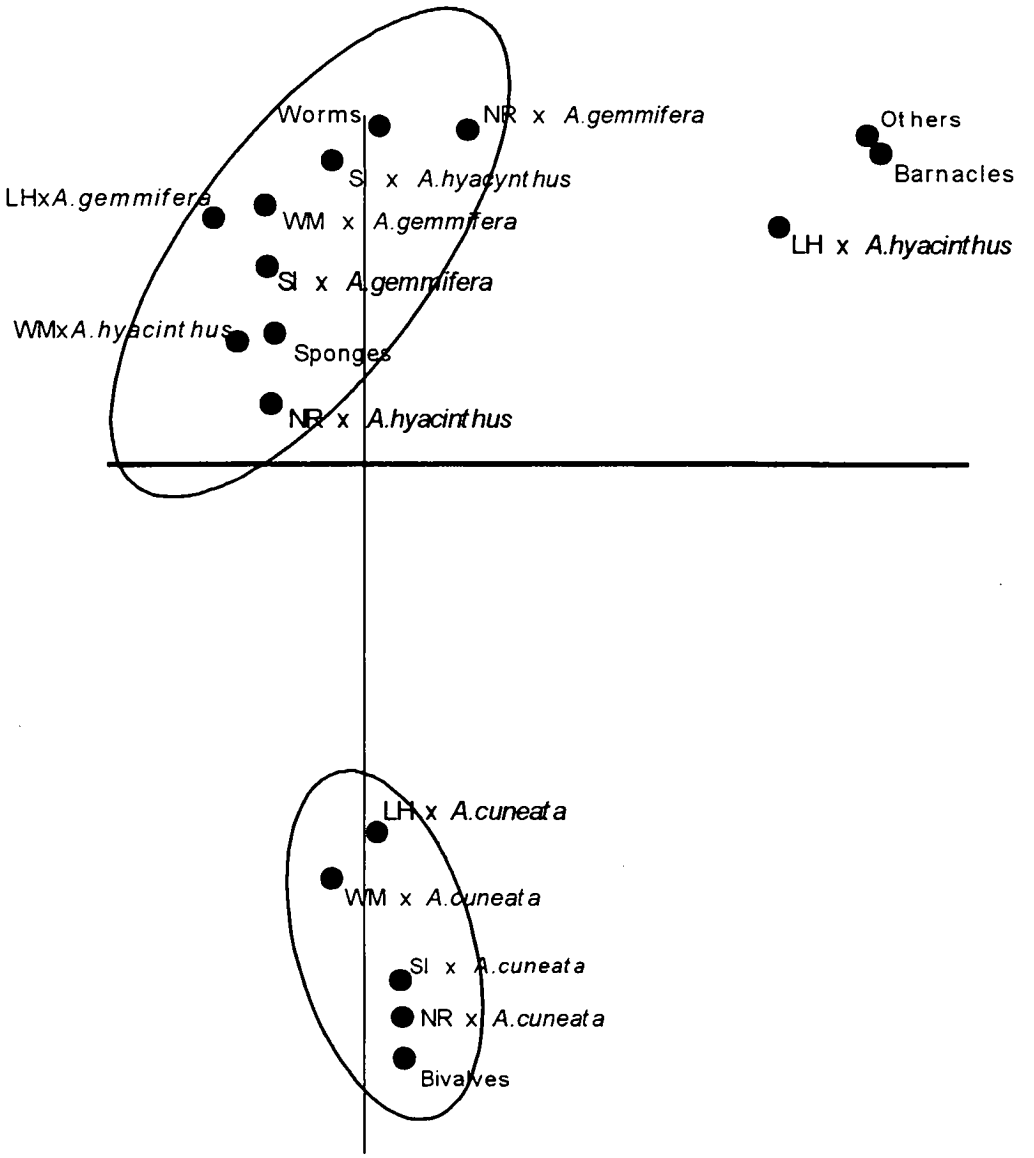


Figure 2.7: Projection of row and column profiles in the reduced space identified by Simple Correspondence Analysis. Row profiles are combinations of site and coral species, and column profiles are taxa of borers.

Simple correspondence analysis of the data relative to proportion of total bioerosion removed by each taxon, identified four axes. The majority of total inertia was represented by the first two axes (96.75%), with the first axis representing 82.81% and the second 13.94%. The association among the taxa and the combinations of sites and coral species was represented on the reduced space identified by the coordinates of the first two axes (Figure 2.7). The first axis emphasises the distance of the row profile points associated with *A.cuneata* at all sites from the other two species which are closer to the origin. The column profile point associated with bioerosion by bivalves projects

in the same direction as the *A.cuneata* points. The second axis projects the column profile points of bioerosion by barnacles and OTHERS very distant from the origin, i.e. from the expected profile. This may be due to the high numbers of zeros for these two taxa, and cannot be meaningfully interpreted. To summarise, the major pattern in the relative importance of the boring agents in the three species and across the sites is the one of bivalves being associated with *A.cuneata* at all sites.

2.3.5 Patterns of total bioerosion

Total bioerosion, unstandardised for dead surface area, differed among species (F_s=106.95, $F_{0.05;2,4}$=6.94; p=0.0003), with *A.cuneata* being more extensively excavated than both *A.hyacinthus* and *A.gemmifera* (Tukey's test α<0.05, n=90). *A.gemmifera* did not vary significantly from *A.hyacinthus*. The total variance was equally partitioned between within-site and inter-specific variability. The other factors accounted for a minimum part of the overall variation of the data. Power to detect location effect was low (ϕ<1, ν_1=1, ν_2=2).

	Total	sponges	WORMS	bivalves	barnacles	OTHERS
Unstandardised:						
C.V.	40.8	31.9	40.3	56.3	330.0	100.3
R^2	*0.50*	*0.10*	*0.24*	*0.68*	*0.11*	*0.09*
Standardised:						
C.V.	22.4	26.2	6.7	28.9	1.9	11.7
R^2	*0.50*	*0.16*	*0.21*	*0.60*	*0.09*	*0.16*

Table 2.7: *Coefficients of variation of the Grand Mean for total bioerosion and bioerosion by individual taxa, before and after standardisation of the variables against unit of colony dead surface area. Coefficients of determination for each variable of the model are showed also.*

When total bioerosion was standardised per unit of dead surface area, the portion of variance due to inter-specific variation decreased, but the difference among the three species remained significant (F_s=15.78, $F_{0.05;2,4}$=6.94; p=0.012; Table A7, Figure 2.8). A considerable decrease in the overall variability of total bioerosion between colonies (as measured by the coefficient of variation of the Grand Mean) occurs when the differences in extent of dead surface area are accounted for (Table 2.7). Total bioerosion expressed as percent colony volume was approximately 3 to 6 times larger in *A.cuneata* than *A.gemmifera* and *A.hyacinthus* respectively (Figures 2.9 and 2.10).

2.3.6 Patterns of bioerosion by individual taxa

Bioerosion by sponges, WORMS and bivalves differed among the three coral species; however, the patterns differed with taxa. The extent of bioerosion by sponges in the three species was in descending order; *A.cuneata* > *A.gemmifera* > *A.hyacinthus*, with the difference between *A.cuneata* and *A.hyacinthus* being significant (Tukey's test α=0.05, df=78). When bioerosion by sponges was standardised for the extent of dead surface area, the difference among the species was not significant (Table A8; Figure 2.11). This indicates that differences in the extent of dead surface area among species are responsible for the species effect on sponge bioerosion. Bioerosion by WORMS was significantly higher in *A.gemmifera* than *A.cuneata* (Table A9; Figure 2.12). A significant species effect remained following standardisation for extent of dead surface area, and the difference between *A.hyacinthus* and *A.cuneata* became significant. The coefficient of variation of the Grand Mean was reduced considerably following the standardisation of the variable for unit of dead surface area (Table 2.7). Bioerosion by bivalves was significantly higher in *A.cuneata* than either *A.gemmifera* or *A.hyacinthus* (F_s=71.49; p=0.0007; Table A10; Figure 2.13).

Source of variation	Total	Sponges	Worms	Bivalves	Barnacles	Others
Location	0.53	0.54	0.15	0.30	0.09	0.94
Site	3.25	4.18	0.52	1.23	2.73	0.94
Species	38.82	3.95	16.49	55.40	0.28	3.02
SpeciesXLoc	0.52	0.74	0.52	0.47	1.64	8.30
SpeciesXSite	4.93	6.56	2.06	1.54	3.64	3.21
Error	49.69	83.50	78.35	39.77	93.64	83.77

Table 2.8: Variance components for total bioerosion and bioerosion by the individual taxa.

Bioerosion by bivalves was small in species other than *A.cuneata.* For all taxa except bivalves, the majority of the total variance was due to within site variability. For bivalves the major source of variation was the factor coral 'species'. Bioerosion by both barnacles and OTHERS was negligible and no significant effect was detected with the implemented design (Tables A11 and A12; Figures 2.14 and 2.15). Neither of the two spatial factors considered in the design contributed significantly to the overall variation for the boring taxa considered (Table 2.8). However, the power for the factor 'location' was low for all taxa (Table 2.9).

	Total	Sponges	Worms	Bivalves	Barnacles	Others
Location	0.58	0.61	0.56	0.50	0.69	0.60
Species	3.14	0.37	2.92	6.86	0.77	0.79

Table 2.9: Powers (values of ϕ, $v_1=1$, $v_2=2$ for location and $v_1=2$, $v_2=8$ for species) of the tests to detect location and species effect for total bioerosion and bioerosion by individual taxa.

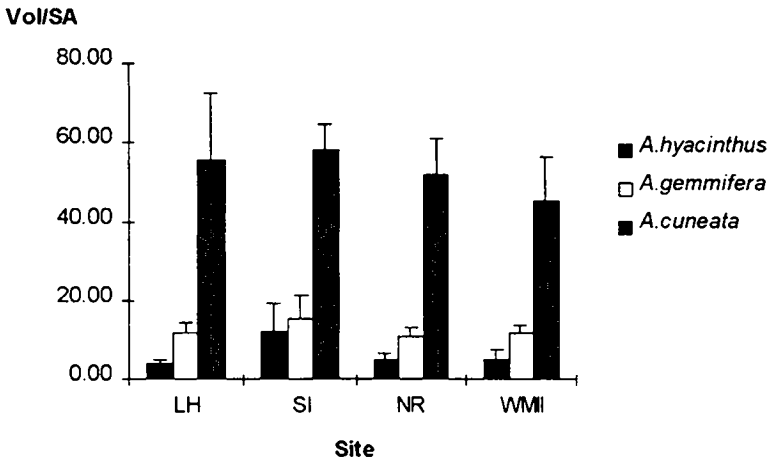


Figure 2.8: Mean total volume of skeleton removed by all borers per unit of dead surface area in A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Error bars are standard errors. Data are untransformed.*

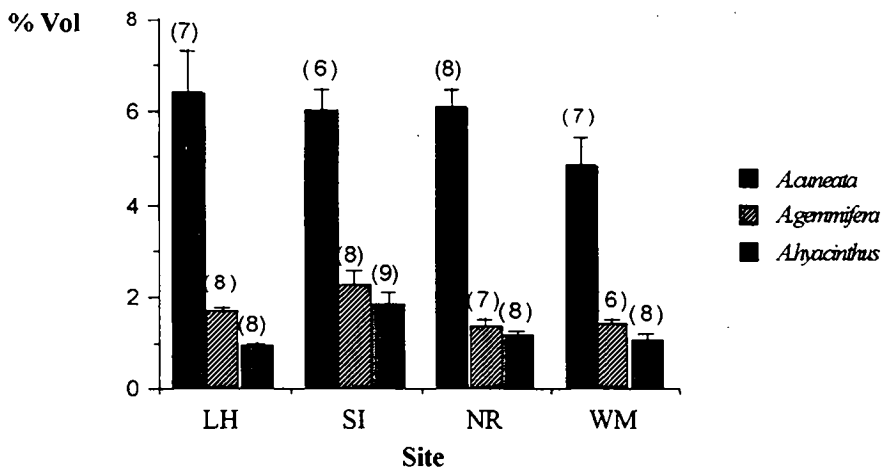


Figure 2.9: Extent of internal bioerosion, expressed as percent volume removed per colony, for A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Error bars are standard errors. Data are untransformed.*

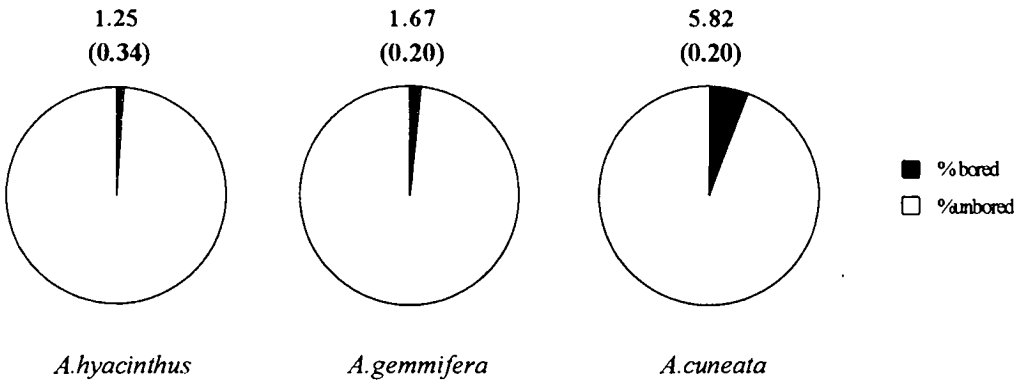


Figure 2.10: Mean percent of colony volume removed from A.hyacinthus *(n=33),* A.gemmifera *(n=29) and* A.cuneata *(n=28), pooled over the four sites. Standard errors are given in parenthesis.*

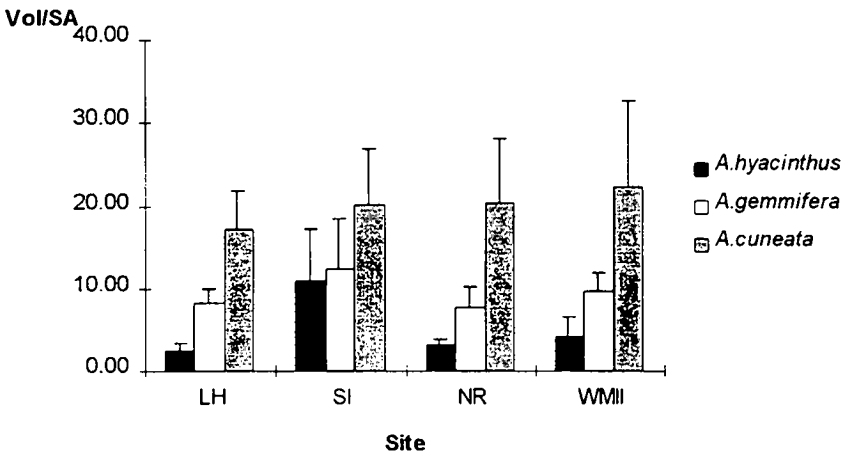


Figure 2.11: Mean total volume of skeleton removed by sponges per unit of dead surface area in A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Error bars are standard errors. Data are untransformed.*

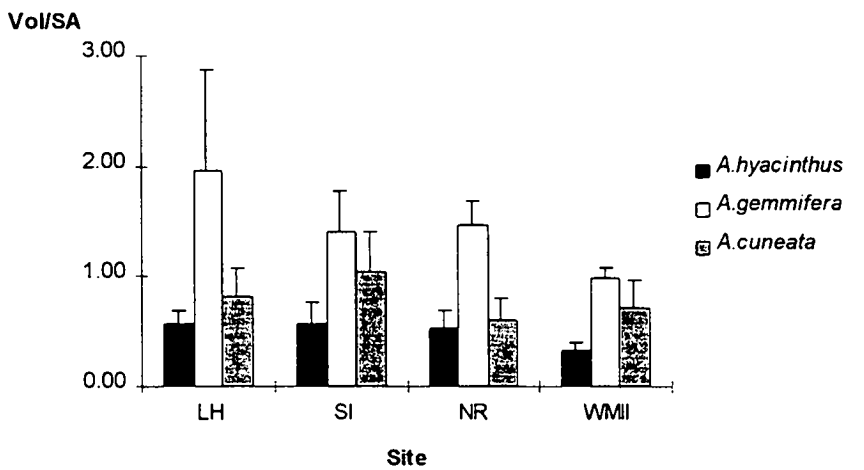


Figure 2.12: Mean total volume of skeleton removed by worms per unit of dead surface area in A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Error bars are standard errors. Data are untransformed.*

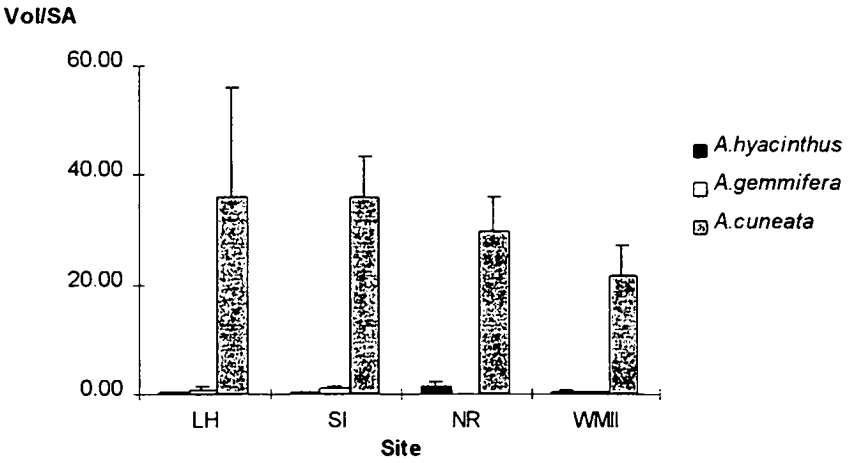


Figure 2.13: Mean total volume of skeleton removed by bivalves per unit of dead surface area in A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Error bars are standard errors. Data are untransformed.*

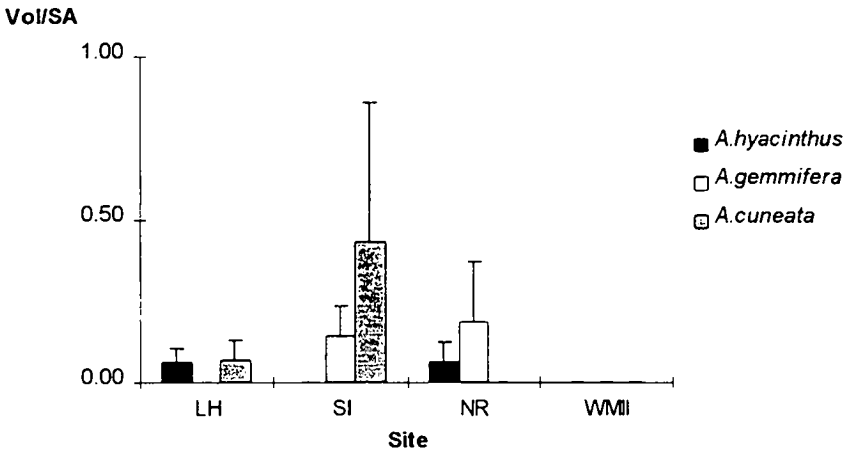


Figure 2.14: Mean total volume of skeleton removed by barnacles per unit of dead surface area in A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Error bars are standard errors. Data are untransformed.*

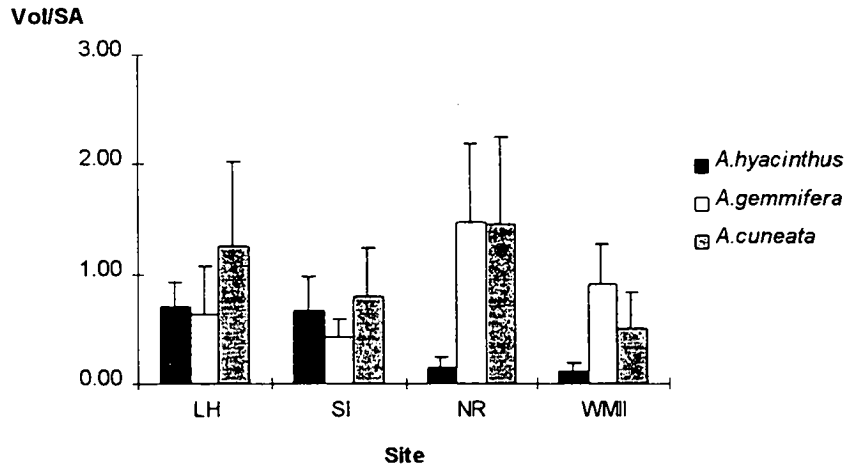


Figure 2.15: Mean total volume of skeleton removed by others per unit of dead surface area in A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Error bars are standard errors. Data are untransformed.*

2.3.7 Calcium carbonate removed by internal bioeroders from living coral colonies

Skeletal density was calculated for the three coral species in order to convert estimates of volume excavated by borers into estimates of weight of $CaCO_3$ removed. *A.cuneata* had the highest density and *A.hyacinthus* the lowest (Table 2.10).

	A.hyacinthus	*A.gemmifera*	*A.cuneata*
Skeletal density	1.50 ± 0.10	1.88 ± 0.08	2.03 ± 0.12
Sample size	*10*	*10*	*10*

***Table 2.10**: Skeletal bulk densities (g x cm^{-3}) of the three coral species* Acropora hyacinthus, A.gemmifera *and* A.cuneata *(errors are Standard Errors).*

Internal bioeroders removed little calcium carbonate from the colonies of the three species. Table 2.11 reports the estimates of $CaCO_3$ weight removed per unit of dead exposed surface area. These estimates refer to a square metre of exposed surface area. The weight of $CaCO_3$ excavated from colonies of the three species ranged from 0 up to 1.152 kg per m^2 of exposed surface area.

	Total	Sponges	Worms	Bivalves	Barnacles	Others
SE sites						
A.hyacinthus	126.45	103.31	8.48	4.02	0.43	10.20
	54.57	*50.45*	*1.74*	*1.91*	*0.29*	*2.69*
A.gemmifera	253.424	193.34	31.75	17.01	1.34	9.98
	60.61	*55.13*	*8.74*	*6.64*	*0.89*	*4.12*
A.cuneata	1152.74	377.02	18.90	730.98	4.74	21.10
	181.92	*74.51*	*4.00*	*212.54*	*3.87*	*8.78*
NE sites						
A.hyacinthus	77.77	55.22	6.37	13.78	0.45	1.94
	20.66	*17.70*	*1.43*	*6.97*	*0.44*	*0.81*
A.gemmifera	212.41	161.84	23.23	2.57	1.87	22.89
	30.41	*29.23*	*2.56*	*1.39*	*1.80*	*7.41*
A.cuneata	1010.05	452.59	12.67	522.89	0	21.90
	155.52	*128.60*	*3.11*	*91.47*	*0*	*9.33*

***Table 2.11**: Grams of $CaCO_3$ per unit of colony dead surface area (m^2) removed by each group of borers from the colonies of each species at the two locations.*

2.4 Discussion

This study demonstrated that the extent of internal bioerosion in living colonies was generally small, but differed strongly among the three coral species. The major source of the inter-specific variation was the presence of *Lithophaga* cf. *lessepsiana* boring into the living tissue of *A.cuneata*, while no borers were present in the portions of skeleton covered by living tissue in the other two coral species. The majority of the remaining variation among species was explained by inter-specific differences in the extent of dead surface area. This was species-specific and, in the case of *A.hyacinthus*, differed in the two locations, with colonies on the SE sites having a larger ratio of dead to living surface area. However, the effect of the extent of dead surface area on excavation varied among bioeroding taxa also. Within-site variability was high for all coral species and all boring taxa. There were no apparent patterns of bioerosion among or within the spatial scales considered. Sponges (*Cliothosa hancocki* in particular) were by far the most destructive borers in living colonies of the three species, together with the bivalve *L. cf. lessepsiana* which bored exclusively in *A.cuneata*. Worms (mostly polychaetes) although numerically abundant, accounted for little of the total bioerosion in living corals.

Living colonies of the three species of *Acropora* considered in this study were subject to only a small extent of excavation by borers. This supports previous findings that, on the reef surface, bioerosion of living coral colonies contributes little to overall reef erosion (Hutchings 1986). Few species of borers are known to settle on living coral tissue. Sponges of the genus *Siphonodictyon* (Family Adociidae), are capable of infesting living coral colonies (Rutzler 1971) via biochemical competition (Sullivan *et al* 1983). Also few species of the genus *Cliona* can succesfully compete with living corals. These species, which include *C.caribbea* and *C.viridis* (Acker and Risk 1985; Bergman 1983) are however an exception to the norm, in that they display an encrusting or even massive, external growth (β and γ growth stages). While this type of boring clionidae is very abundant in some areas of the tropical Atlantic, representing a major agent of bioerosion, *C.viridis* from the GBR is rarely found in the encrusting and massive growth stages (Bergman 1983; the author, pers. obs.).

Several species of bivalves of the genus *Lithophaga* are known to occur in living portions of coral colonies. The boring bivalve *Lithophaga bisulcata* has been found to settle more successfully on living than dead corals (higher survival and reproductive output, Scott 1988a) and to display a degree of species specificity during settlement. In the Caribbean, *Lithophaga dixonae* bores exclusively into living colonies of three *Madracis* spp. (Scott 1986). Mokady *et al.* (1992) also reported that *Lithophaga simplex* occurs only in living corals, although the larvae appear to settle on small areas of bare skeleton. In the present study of three acroporid corals, the bivalve *Lithophaga cf. lessepsiana* was only found boring among the living polyps of *A.cuneata*. The correlation between the extent of *L.cf. lessepsiana* boring and the colony volume was probably due to the age of the colony. *L. cf. lessepsiana* had previously been reported as boring into living corals of *Porites* sp., *Favia* sp. (Wilson 1979), *Symphillia* sp. (Iredale 1939) , *Acropora palifera* and *Pocillopora eydouxi* (Wilson 1979) and *Stylophora pistillata* (Mokady *et al.* 1991). It has been reported as boring only into living corals (Wilson 1979) and it was not found by Kleemann (1984) during a revision of *Lithophaga* species from dead coral substrates on the GBR.

Lithophaga cf. lessepsiana, found in this study in living colonies of *Acropora cuneata*, is considered a true borer. However, Morton and Scott (1980) have suggested that active erosion decreases in *Lithophaga* spp. that have become specialised to bore in live corals. This specialisation is reflected both in the tendency towards host specificity (Morton and Scott 1980; Mokady *et al.* 1992) and in the concomitant morphological modifications (Morton and Scott 1980). Morton and Scott (1980) suggested that *Lithophaga* spp. which display high specificity for their coral hosts, do not actively bore, but let the coral grow around them. It has to be demonstrated whether *L.lessepsiana* is not a true borer. The implications of the lack of active boring would be important for calculating rates of bioerosion and estimating the production of carbonate sediments. However, *Lithophaga* excavations in living corals, whether actively bored or the results of passive resistance, create important micro-habitats and contribute to the overall increase in porosity of the reef framework. These excavations are also important

as they constitute points of high fracture moment which contribute to diminish the coral mechanical strength (Schuhmacher and Plewka 1981; Mitchell-Tapping 1983).

The presence of *L.cf. lessepsiana* in living portions of *A.cuneata* skeletons increased the extent of excavation 4 to 5 times compared to the other two species. This implies that the composition of the coral community and the existence of specific relationships among corals and borers must be considered when assessing the contribution of living corals to the overall reef bioerosion. Furthermore, the differences in the extent of bioerosion observed among the three species, underscore the contention (Hutchings 1986) that estimates of bioerosion should not be extrapolated beyond the type of substrates from which they were derived (as in Scoffin *et al.* 1980; Stearn and Scoffin 1977).

Although the majority of interspecific variation resulted from the association of *A.cuneata* and *L. cf. lessepsiana*, differences among species were also caused by different levels of dead surface area among colonies of the three species. MacGeachy and Stearn (1976) showed that the ratio of living to dead surface area in colonies of *Montastrea annularis* was the most important factor in determining bioerosion. Highsmith (1981a) and Highsmith *et al.* (1983) found that in massive living coral heads bioerosion was confined to within two centimetres of the dead basal portion of the colony. Despite these findings, previous studies have estimated bioerosion in living corals as a proportion of the colony volume (Hein and Risk 1975; MacGeachy and Stearn 1976; Highsmith 1981a; Sammarco and Risk 1990), rather than standardising by the extent of dead surface area.

The comparison of results from this study with most of the previous research on bioerosion in living corals is made difficult by the widespread use among past and recent studies of measurements of internal bioerosion expressed as proportion of the colony volume (Hein and Risk 1975; MacGeachy and Stearn 1976; Highsmith 1981a; Risk and Sammarco 1982; Highsmith *et al.* 1983; Sammarco and Risk 1990; Risk *et al.* 1995). Although in this study the mean values of the proportion of colony volume removed (Figures 2.10 and 2.11) are similar to values previously reported for different

coral species (genera *Goniastrea, Porites*, *Favia* and *Montastrea*) from both Pacific (Highsmith 1981a) and Atlantic (MacGeachy and Stearn 1976; Highsmith *et al.* 1983), such comparison is in fact meaningless and impossible to interpret. Bioerosion expressed as percent of the total colony volume is a function of the volume and, not surprisingly, small colonies have been found to be more excavated than large colonies (Highsmith 1981a). Such a measure of bioerosion therefore is likely to introduce a considerable portion of variability in data on bioerosion in living colonies, even when comparing similar sized colonies. Furthermore, measuring bioerosion as percent volume removed does not allow comparison among different studies, although it may allow some degree of comparison if the size of the colonies is reported. Failure to standardise by the proportion of dead surface area increases the unexplained portion of variability in the data. As this study has demonstrated, a large and significant relationship exists between the amount of bioerosion and the extent of dead surface area. Depending on the taxa, standardisation by the extent of dead surface area when comparing colonies within and among species, can considerably reduce the overall variation in the data. Therefore, it is recommended that future studies of internal bioerosion in living coral colonies standardise for among colony differences in the extent of dead surface area.

Skeletal density in corals, although highly correlated to colony morphology, is to some extent species dependent (Hughes 1987). Highsmith (1981b) found that in living massive corals damage by borers is positively correlated to the bulk density. He advocated increased protection from predation as a possible explanation for borers to prefer denser substrates. However, denser, slower growing corals tend to have larger portions of dead tissue, which may confound the effect of density (Highsmith 1981b). White (1980) also addressed the relationship between bioerosion and substrate density. She found the highest number of borers per gram of substrate in the densest of three branching coral species in Hawaii. Unfortunately her conclusions were based on one sample per species, and the samples had been subjected to unknown durations of exposure to bioeroders. In this study, the effect of density on bioerosion was not specifically addressed. The design, which included only 3 species with different skeletal density was inappropriate to answer such question. It is worth noting that the three species in this study followed the model proposed by Highsmith (1981b), with the densest coral species, *A.cuneata* being also the most excavated, and

A.hyacinthus, which has the lowest density, being the least affected by borers. Additional studies which partition out relationship between exposed surface area and growth rate are required to establish a relationship between coral density and internal bioerosion. Such studies should also acknowledge the potential confounding of skeletal density with coral morphology (Hughes 1987) and other factors that may affect settlement.

The extent of dead exposed skeleton explained the majority of the interspecific variation in bioerosion by sponges, and accounted for part of the variation among colonies within individual species. Even more so for worms, for which overall variation in bioerosion was substantially reduced when the extent of dead surface area available for settlement was accounted for (Table 2.7). This relationship can be interpreted both as a response of borers to availability of substrate for settlement, and as a result of the physiological constraints of endolithic life styles. However, the similar response of these two groups of borers to availability of substrate in living colonies probably reflects different mechanisms of infestation. Worms, which recruit to available substrate via pelagic larvae (McCloskey 1970), are restricted to patches of dead substrate as they are generally unable to settle on living coral tissue. Hence, their distribution and abundance in living corals is likely to be determined by the extent of dead surface area available for recruitment. Boring sponges however, are colonial organisms which continuously expand through the substrate and do not rely solely on pelagic larvae for local dispersal (Acker and Risk 1985). Their excavation is constrained by their inability to extend their internal galleries further than approximately 2 cm from their external inhalant and exhalant papillae (Highsmith 1981a). As most species of boring sponge cannot compete with coral polyps (their papillae cannot grow amid living coral tissue) their excavation is limited to a maximum of 2 cm into substrates covered with living coral. The excavation of a living coral colony will therefore depend on the extent of dead skeleton on which the sponge tissue can emerge with its papillae.

Areas not covered by living tissue on coral colonies are usually found at the base of the colony. Tunnicliffe (1981) suggested that for *Acropora cervicornis*, which reproduces mainly and successfully by fragmentation, susceptibility to borers may have adaptive significance. Within the theory of the adaptive significance of fragmentation

(Highsmith 1982), corals with high fragment survival might be expected to have high extent of basal area exposed to borers. A recent study at Lizard Island, GBR, has found high rates of fragmentation and high fragment survival for *A.hyacinthus* (Nelson 1994). In the three species investigated in this study, the extent of the basal area not covered by living tissue had a signifcant interspecific variation. However, the plate coral *A.hyacinthus* had the smallest extent of dead basal area, while the sub-massive *A.cuneata* had the largest. Moreover, there was evidence that for *A.hyacinthus* the extent of basal dead area is different among locations, possibly in relation to wave energy. Colonies at the SE sites that are likely to experience the largest strain by wave action, were also the ones with the largest extent of skeleton exposed and therefore the most excavated. Interpretation of this pattern in the light of Highsmith's (Highsmith 1982) and Tunnicliffe's theory (Tunnicliffe 1981) is difficult. The question should be addressed of what determines the inter- and intra-specific patterns in the extent of exposed area as described in this study, and what is the significance of these patterns in the context of adaptative fragmentation and susceptibility to borers.

Part of the variability which could not be accounted for may have resulted from the lack of stratification for colony age. Duration of exposure to borers and extent of dead basal skeleton are a function of colony age and affect the extent of bioerosion. In this study colony age could not be determined, but during collection care was taken to ensure homogeneity of size among the colonies of each species. However, size in corals is not necessarily related to age, as a result of their modular form of life (Hughes and Jackson 1980). Therefore the samples may have been slightly heterogeneous with respect to duration of exposure to borers.

There was no apparent effect of location on the extent of internal bioerosion in living colonies. Previous studies have indicated that the degree of exposure to wave energy may affect the abundance and diversity of boring communities (Bromley 1978; Peyrot-Clausade and Brunel 1990). The distribution of other sessile organisms within reefs is affected by wave exposure (Done 1983). In this study the lack of location effect is not conclusive, due to the low power of the tests associated with this factor. The overall variation and the proportion of the variance due to within-site variation was high for all

coral species. This suggests that experimental studies which investigate spatial patterns of bioerosion in living corals should allocate sampling resources towards a high number of colonies at small spatial scales (i.e. meters).

The high variation observed within sites may reflect the spatial distribution of boring organisms. On coral reefs, the distribution of corals and other benthic organisms have been shown to be very variable at small spatial scales (Nelson 1992; Green *et al.* 1987; Bradbury *et al.* 1986; Fisk and Harriot 1990; Hutchings 1985). For boring organisms, the only previous work including multiple spatial scales, showed that the highest variability occurred among colonies within sites and that a smaller, but important, portion of variation was at the within colony scale (Sammarco and Risk 1990). The present study demonstrated that within forereef habitats, internal bioerosion in living colonies was considerably more variable, i.e. less predictable, at a scale of few meters than at a between-site scale of few hundred meters (see also results from Chapters 3 and 5). Although this may reflect the effect of stochastic phenomena, it highlights the necessity of addressing small-scale processes for understanding the spatial distribution of internal bioeroders within reefs.

To summarise, this study confirmed that coral substrates covered by living tissue are little excavated by boring organisms. However, when a specific relationship exists between a coral species and a particular borers, as is the case between *A.cuneata* and *Lithophaga cf. lessepsiana*, the extent of excavation can be considerably higher. In the three coral species studied, there are species-specific and spatial patterns in the extent of the dead exposed skeleton. This significantly affected the extent of internal bioerosion among the different coral species and should be accounted for in future studies of internal bioerosion of *in situ* substrates.

Chapter 3

Internal bioerosion in coral colonies killed *in situ*

3.1 Introduction

The dynamics of destructive processes acting on *in situ* dead coral skeletons on the reef surface have not previously been investigated experimentally. A manipulative approach was used to investigate the patterns and extent of internal bioerosion in three species of *Acropora* corals. Colonies were killed *in situ* and left exposed to borers for a period of 21 months. The major objectives were i) to investigate the effects of coral species, location and spatial variability on both the extent and the broad taxonomic composition of the boring infauna; and ii) to obtain short-term (21 months) rates of internal bioerosion in naturally occurring and abundant coral substrates.

This study uses *in situ* dead coral colonies to investigate patterns of bioerosion. Previous studies have used either experimental blocks cut from coral skeletons (Davies and Hutchings 1983; Sammarco *et al.* 1987; Kiene 1988; Kiene and Hutchings 1992) or living colonies (MacGeachy and Stearn 1976; Stearn and Scoffin 1977; Sammarco and Risk 1990). For example, Sammarco and Risk (1990) used living colonies of *Porites* spp. in a sampling study which investigated patterns of bioerosion on a cross-shelf gradient on the GBR. However dead coral substrates are a more representative study substrate for investigating patterns of bioerosion as they are more extensively eroded by a wider range of taxa (Hutchings 1986). Moreover, the use of *in situ* dead coral colonies, rather than experimental blocks, ensures that the results are more directly relevant to naturally occurring coral substrates and the reef area under study.

Presently it is not known whether coral species are differentially excavated following death. The effect of coral species on the process of bioerosion and the composition of boring infauna has not been investigated experimentally, although various features of dead coral substrates have been suggested to affect or determine the extent of internal bioerosion. These include skeletal density (Highsmith 1981b), degree of branching (Peyrot-Clausade and Brunel 1990) and extent of encrustation by coralline algae (Peyrot-Clausade and Brunel 1990). This study relates the extent of bioerosion to coral colony features such as volume, surface area, rugosity index and extent of encrustation

by coralline algae, and investigates the effect of coral species on the extent and agents of internal bioerosion.

The species studied have different morphologies characterised by different degrees of structural complexity within a relatively small range of bulk density and corallite size. This makes them convenient subjects for examining the effect of structural complexity on bioerosion. Peyrot-Clausade and Brunel (1990) compared a variety of dead coral substrates and suggested that the degree of branching in dead corals is more important in determining boring communities than coral species. However, their samples were not homogeneous with respect to duration of exposure to borers and the brief and incomplete description of the sampling design prevents a critical evaluation of their results. The effect of different types of dead coral substrates on extent of excavation has only been studied for few individual taxa. Rice and Macintyre (1982) investigated the distribution of boring sipunculans in dead coral rocks in Belize. The highest numbers of sipunculans per unit of surface area occurred in relatively unaltered dead corals of *Acropora* and *Porites* species. Few animals occurred in substrates with evidence of secondary infilling of calcite cement or in substrates highly eroded by boring sponges. Their samples consisted of coral rocks detached from the reef surface, and it is likely that the highly eroded and infilled rocks had been part of the rubble component for considerably longer than the unaltered dead coral rocks. Their result may, therefore, reflect a difference between freshly detached coral substrates and coral rubble and be due to duration of exposure rather than type of substrate.

This experiment focuses on the reef crest environment at two locations which differ also in the exposure to wave impact. Davies and Hutchings (1983) found diverse and extensive boring communities to occur on the windward side of Lizard Island. In the same areas, Bellwood and Choat (1990) found high rates of external bioerosion by parrotfish of the 'excavator' group. According to Davies (1983) the exposed side of the reef is the major source of sediments and it also appear to be the area of the reef where calcification rates are the highest (Kinsey 1977). This evidence suggests that exposure to wave energy is an important factor for reef morphological processes (Marshall and Davies 1982).

Previous works has highlighted the high levels of spatial variation in measures of bioerosion (Hutchings and Bamber 1985; Sammarco and Risk 1990; Hutchings *et al.* 1992). Spatial variability was investigated here at multiple scales, from centimetres (within colony), to metres (within site), to hundred metres (between sites). A major aim of this experiment was to understand at which scale within one habitat the majority of the variability in the process of internal bioerosion occurs. This question is fundamental in two respects: to understand the dynamics of the processes which determine the distribution of borers and ultimately the patterns in the extent of internal bioerosion. Secondly, to obtain estimates of the variance at hierarchical levels which may help to optimally allocate resources in future studies.

The experiment simulated episodes of total mortality of coral colonies belonging to three species of *Acropora* on restricted and replicated areas of the reef crest. These episodes mimicked the consequences of the localised and gregarious feeding behaviour of *Acanthaster planci* on reefs with starfish populations at outbreak levels (Moran 1986). Therefore the present study provides an unique opportunity to investigate the potential consequences of *A.planci* predation on the process of degradation of the reef surface in the short-term following infestation. Several authors have pointed to the likely increase in bioerosion rates on reefs following *A.planci* outbreaks (Sano *et al.* 1984; Hutchings 1986; Glynn 1988). However no information on the rate of destruction of *in situ* dead coral colonies is presently available. This study provides data on which to base predictive models of the calcium carbonate reworked through internal bioerosion and external degradation (see Chapter 4) from dead coral colonies standing on the reef surface.

As a result of bioerosion, calcium carbonate is transferred from coral skeletons and reef framework to other carbonate compartments of the reef (coral rubble, coarse to fine sediments, dissolved calcium carbonate) or is lost from the reef system (Davies 1983). The focus of many studies investigating bioerosion has been to determine the rates of reworking of calcium carbonate and to identify the pathways through which it occurs (Davies 1983). As more and more researchers have reported rates of bioerosion of the same orders of magnitude of calcium deposition rates, bioerosion has assumed an

increasingly important position in studies of morphological development of coral reefs (Davies 1983; Hubbard *et al.* 1990). There is a need for reliable information on rates of reef bioerosion, in order to fully understand the significance of the process for reef morphology (Hutchings 1986). A series of studies have provided rates for various forms of bioerosion on coral reefs around the world (Hein and Risk 1975; Hudson 1977; Scoffin *et al.* 1980; Davies and Hutchings 1983; Kiene 1988; Glynn 1988; Kiene and Hutchings 1992). Many of the published rates of internal and external bieorosion, however, are reported without an estimate of the dispersion of the observed data. Moreover, data have been often obtained from a very small number of samples within a single type of substrates. Therefore, it is difficult to assess the reliability and the representativeness of many of the published rates. As a result, we now have a range of estimates for rates of internal bioerosion on coral reefs, that spans several orders of magnitude. These may indeed reflect true differences, but may as well be the result of inadequate sampling regimes. A major aim of the present study was to provide reliable estimates of rates of bioerosion by macroborers within one reef habitat.

3.2 Methods

3.2.1 Study sites

The experiment was carried out at Lizard Island, at two locations within the reef crest habitat, with three sites per location (Figure 3.1). The SE sites sites were Lizard Head (LH), South Island (SI) and Bird Islet (BI). The NE sites sites were North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). The experimental sites were adjacent to the sampling sites described in 2.2.2.

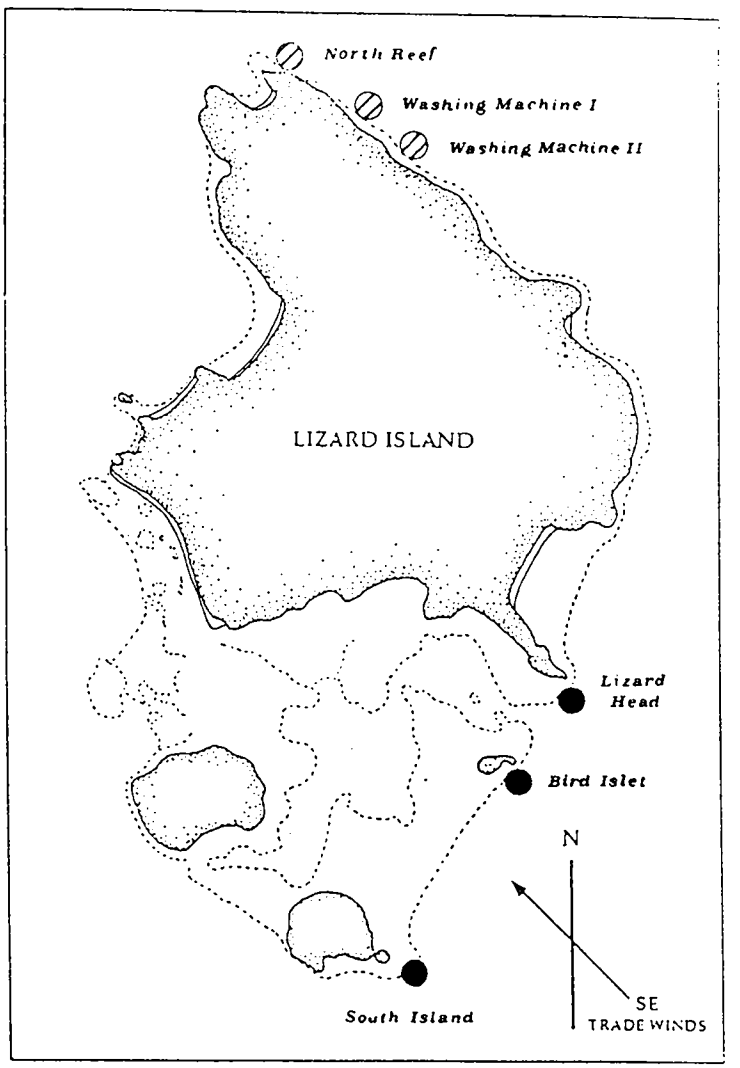


Figure 3.1: Map of Lizard Island with the six study sites: South Island, Bird Islet and Lizard Head (South East sites); and North Reef, Washing Machine I and Washing Machine II (North East sites).

3.2.2 Experimental procedure

The coral species used in the experiment were *Acropora hyacinthus, A.cuneata* and *A.gemmifera*. For a description of these species see 2.2.1. The field experiment involved the killing of *in situ* coral colonies of the three species. The colonies were killed in February 1991, left *in situ* for a period of 21 months and then collected and analysed for the extent of excavation of the skeletons by boring organisms (3.2.4). The volume, surface area and degree of cover of coralline algae was also measured for each colony.

Experimental colonies were chosen according to the criteria described in 2.2.1. All experimental colonies were of similar size within each species (see 4.3.1) and evenly distributed within each site. Colonies were killed by covering them with aluminium foil and a heavy-duty plastic bag. The time necessary for each colony to die varied between three to six days. All colonies were killed within a single 3 week period. Once the colonies were dead, the foil and the plastic bag were removed and the remains of the living tissue displaced from the skeleton by moving the water around it.

Colonies were photographed before and after death and marked with a numbered perspex tag nailed to the reef substrate. The location of the colonies was marked on detailed maps of each site. This made it possible to find the colonies even in conditions of low visibility or in the cases where tags were lost. Colonies were surveyed and photographed at three monthly intervals (Chapter 4).

In November 1992 the experiment was concluded and the colonies collected for analysis of the bioeroding infauna. Of the 180 colonies killed at the beginning of the study, 158 were photographed and retrieved by removing them from the substrate with hammer and chisel. Colonies were left overnight in bags full of sea water to extract infaunal organisms, which come out from the substrate in condition of increasing anoxia (Hutchings and Weate 1977). The present study considers only broad taxonomic groups. However the infauna was collected and sorted into major taxa and preserved in formalin or alcohol for further identification.

3.2.3 Experimental design

The experiment included three coral species, two locations with three sites per location and ten replicates per species per site. It followed a three-way, mixed model nested ANOVA, with location and species as fixed factors and site nested within location.

The original experimental plan included two sampling occasions in which 5 replicates per species per site would have been collected on each occasion and analysed for the extent of bioerosion. The sampling would have been carried out after 12 and 24 months. This schedule was meant to provide an indication of the temporal variability of the process. However, results from the analysis of the living colonies (see Chapter 2) soon after the beginning of the experiment indicated that with the variance estimated for the living colonies, the power of detecting differences among locations using five replicates was low ($\phi<1$; $\nu_1=1$, $\nu_2=4$). Therefore it was decided to reduce the sampling to one collection of all the colonies (ten replicates per species per site), to be carried out after 21 months from the beginning of the experiment. Therefore this study does not provide data on temporal patterns, on the extent of bioerosion, but rather focusses on the spatial variability at different scales.

3.2.4 Sample processing

A total of 158 colonies were retrieved at the conclusion of the experiment. Photographs of the colonies taken before collection were compared with photographs of the same colonies taken at the start of the experiment. All colonies that could not be identified were discarded. Table 3.1 summarises the numbers of colonies per site that were processed and included in the analysis. The samples were processed as described in 2.2.3 which included cutting the colonies into slices, xeroxing the slices and identifying and digitising the borings on the cut surfaces.

	SE Location			NE Location			
	SI	LH	BI	NR	WMI	WMII	Total
A. hyacinthus	8	9	9	10	7	8	51
A. gemmifera	8	8	8	9	8	8	49
A. cuneata	6	5	5	8	8	10	42
Total	22	22	22	27	23	26	**142**

Table 3.1. Number of colonies per species recovered at the end of the experiment at the six sites.

In order to estimate the minimum number of slices per colony required for an accurate estimate of colony bioerosion per unit of surface area, an iterative process with t-test analysis for paired comparisons was used. The most accurate estimate of bioerosion was assumed to be obtained by using all the slices of a colony (the total number of slices per colony varied with the colony size and ranged from 9 to 16). This was justified by the following considerations. a) The colonies were sliced perpendicular to the major axis in order to maximise the number of slices obtained. b) The thickness of the slices (0.5 cm) was considered the minimum feasible thickness, as thinner slices (0.3-0.4 cm) tended to break in most cases during the cutting process. Consequently, estimates obtained using the total number of slices per colony were compared with estimates obtained using 5 and 4 slices per colony. The estimates from the total number of slices and from five slices were compared using a t-test for paired comparisons and found not to be significantly different (t_s=1.0045; $t_{0.05(2),71}$=1.994; n=72). The power calculated to detect an effect size of δ=0.015 when the average difference of the two estimates was d=0.0316±0.0315 (SE), was very high (1-ß=0.979). Although the t-test for paired comparisons between the total number of slices and four slices per colony was also not significant (t_s=0.93; $t_{0.05(2),20}$=2.086), its power was considerably lower (1-ß=0.645). Therefore it was decided to use five slices per colony.

3.2.5 Summary of data obtained

For each colony five non-adjacent slices were analysed and the following measurements were recorded for each slice:

1) Total area. This was used to estimate the volume of the slice.

2) Area of individual macroscopic boreholes belonging to each of the five broad groups of borers (as in Figure 2.2). The sum of the borings within a group was used to estimate the volume of skeleton removed per slice by each group.

3) Number of individual borings per slice by each non colonial group.

4) Distance along the perimeter of the slice which was exposed to borers (it excludes the portion of the perimeter which was attached to the substrate; see Figure 2.2). This measure was used to estimate the surface area of the colony exposed to borers.

5) Distance along the exposed perimeter which was covered with encrusting coralline algae.

The five non adjacent slices per colony were considered as true colony subsamples for the group WORMS in all species and bivalves in *A.hyacinthus* and *A.gemmifera* only. The average size of the boreholes excavated by worms was much lower than the minimum distance between the closest slices. However for the other groups, slices could not be considered as subsamples, i.e independent. Non-independence of slices was due to bivalves, whose boreholes extend throughout several non-adjacent slices and to sponges where chambers can extend throughout the whole colony. Thus only for the group WORMS it was possible to obtain an estimate of within-colony variance.

3.2.6 Comparison of living and dead colonies

In order to be able to obtain rates of bioerosion in the experimental colonies (= amount of $CaCO_3$ removed over the duration of the experiment) it was necessary to estimate the extent of excavation in the colonies prior the start of the experiment. For this purpose, I used the estimates of excavation obtained by sampling living colonies of the three species (Chapter 2). The living colonies were sampled in the same size class as the ones used for the experiment. It is assumed that the average bioerosion in the experimental colonies minus the average bioerosion in the living colonies is an estimate of the bioerosion that took place during the 21 months of the experiment. For this assumption to hold, it was necessary that the extent of bioerosion in dead versus living colonies was significantly different. This was tested by combining the two datasets (bioerosion in living and dead colonies by each borer group) into one and analysing the combined dataset with an ANOVA which included the factor 'status' (two levels: dead and alive), species, location and site. To balance the design, only the four sites where sampling of the living colonies had been carried out were considered (Table 3.2).

	Dead colonies			Living colonies			Tot
	A.hyacinthus	*A.gemmifera*	*A.cuneata*	*A.hyacinthus*	*A.gemmifera*	*A.cuneata*	
SI	8	8	6	9	8	6	45
LH	9	8	5	8	8	7	45
NR	9	9	8	8	7	8	49
WMII	8	8	10	8	6	7	47
Tot	34	33	29	33	29	28	**186**

Table 3.2: Summary table of the number of colonies per treatment. Treatments are identified as combination of coral species and site. Sites are SI=South Island, LH=Lizard Head, NR=North Reef, WMII=Washing Machine II (see Fig.3.1).

Due to limitations imposed by the permit conditions on the number of living colonies that could be collected at the study sites, a control treatment for increase in bioerosion in living colonies during the course of the experiment, was not available. Such control would have consisted of living colonies of the same size as the experimental ones, tagged at the start of the experiment and collected after the 21 month exposure period. A comparison between living colonies at the start of the experiment, living colonies after 21 months and dead colonies after 21 months, would have allowed to statistically confirm that the observed increase in bioerosion is actually due to colony death followed by 21 months exposure. Without such control, this remains an assumption of this study, to be considered when evaluating its results. This assumption, and the likelihood of its validity, is discussed in Section 3.4.2.

3.2.7 Estimates of rates of internal bioerosion

Rates of bioerosion were estimated from the differences between the mean extent of bioerosion in the experimental colonies ($\bar{x}_D$) at each site and species and the mean bioerosion in the living colonies ($\bar{x}_L$) at each site and species. This difference ($\bar{x}_D$ - $\bar{x}_L$) was an estimate of the amount of excavation that occurred during the 21 months of exposure at each site and species. Standard errors for the difference ($\bar{x}_D$ - $\bar{x}_L$) were calculated as the square root of the sum of the ratios of the pooled variance on n_D and n_L (Zar 1984). Rates of bioerosion were expressed as weight of calcium carbonate removed per unit of surface area per year. Data of the volumes excavated by borers per unit of colony surface area were converted into $CaCO_3$ weight (g) by using the estimated bulk densities for the three species (Table 3.3). Yearly rates per unit of surface area (m^2) were obtained from untransformed data (volume, mm^3, per unit of surface area, mm^2) by using the conversion factors shown in Table 3.3.

	A.hyacinthus	*A.gemmifera*	*A.cuneata*
Skeletal density	1.50 ± 0.10	1.88 ± 0.08	2.03 ± 0.12
Sample size	*10*	*10*	*10*
Conversion factor	857	1073	1159

Table 3.3: *Skeletal bulk densities (g x cm^{-3}) of the three coral species* Acropora hyacinthus, A.gemmifera *and* A.cuneata *(errors are Standard Errors). Conversion factors used to obtain estimates of rates of bioerosion (g x m^2 x y^{-1}) from the untransformed data of volume removed (mm^3) per unit of surface area (mm^2).*

3.2.8 Data analysis

All analyses were performed using the SAS/STAT package for PCs. Ungrouped data were tested for normality using D'Agostino's test (Zar 1984). Raw data for total bioerosion and bioerosion by individual taxa departed significantly from normality and were transformed as 1) $x^1=\log(x+1)$ and 2) $x^1=\text{sqrt}(x+3/8)$ and tested for normality (Table A13)* . Multivariate normality was assessed graphically (McArdle pers. comm.). Homoscedasticity of the raw and transformed data was assessed graphically on ungrouped and grouped data, by plotting the expected values of the observations over the residuals. Multivariate homogeneity of variance-covariance matrices was tested using Levene's test.

Following transformation, ungrouped data were analysed as follows:

- Canonical Correlation Analysis was performed to examine the relationships between bioerosion by individual taxa (Dependent Variables, DV) and colony properties (volume, surface area, cover of coralline algae and rugosity index; Independent Variables, IV) and to assess the degree of correlation within DVs and IVs. Scatterplots of the canonical variate scores confirmed normality, linearity and homoscedasticity of the variables.
- Partial and simple correlation were performed on total bioerosion data to examine the relationships with each of the colony variables (surface area, volume, coralline algae cover and rugosity index).

Grouped data were analysed as follows:

- Univariate ANOVAs were used to test for homogeneity of colony volume, surface area, coralline algae cover and rugosity index of the experimental units in the different treatments. Significance level for each F-test for the ANOVAs of bioerosion by sponges, WORMS, bivalves, barnacles and OTHERS was set at $\alpha=0.01$ (Bonferroni corrected significance level), yielding an overall significance level for the five ANOVAs of $\alpha=0.049$.

* All Tables denoted with A are to be found in Appendix A, at the end of the Thesis.

- Mixed model, 3-way, nested ANOVAs were performed to test for effects of location, site and coral species on the extent of total bioerosion and bioerosion by sponges, bivalves, WORMS, barnacles and OTHERS. Significance level was α=0.01.
- A mixed model, 4-way, nested ANOVA was performed to test for the effect of coral species, location, site and colony on data of bioerosion by WORMS and bivalves in *A.hyacinthus* and *A.gemmifera*,. The aim was to investigate the variability in the extent of bioerosion by WORMS and bivalves within individual colonies. Colony was nested within site, with five replicates per colony. For the group WORMS and for bivalves in *A.hyacinthus* and *A.gemmifera* the slices can be considered as colony subsamples, as the dimensions of the borings are small compared to the minimum distance among slices. For the other taxonomic groups, and for bivalves in *A.cuneata*, for which borings may extend throughout the colony, slices cannot be considered independent subsamples.

For grouped data of bioerosion by individual taxa, separate univariate ANOVAs with corrected significance levels were considered more appropriate than a MANOVA given 1) the low correlation within both bioerosion and colony variables, as indicated by the canonical correlation; 2) the deviation from normality of the variables barnacles and OTHERS (Table A13); 3) the assumption of homogeneity of variance-covariance matrices was not met for either raw or transformed data (Levene's test).

For the dataset combining dead and living colonies, variables of total bioerosion, bioerosion by individual taxa and bioerosion per unit of surface area were tested for normality and appropriately transformed when necessary. Data were analysed with a 4-way mixed model ANOVAs, with the factors being colony "status" (alive vs dead), location (SE and NE), site nested within location (LH and SI at the SE location, and NR and WMII at the NE location) and species (*A.hyacinthus, A.gemmifera* and *A.cuneata*).

3.3 Results

3.3.1 Relationship between extent of bioerosion and colony surface area, volume, structural complexity and cover of coralline algae

Results from the canonical correlation analysis showed that the first canonical correlation was 0.76 (58% of overlapping variance between the first pair of canonical variates) and the second was 0.63 (40% of the variance). The probability for the null hypothesis that all canonical correlations are zero was $p<0.0001$, and the probability that the canonical correlations after removing the first one are zero was also $p<0.0001$. The remaining canonical correlations were not significantly different from zero and interpretation of these was not attempted. Thus the first two pairs of canonical variates explained the significant relationship between the two sets of variables. Correlations between the variables and the first pair of variates (Table 3.4) indicated that colonies with high exposed surface area (0.98) and, to a lesser extent, large volume (0.46) and rugosity index (0.48) had high levels of bioerosion by worms (0.91) and low levels of bioerosion by bivalves (-0.51).

	1st canonical variate		2nd canonical variate		
	Correlation	Coefficient	Correlation	Coefficient	
Colony variables:					
Surface area	0.98	0.71	-0.02	-0.25	
Volume	0.46	0.35	0.88	0.84	
Cor.algae	0.14	-0.17	0.10	-0.01	
Rug. index	0.48	0.32	-0.85	-0.28	
% of variance	0.35		0.37		tot=0.72
Redundancy	0.20		0.14		tot=0.34
Bioerosion variables:					
Sponges	0.05	0.20	0.84	0.73	
Worms	0.91	0.85	-0.10	0.18	
Bivalves	-0.51	-0.24	0.61	0.55	
Barnacles	0.16	0.12	0.13	-0.01	
Others	0.29	0.21	0.22	0.26	
% of variance	0.24		0.23		tot=0.47
Redundancy	0.15		0.09		tot=0.24
Canonical correlation	0.76		0.63		

Table 3.4: Canonical correlation statistics between 4 colony variables and 5 bioerosion variables. Correlations between variables and canonical variates; standardized canonical coefficients; percent of variance; redundancies between colony and bioerosion variables; canonical correlations.

Correlations between variables and the second pair of canonical variates indicated that large colony volume (0.88) but small rugosity index (-0.85) was associated with high

levels of bioerosion by sponges (0.84) and bivalves (0.61). Coralline algae cover did not contribute to either of the canonical variates (correlations of 0.14 and 0.10 respectively).

Canonical redundancy analysis showed that neither of the first two pairs of canonical variates is a good overall predictor of the opposite set of variables, with the proportions of variance explained being 20% and 14% for the colony variables, and 15% and 9% for the bioerosion variables (Table 3.4). However, squared multiple correlations showed that the first canonical variate of the colony variables was a moderately good predictor of the bioerosion by worms (0.48), while the first canonical variate of the bioerosion variables is a good predictor of the colony surface area (0.56).

	Surface Area	Volume	Corall.Algae	Rugos.Index
Total Bioerosion	-0.15	**0.25**	0.02	0.001
	(0.06)	(0.002)	(0.78)	(0.98)

Table 3.5: Partial correlation coefficients between total bioerosion and the 4 colony variables (colony surface area, volume cover of coralline algae and rugosity index). Values in bold and underlined are significant at α=0.05. Numbers in brackets are the probability of the coefficients to be different from zero.

Total bioerosion was poorly but significantly correlated with colony volume and was not correlated with colony surface area, coralline algal cover and rugosity index when the other variables were partialled out (Table 3.5). Simple correlations between colony rugosity and bioerosion by borers was significant and positive for WORMS ($r=0.42$; $p<0.001$; $n=130$) and significant and negative for sponges ($r=-0.36$; $p<0.001$; $n=130$).

3.3.2 Patterns of cover of coralline algae

Coralline algal cover per unit of colony surface area differed greatly among all the species ($F_s=62.32$, $F_{0.01;2,8}=8.65$; $p=0.0001$) and among sites ($F_s=7.59$, $F_{0.01;\ 4,123}=3.48$; $p=0.0001$) (Table A14). Cover of coralline algae per unit of surface area in the three species followed the order *A.cuneata* > *A.gemmifera* > *A.hyacinthus*. The site effect was mainly due to Lizard Head having a higher coralline algae cover than the other sites (Figure 3.2). Bioerosion by individual taxa and total bioerosion were not correlated with extent of cover by coralline algae.

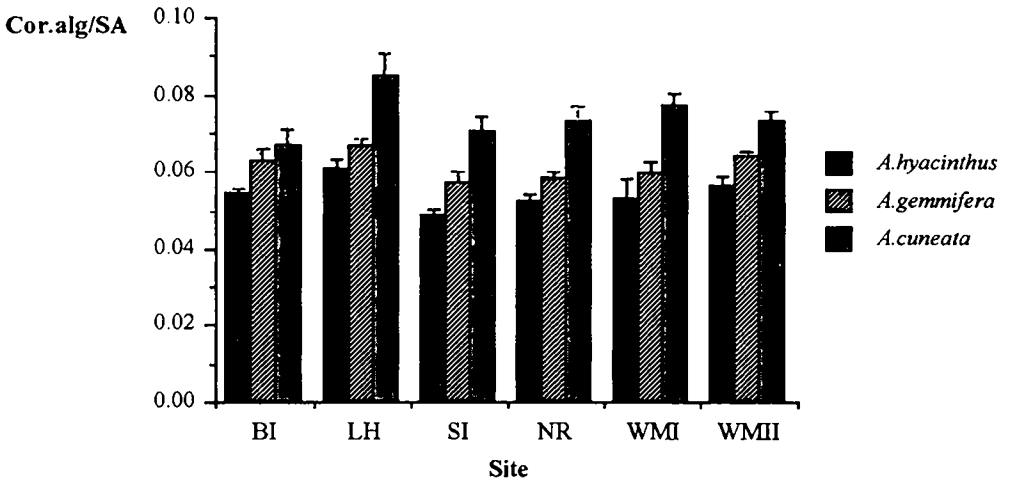


Figure 3.2: Mean cover of coralline algae per unit of surface area for A.hyacinthus, A.gemmifera *and* A.cuneata *at Bird Island (BI), Lizard Head (LH), South Island (SI), North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). Data are untransformed. Error bars are standard errors.*

3.3.3 Excavation of the experimental colonies by macroborers

Extent of volume excavated from the experimental colonies following 21 months of exposure to bioeroders ranged from 21 mm^3 to 150 mm^3 per centimetre square of colony surface area (Table 3.6). Most of the bioerosion was concentrated in the basal portion of the colonies as in the living colonies, but considerable bioerosion had taken place throughout the whole of the colony surface (Figures 3.3 to 3.8). Sponges and, to a lesser extent, bivalves were the most destructive borers in the experimental colonies. Excavation by sponges ranged from 17.1 to 85.7 mm^3 per cm^2 of colony exposed area, amounting up to the 76% of total internal bioerosion (Table 3.7, Figure 3.9). bivalves removed 1.4 - 79.6 mm^3 per cm^2 of exposed area. The highest level of excavation was in *A.cuneata*, where large BIVALVE boreholes were already present at the start of the experiment (see Chapter 2). In *A.cuneata*, bivalves represented up to 59% of total excavation, while for the other two coral species, which are unbored by bivalves while alive, they accounted to a smaller proportion of the total bioerosion, from 3.4% (*A.hyacinthus*) to 34% (*A.gemmifera*). WORMS borings resulted in little volume removed (4.2 to 9.3 mm^3 per cm^2 of area exposed) and had the largest percent of total bioerosion in *A.hyacinthus* (up to 29%), while accounting for only 3.2 - 6.1% in *A.cuneata*. The groups barnacles and OTHERS were absent from 5 and 1 sites, respectively (Table 3.6).

		n	Total	Sponges	Worms	Bivalves	Barnacles	Others
A.cuneata								
SE Sites	BI	6	150.0	61.2	5.8	79.6	2.2	1.2
			6.1	*4.1*	*1.2*	*7.6*	*1.7*	*0.8*
	LH	5	148.9	85.7	4.8	58.3	0.2	-
			20.1	*20.1*	*1.2*	*10.5*	*0.2*	-
	SI	6	144.3	83.9	6.0	53.4	0.3	0.8
			18.8	*14.5*	*1.5*	*11.6*	*0.3*	*0.5*
NE Sites	NR	8	111.8	63.5	4.2	41.8	-	2.3
			9.4	*11.6*	*0.6*	*7.0*	-	*2.2*
	WMI	8	115.3	39.8	7.1	67.8	-	0.7
			16.6	*11.5*	*1.0*	*12.0*	-	*0.4*
	WMII	10	98.5	40.4	5.6	47.1	0.9	4.6
			12.7	*7.3*	*0.9*	*10.2*	*0.6*	*4.2*
A.gemmifera								
SE Sites	BI	8	47.2	24.8	6.4	12.4	2.8	0.9
			6.9	*6.4*	*0.9*	*3.8*	*2.1*	*0.6*
	LH	8	36.4	17.1	6.0	12.4	0.2	0.7
			5.1	*5.0*	*0.6*	*3.2*	*0.2*	*0.4*
	SI	8	44.4	27.7	7.5	7.7	-	1.5
			3.6	*3.3*	*0.9*	*1.7*	-	*0.6*
NE Sites	NR	9	45.7	30.7	6.7	6.4	0.3	1.7
			7.4	*6.1*	*0.9*	*2.2*	*0.3*	*1.2*
	WMI	8	61.9	44.5	8.8	3.2	3.5	1.9
			9.5	*7.3*	*1.3*	*1.8*	*3.0*	*1.4*
	WMII	8	49.0	32.7	7.4	6.2	0.2	2.4
			13.4	*13.7*	*0.9*	*2.4*	*0.2*	*0.8*
A.hyacinthus								
SE Sites	BI	9	34.9	21.4	6.7	6.6	0.2	0.3
			5.2	*4.8*	*0.5*	*0.9*	*0.1*	*0.1*
	LH	9	31.8	16.0	7.6	7.0	0.7	0.6
			4.1	*3.5*	*0.7*	*1.5*	*0.5*	*0.3*
	SI	8	38.0	22.5	9.2	5.5	-	0.8
			3.8	*4.0*	*1.5*	*1.2*	-	*0.3*
NE Sites	NR	9	41.0	31.3	6.2	1.4	0.3	1.8
			11.2	*11.5*	*0.9*	*0.4*	*0.2*	*0.6*
	WMI	6	32.0	20.3	9.3	2.0	-	0.4
			8.2	*8.4*	*1.4*	*0.7*	-	*0.3*
	WMII	8	21.0	13.0	5.2	1.5	0.2	1.0
			4.1	*3.3*	*0.5*	*0.5*	*0.1*	*0.4*

Table 3.6: *Means, standard errors of volume (mm^3) per unit of surface area (cm^2) removed from each experimental colony by the five groups of borers after 21 months of exposure. Sample sizes (number of colonies) are given for each species and site.*

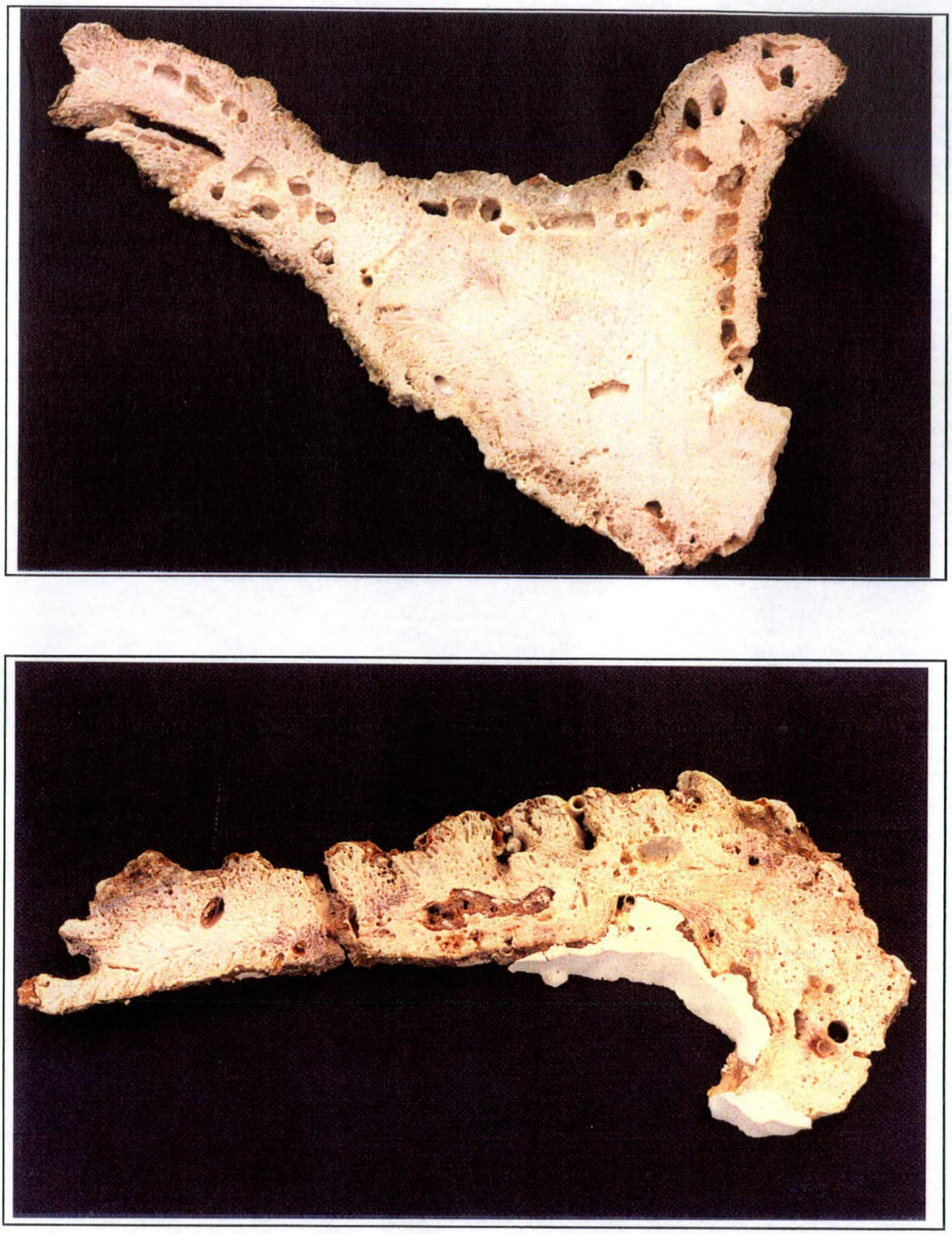


Figure 3.3: *Sections of two colonies of* Acropora hyacinthus *collected after 21 months since death of the living tissue. Most of the boreholes in the first section (top) were produced by a boring sponge (*Cliothosa hancocki*) whose orange tissue can be seen inside the borings. Smaller borings of a second, unidentified sponge can be seen at the base of the colony. The second section (bottom) is perforated by at last two species of sponges (of which one, produced a large boring evident in the centre of the section) and some bivalves (the subspherical borehole on the left of the section still contains fragments of the shell). Some polychaete boreholes are evident also.*

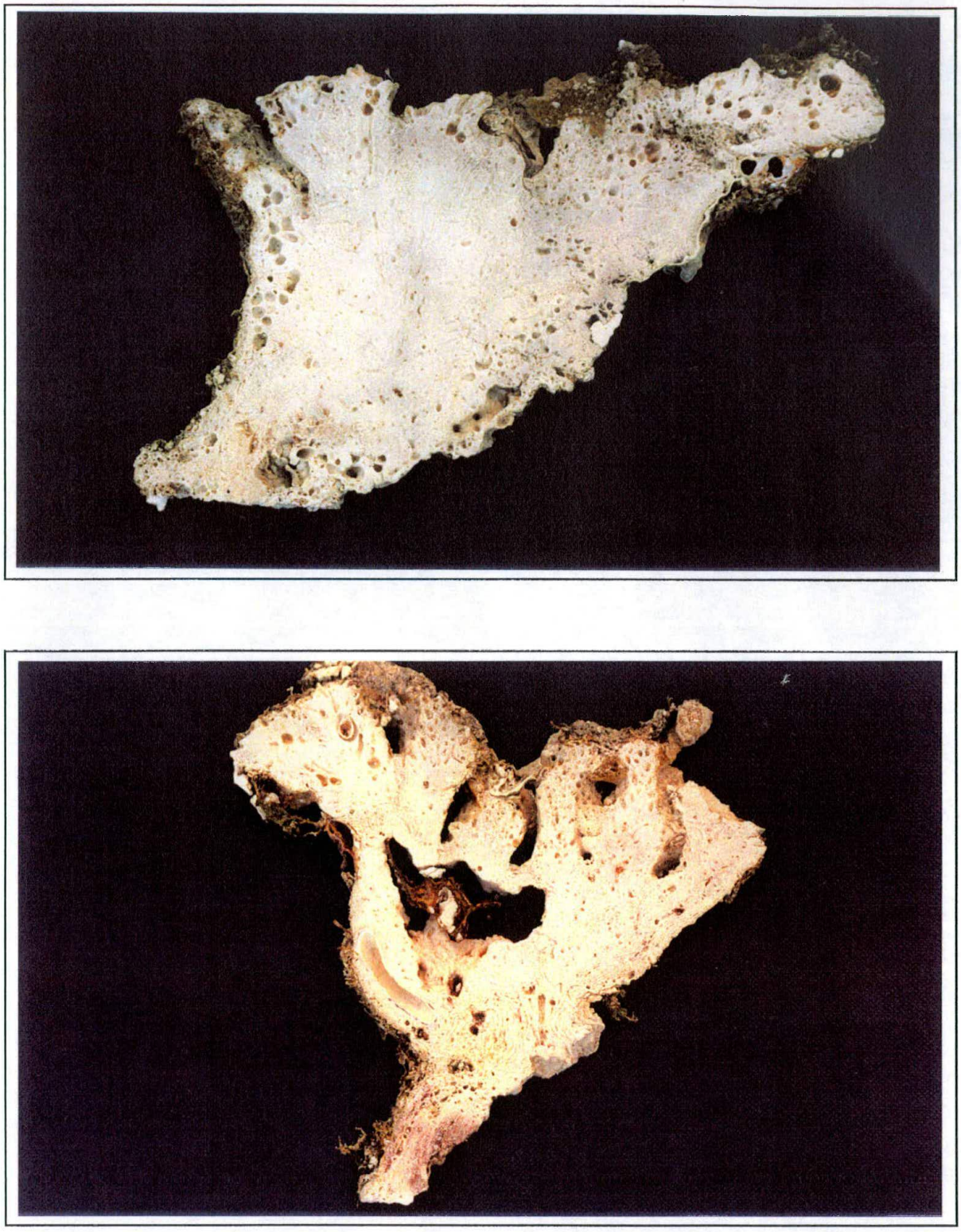


Figure 3.4: *Sections of two colonies of* Acropora hyacinthus *collected after 21 months since death of the living tissue. The section at the top was excavated peripherally by* Cliona vermifera. *A bivalve borehole containing shell fragments is evident at the right of the section. Notice in this as in the other sections from* A.hyacinthus, *how external degradation has produced the loss of the branchlets typical of this coral species (compare with Figure 2.3 top, see also Chapter 4 on decreased rugosity due to external degradation). The section at the bottom shows a large central borehole produced by an unidentified sponge whose brown tissue is evident in the hole. Below this large boring a lined long hole is evident. This was produced by a* Spyrobranchus *sp. polychaete, which is not a boring species. In this section some worm and bivalve boreholes can be seen.*

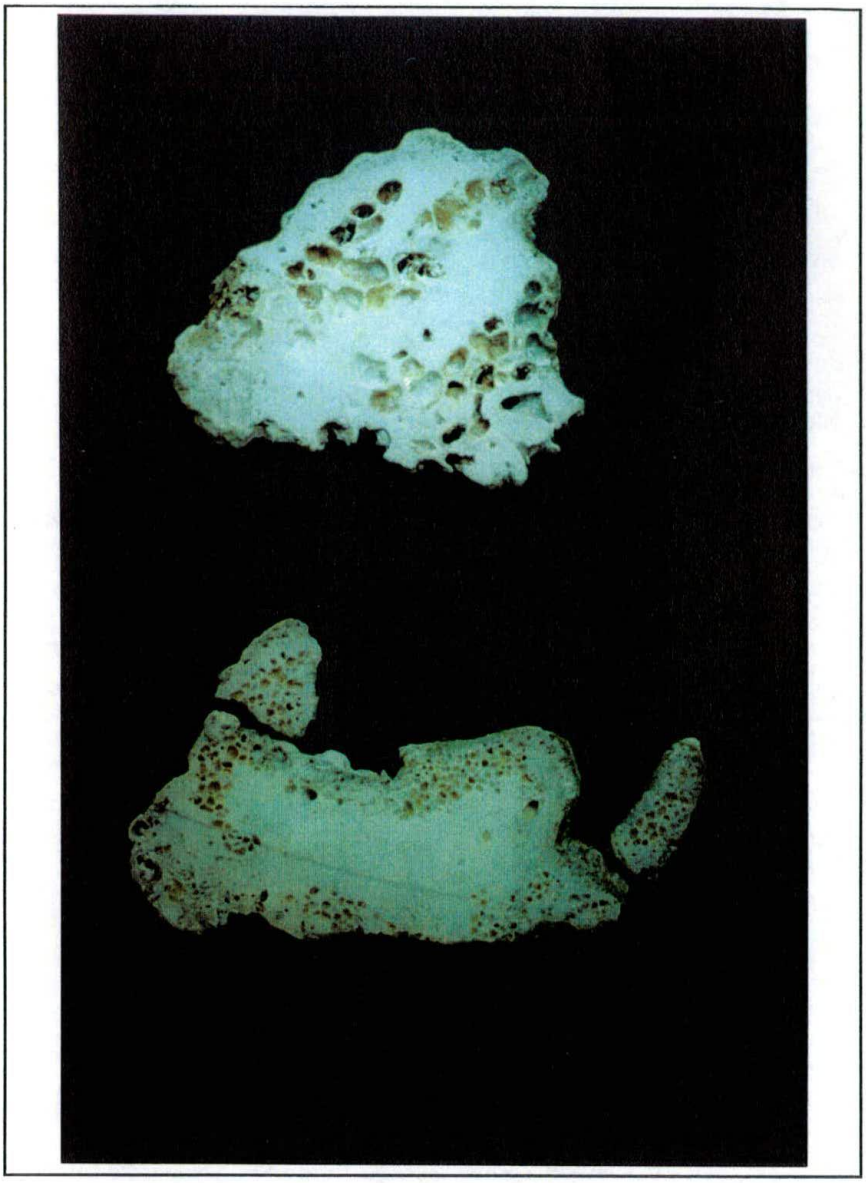


Figure 3.5: *Sections of two colonies of* Acropora gemmifera *following 21 months since death of the living tissue. The colony at the top is heavily eroded by* Cliothosa hancocki. *The colony at the bottom is eroded by* Cliona cf. vermifera.

Figure 3.6: *Section of a colony of* Acropora gemmifera *following 21 months since death of the living tissue. Notice the small extent of bioerosion in this colony compared to the colonies in Figure 3.5. Here the major borer is a bivalve of the genus* Lithophaga. *Fragments of the shell are still evident in the borehole.*

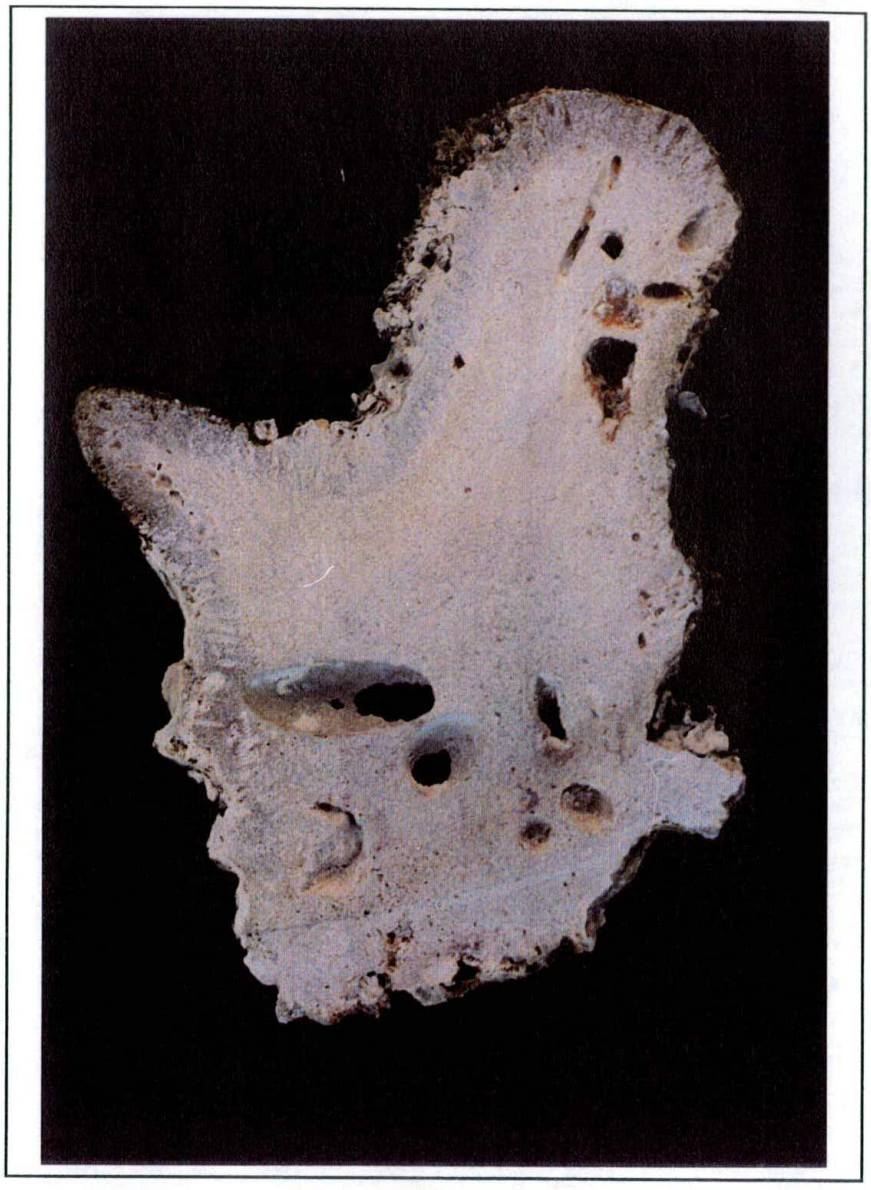


Figure 3.7: *Section of a colony of* Acropora cuneata *after 21 months of exposure to borers. Notice the long and narrow borehole excavated by a large polychaete worm (top right of the colony). The large bivalve borings were most likely excavated by* Lithophaga cf. lessepsiana *when the colony was still alive. An orange sponge (possibly* Cliothosa hancocki*) is excavating the colony as well.*

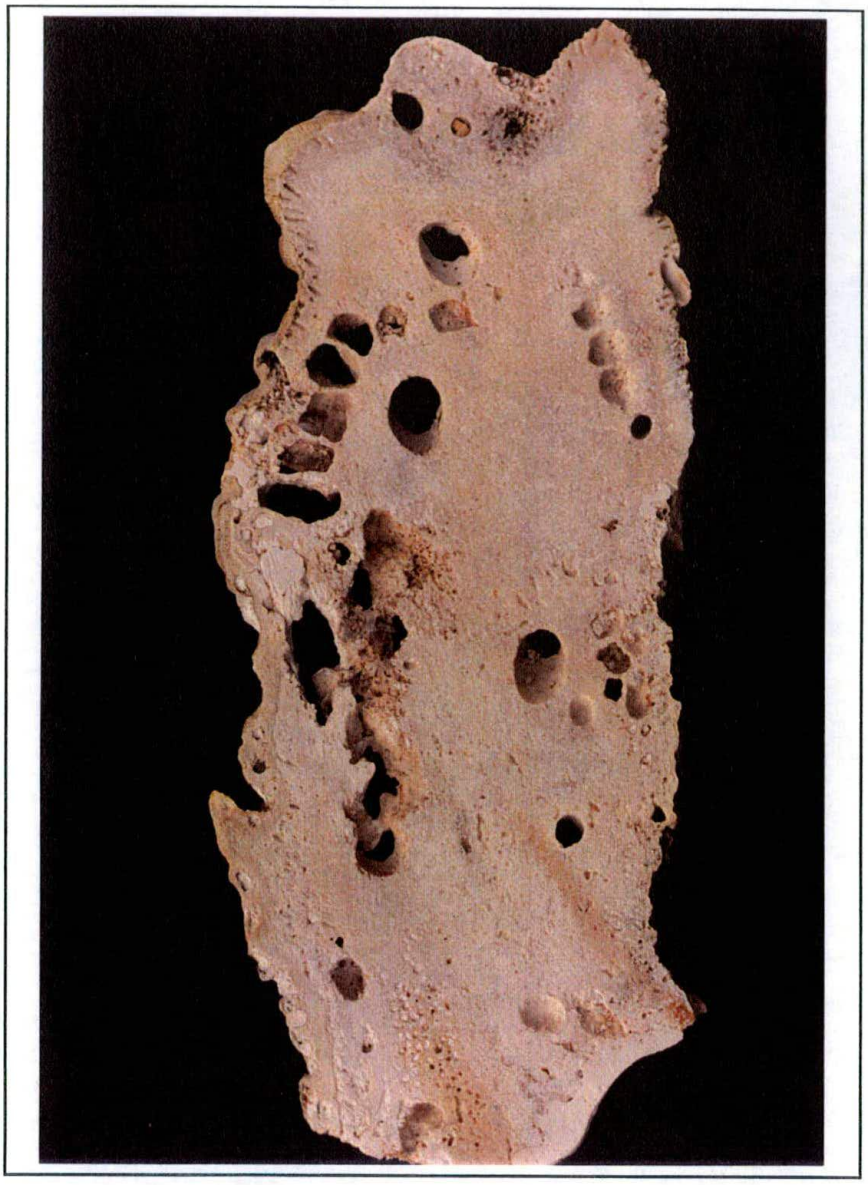


Figure 3.8: *Section of a colony of* Acropora cuneata *after 21 months of exposure to borers. Notice the large bivalve borings and, adjacently the large excavation by* Cliothosa hancocki. *A close-up detail of this section is given in Figure 3.25.*

Where they occurred they were responsible for excavating only up to 3.5 and 4.6 mm^3 per cm^2 respectively. Their contribution to the total bioerosion was minimal (up to 5.9% for barnacles, and 4.8% for OTHERS), however this seemed to depend on the coral species to some extent (Table 3.7).

		sponges %	WORMS %	bivalves %	barnacles %	OTHERS %
A.cuneata						
SE Sites	BI	40.8	3.9	53.1	1.5	0.8
	LH	57.5	3.2	39.1	0.1	0
	SI	58.1	4.2	37	0.2	0.5
NE Sites	NR	56.8	3.7	37.4	0	2.1
	WMI	34.5	6.1	58.7	0	0.6
	WMII	41	5.7	47.8	0.9	4.6
A.gemmifera						
SE Sites	BI	52.4	13.5	26.2	5.9	1.9
	LH	47	16.5	34.1	0.5	1.9
	SI	62.4	16.9	17.3	0	3.4
NE Sites	NR	67	14.6	14	0.7	3.7
	WMI	71.9	14.2	5.2	5.6	3.1
	WMII	66.9	15.1	12.7	0.4	5
A.hyacinthus						
SE Sites	BI	60.8	19	18.7	0.6	0.8
	LH	50.2	23.8	21.9	2.2	1.9
	SI	59.2	24.2	14.5	0	2.1
NE Sites	NR	76.3	15.1	3.4	0.7	4.4
	WMI	63.4	29	6.2	0	1.2
	WMII	62.2	24.9	7.2	0.9	4.8

Table 3.7: Percent of volume excavated by each group of borers, for the three species at the six sites.

The relative importance of the taxonomic groups was uniform across the treatments, with sponges consistently eroding the largest portion of the experimental colonies. Patterns in the relative extent of bioerosion were detected graphically (Figure 3.9) and by performing a correspondence analysis on data expressed as proportion of the total volume of skeleton removed per colony (Figure 3.10). The analysis identified four axes. The portion of total inertia represented by the first two axes was 96.4%, with the first axis alone representing the 92.12%. Therefore the association among the taxa and the combinations of location and coral species is explained mainly by one dimension. Along the first axis a data cloud including the group bivalves was associated with *A.cuneata* at both locations, separates from the other major cloud of sponges, OTHERS and WORMS, which were associated with *A.gemmifera* and *A.hyacinthus*. Within this second data cloud, *A.hyacinthus* separates with WORMS (Figure 3.10). The second axis is due mainly to the group barnacles and it is likely to be an artefact of the high number

of zeros. All the points were well represented on the first axis with the exception of barnacles, OTHERS and, to a small extent, *A.gemmifera* at the SE sites (Table 3.8).

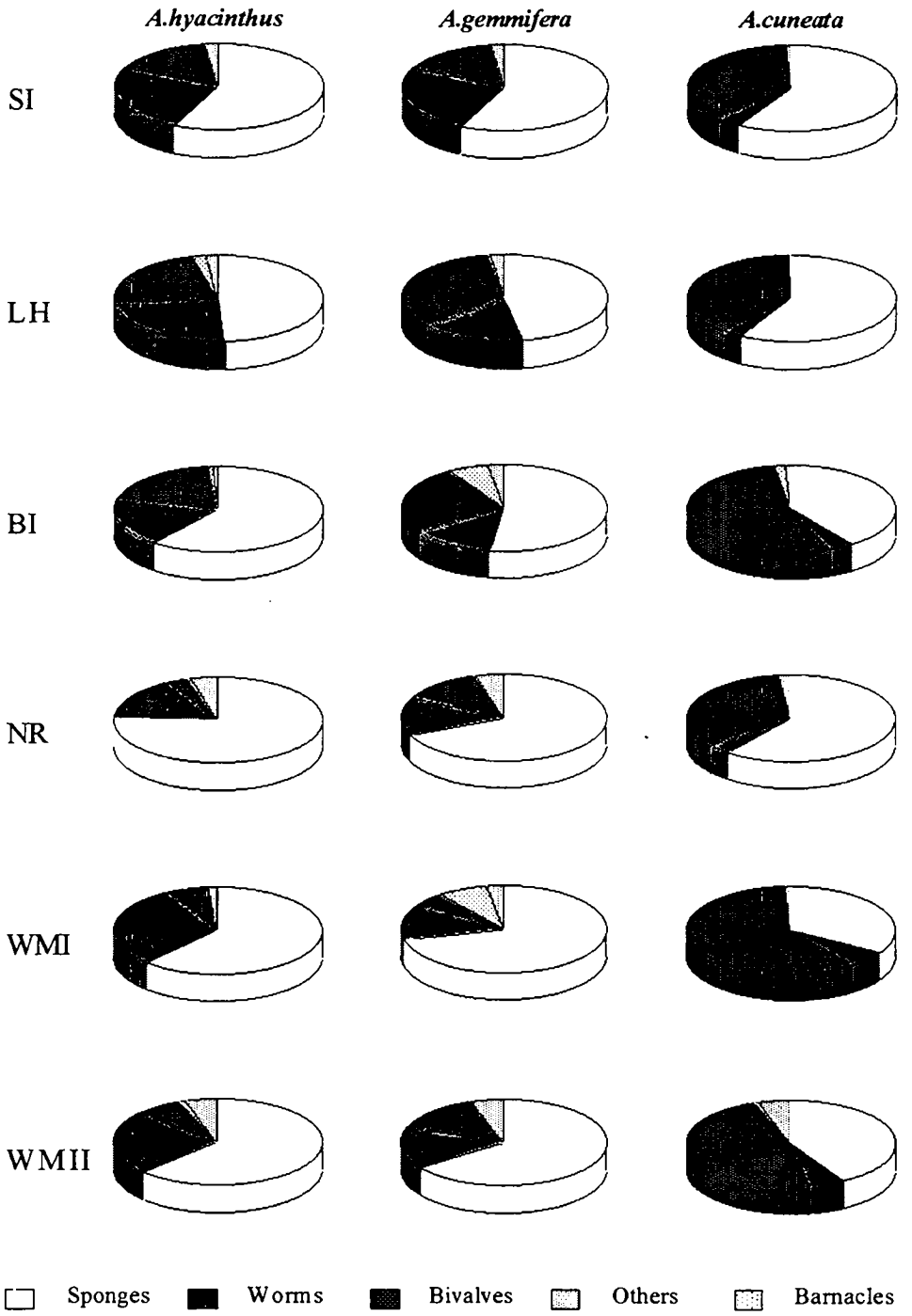


Figure 3.9: Proportion of volume of skeleton removed from A.hyacinthus, A.gemmifera *and* A.cuneata *by the major boring groups at South Island (SI), Lizard Head (LH), Bird Island (BI), North Reef (NR), Washing Machine I (WMI), Washing Machine II (WMII).*

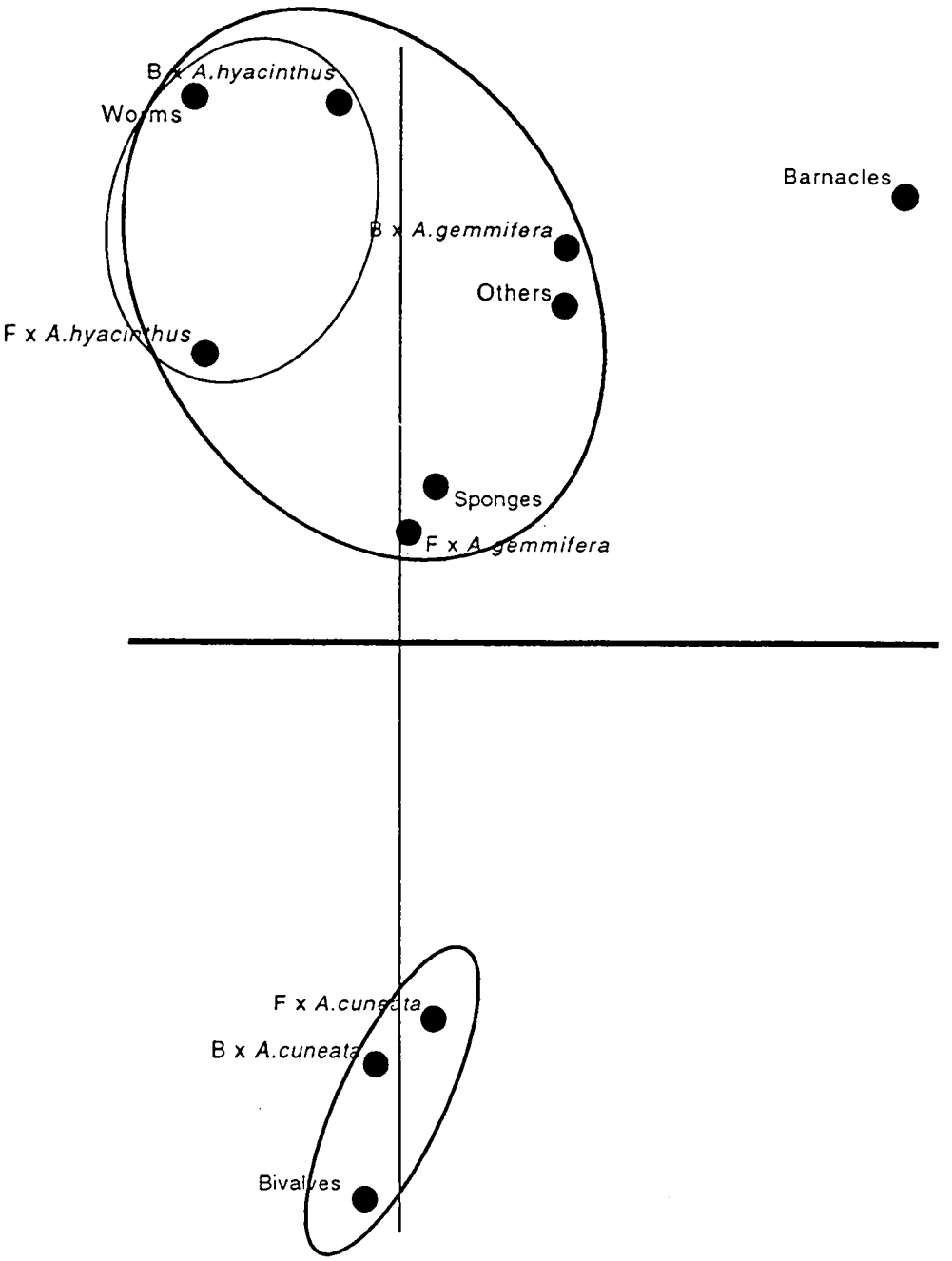


Figure 3.10: Projection of row and column profiles in the reduced space identified by Simple Correspondence Analysis. Row profiles are combinations of site and coral species, and column profiles are taxa of borers.

	1st Axis	2nd Axis
sponges	0.85	0.07
WORMS	0.84	0.14
bivalves	0.99	0.004
barnacles	0.27	0.44
OTHERS	0.42	0.13
NE Sites X *A.cuneata*	0.97	0.002
NE Sites X *A.gemmifera*	0.83	0.16
NE Sites X *A.hyacinthus*	0.93	0.01
Front X *A.cuneata*	0.93	0.009
Front X *A.gemmifera*	0.43	0.006
Front X *A.hyacinthus*	0.62	0.34

Table 3.8: Squared cosines for the profile points obtained by correspondence analysis, which describe the contributions of the axes to the inertia of the row and column profile points. The values arbitrarily underlined show the row and column profiles that most contributed to the inertia (viz. their position in the reduced space) for each axis.

In general, bioerosion by sponges was consistently higher at all sites in the three species. However the relative importance of sponges was greater in *A.hyacinthus* and *A.gemmifera* at the NE sites (Figure 3.9). *A.cuneata* had a larger proportion of bioerosion by bivalves, and in this species bivalves caused more excavation than sponges at three sites. The relative importance of bioerosion by WORMS was greater in *A.hyacinthus.*

3.3.4 Patterns of total bioerosion

Total bioerosion and bioerosion by sponges, WORMS and bivalves were normal following square root transformation (Table A13). Total bioerosion was significantly different among species of corals (F_s=64.74 with $F_{0.05;2,8}$=4.46; p<0.0001) (Table A15; Figure 3.11). Tukey test for multiple comparisons showed that total bioerosion was different between *A.cuneata* and *A.gemmifera*, and between *A.cuneata* and *A.hyacinthus* (p<0.05; df=123), but not between *A.gemmifera* and *A.hyacinthus*. Total bioerosion was also significantly different among sites within a location (F_s=2.51 with $F_{0.05;4,123}$=2.45; p=0.045) (Table A15; Figure 3.11). There was no significant difference between the two locations (F_s=0.19 with $F_{0.05;1,4}$=7.71; p=0.68; but ϕ=0.63; ν_1=1, ν_2=4). There was no significant interaction effect between location and species or between species and site. The majority of the variance in the data was due to within-site variability (61.5%), with a considerable portion accounted for by interspecific variability (30.41%; Table 3.9). However, the larger spatial scales considered in the study (site and location) contributed little to the overall variance of total bioerosion. The majority of this larger

scale spatial variation was accounted for by sites (5%; Table 3.9), with location accounting for little of the total observed variation.

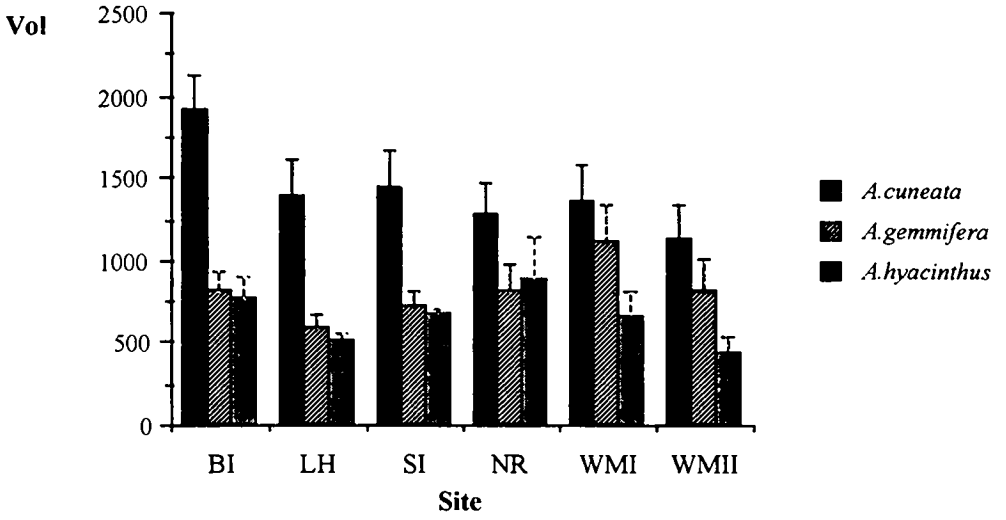


Figure 3.11: Mean volume (mm3) removed by all taxa from colonies of A.hyacinthus, A.gemmifera *and* A.cuneata *at Bird Island (BI), Lizard Head (LH), South Island (SI), North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). Data are untransformed. Error bars are standard errors.*

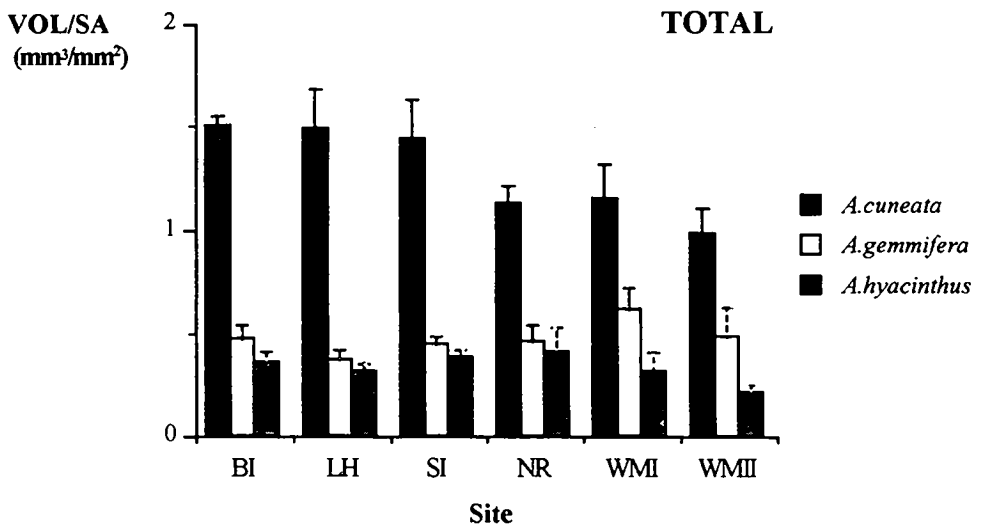


Figure 3.12: Mean volume (mm^3) removed per unit of surface area (mm^2) by all taxa from A.hyacinthus, A.gemmifera *and* A.cuneata *at Bird Island (BI), Lizard Head (LH), South Island (SI), North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). Data are untransformed. Error bars are standard errors.*

Source of Variation	Total Bioerosion	Total Bioerosion per unit of Surface Area
Location	0.24%	1.06%
Site	5.02%	1.23%
Species	30.41%	67.02%
Sp X Loc	2.59%	2.56%
Sp X Site	1.87%	0.88%
Within Site (Error)	61.56%	30.15%
Total	100%	100%

Table 3.9: Variance components of total bioerosion and total bioerosion per unit of exposed surface area.

When total bioerosion was standardised per unit of colony surface area (Table 3.9), the error was then reduced and the factor species explained a larger part of the total variation. In addition, the interaction between species and location was significant (Table A16). This interaction was due to *A.cuneata* being more bioeroded at the SE sites, while this difference was not evident for the other two species (Figure 3.12). Following standardisation, the power to detect a location effect, although still low, doubled (ϕ=1.28; ν_1=1, ν_2=4). In *A.cuneata*, standardised total bioerosion was greater at the SE sites sites than at the NE sites (F_s=31.06 with $F_{0.05;\ 1,4}$=7.71; p=0.005), with location accounting for the 20% of the total variance (Table A17). When total bioerosion, excluding bioerosion by bivalves, was calculated, the general patterns of specific differences remained unaltered, with *A.cuneata* being significantly more eroded than the other two species (Table A18).

3.3.5 Patterns of bioerosion by sponges

Bioerosion by sponges per unit of surface area varied significantly with coral species (F_s=9.33 with $F_{0.01;2,8}$=8.65; p=0.008; Table A19; Figure 3.13), with *A.cuneata* being significantly more eroded by sponges than *A.hyacinthus* (Tukey test, p<0.05, df=123). No other effects on bioerosion by sponges could be detected at the corrected significance level for each F test of α=0.01 (overall α=0.049). Patterns of the means suggest that bioerosion by sponges in *A.cuneata* is greater at the SE sites location. However, power to detect location effect was low (ϕ=0.69; ν_1=1, ν_2=4). Up to 78% of the total variance was due to variation among colonies.

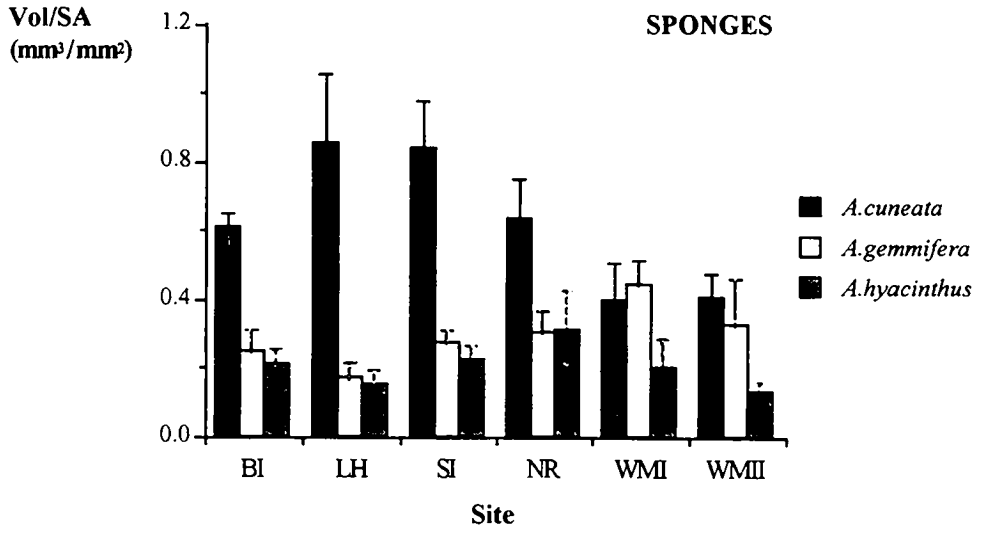


Figure 3.13: Mean volume (mm^3) removed per unit of surface area (mm^2) by sponges from A.hyacinthus, A.gemmifera *and* A.cuneata *at Bird Island (BI), Lizard Head (LH), South Island (SI), North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). Data are untransformed. Error bars are standard errors.*

3.3.6 Patterns of bioerosion by worms

Intra-colony variation was investigated for the group WORMS (see 3.2.5). Bioerosion by WORMS differed significantly among coral species (F_s=118.06, with $F_{0.01;2,8}$=8.65; p=0.0001; Table 3.10), being greater in *A.hyacinthus* and *A.gemmifera* than in *A.cuneata* (Tukey test for multiple comparisons, p<0.05, df=123; Figure 3.14). It also differed significantly among colonies (F_s=3.27, with $F_{0.01;47,563}$<1.76; p=0.0001); the interaction between species and colonies was highly significant also (F_s=2.46, $F_{0.01;76,563}$<1.47; p=0.0001), indicating that for different species the among colony variation was significantly different.

Source of variation	df	SS	MS	Fs	p
Total	703	2294.01			
Species	2	379.04	189.52	**118.06**	0.0001
Location	1	9.03	9.03	0.55	0.49
Site	4	65.21	16.30	2.53	0.053
Colony	47	303.28	6.45	**3.27**	0.0001
SpxLoc	2	12.98	6.49	4.05	0.06
Sp X Site	8	12.84	1.60	0.33	0.95
Sp X Col	76	368.41	4.84	**2.46**	0.0001
Error	563	1109.80	1.97		

***Table 3.10:** Results of 4-way mixed, nested ANOVA for bioerosion by WORMS. Data are transformed as X_1=sqrt(X+1). F values in bold and underlined are significant at α=0.01.*

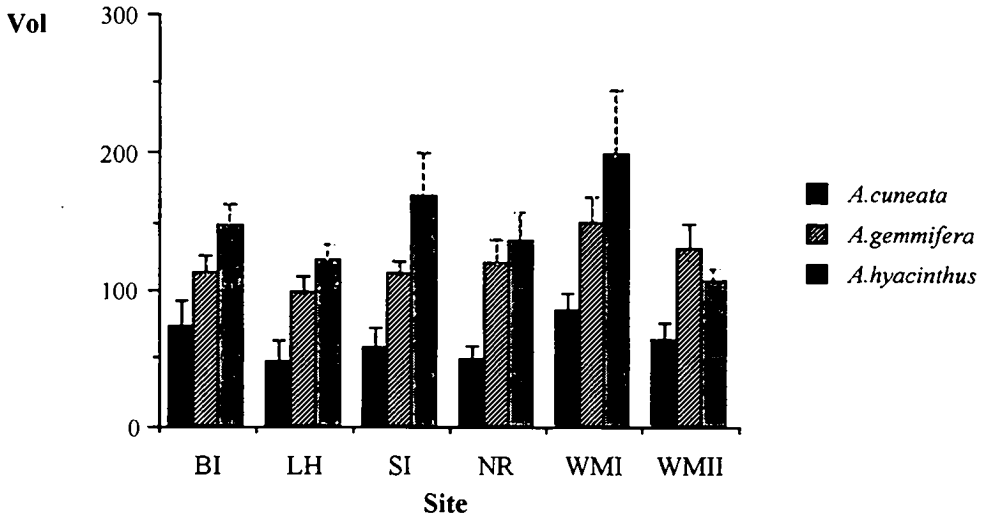


Figure 3.14: Mean volume (mm^3) removed by WORMS from colonies of A.hyacinthus, A.gemmifera *and* A.cuneata *at Bird Island (BI), Lizard Head (LH), South Island (SI), North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). Data are untransformed. Error bars are standard errors.*

When bioerosion by worms was standardised per unit of surface area (Table A20, Figure 3.15) the variability due to coral species effect decreased from 16.5% to 0.8%, suggesting that observed difference among coral species was mainly due to a difference in the availability of surface area. The difference in surface area explained half of the variation among colonies (form 13.2% to 6.8%; Table 3.11) also; while a large portion of variation was due to difference among slices.

Source of Variation	Bioerosion by WORMS	Bioerosion by WORMS per unit of Surface Area
Species	16.52%	0.80%
Location	0.39%	0.08%
Site	2.84%	0.48%
Colony	13.22%	6.79%
Sp X Loc	0.56%	0.74%
Sp X Site	0.55%	0.75%
Sp X Colony	16.05%	13.56%
Within Colony (Error)	48.37%	76.45%
Total	100%	100%

Table 3.11: Variance components of bioerosion by WORMS and bioerosion by WORMS per unit of exposed surface area.

No significant effect of any of the factors was detected after standardisation. Power for detecting a species effect was $1-\beta=0.25$ at $\alpha=0.01$ with $\nu_1=2$ and $\nu_2=8$. Power to detect a location effect was also low ($\phi<1$, $\nu_1=1$ and $\nu_2=2$).

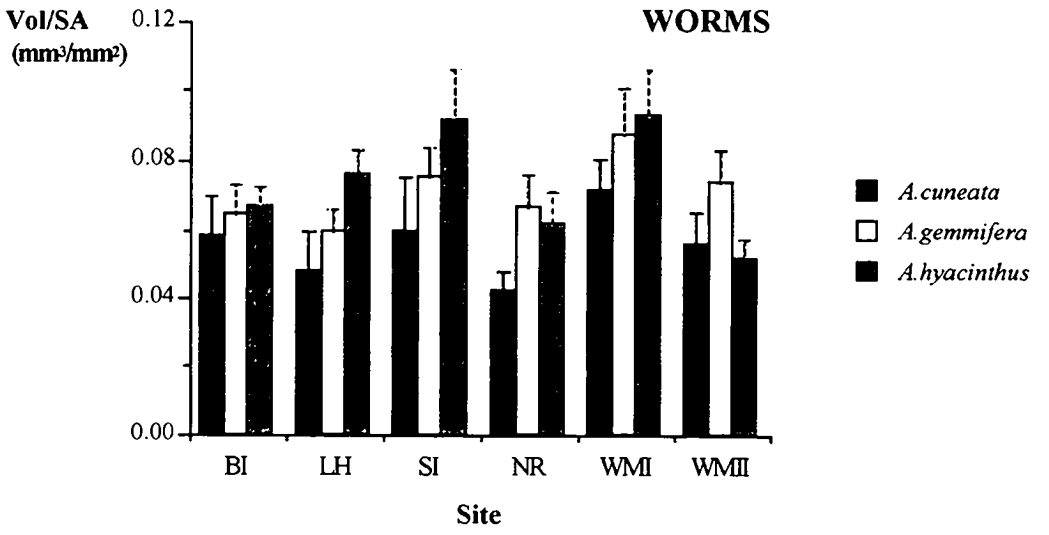


Figure 3.15: Mean volume (mm^3) removed per unit of surface area (mm^2) by worms from A.hyacinthus, A.gemmifera *and* A.cuneata *at Bird Island (BI), Lizard Head (LH), South Island (SI), North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). Data are untransformed. Error bars are standard errors.*

3.3.7 Patterns of bioerosion by bivalves

Bioerosion by bivalves per mm^2 was greater at the SE than the NE sites (F_s=26.09 with $F_{0.01;1,4}$=21.2; p=0.006) (Table A21; Figure 3.16). It also differed among coral species, with *A.cuneata* being more extensively eroded by bivalves than either *A.hyacinthus* or *A.gemmifera* (Tukey test; p<0.05, df=123). The factor location explained 8.4% of the total variation, and within site and interspecific variability accounted for the 49% and 36% respectively.

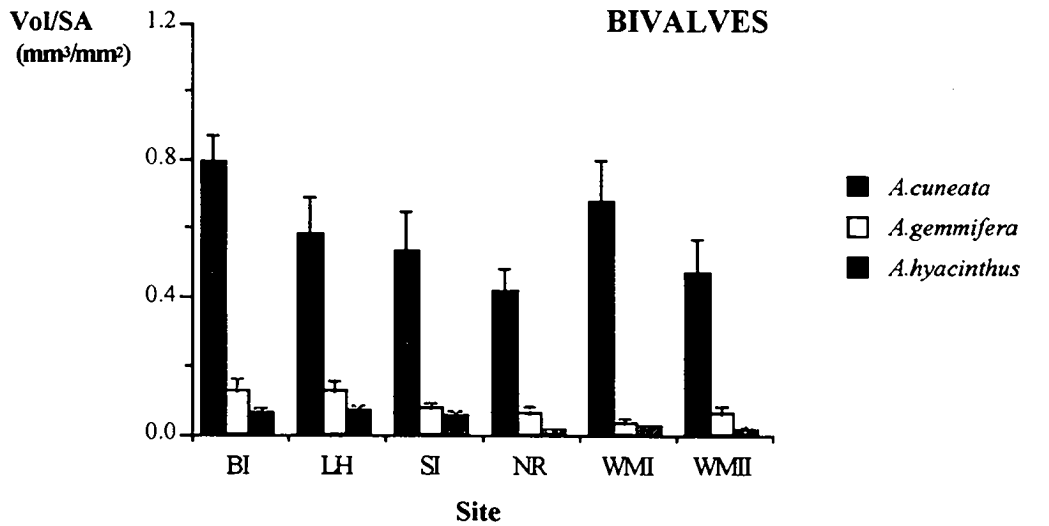


Figure 3.16: Mean volume (mm^3) removed per unit of surface area (mm^2) by bivalves from A.hyacinthus, A.gemmifera *and* A.cuneata *at Bird Island (BI), Lizard Head (LH), South Island (SI), North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). Data are untransformed. Error bars are standard errors.*

When bioerosion by bivalves was analysed for each coral species separately (Table 3.12), it was evident that location had a large and similar effect in *A.hyacinthus* and *A.gemmifera* (18.7 and 19.2% of the variance respectively), which were more eroded by bivalves at the SE sites, but accounted for a small portion of the total variance in colonies of *A.cuneata* (2.8%), which instead displayed a large between-site variation (17%) as a result of higher excavation at Washing Machine I compared to the other sites at the NE location. Power to detect a location effect for *A.cuneata* was therefore low.

Source of variation	df	SS	MS	F_S	P	%
A.cuneata						
Total	42	4.79				100
Location	1	0.13	0.13	0.69	0.45	2.8
Site	4	0.80	0.20	1.95	0.12	17
Error	37	3.81	0.10			80
A.gemmifera						
Total	48	28.70				100
Location	1	5.40	5.40	11.46	0.02	18.7
Site	4	1.88	0.47	0.94	0.45	6.4
Error	43	21.57	0.50			75
A.hyacinthus						
Total	48	22.88				100
Location	1	4.40	4.40	**25.73**	0.007	19.2
Site	4	0.68	0.17	0.42	0.79	2.9
Error	43	17.60	0.41			76.9

Table 3.12: ANOVA tables and percent variance components for bioerosion by bivalves per unit of surface area in each coral species. Data are log transformed. F values in bold and underlined are significant at α=0.01.

While there was no difference between the *A.hyacinthus* and *A.gemmifera* in the extent that they are bioeroded by bivalves per unit area, the location effect was highly significant (F_s=71.07, $F_{0.01;1,4}$=21.20; p=0.0011; Table A22), with the SE sites being more eroded by bivalves than the NE sites, and accounted for 10.8% of the total variance. The factor colony, although not significant at the corrected significance level, accounted for 10.3% of the total variance.

3.3.8 Patterns of bioerosion by barnacles and OTHERS

The large numbers of zeros, especially in the category barnacles, made the data of bioerosion by both groups deviate from normality. Data significantly deviated from normality following either transformations (log and square root), however the deviation was reduced following the logarithmic transformation (Table A13). Bioerosion by

barnacles (Figure 3.17) and borers included in the category OTHERS (see 2.2.4; Figure 3.18) was small. ANOVAs did not detect any effect at the corrected significance level (Tables A23 and A24). However, there was a large effect of site on bioerosion by barnacles (F_s=2.48, $F_{0.01;\,4,123}$>3.46; p=0.047), and there was a large effect of 'species' on bioerosion by OTHERS (F_s=6.21 $F_{0.01;\,2,8}$=8.65; p=0.02). The percent components of the total variance showed that for both variables up to the 85% of the variance was due to within site variation.

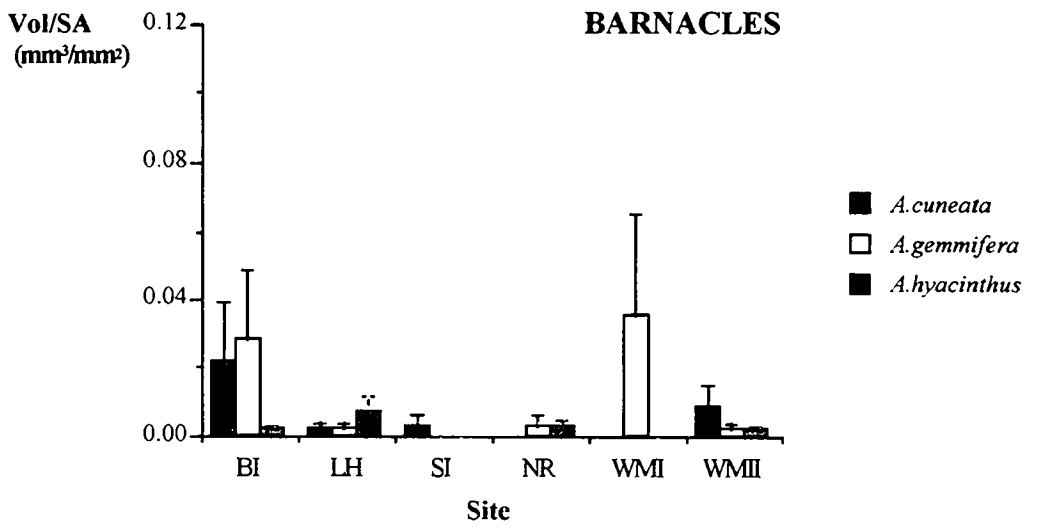


Figure 3.17: Mean volume (mm^3) removed per unit of surface area (mm^2) by barnacles from A.hyacinthus, A.gemmifera *and* A.cuneata *at Bird Island (BI), Lizard Head (LH), South Island (SI), North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). Data are untransformed. Error bars are standard errors.*

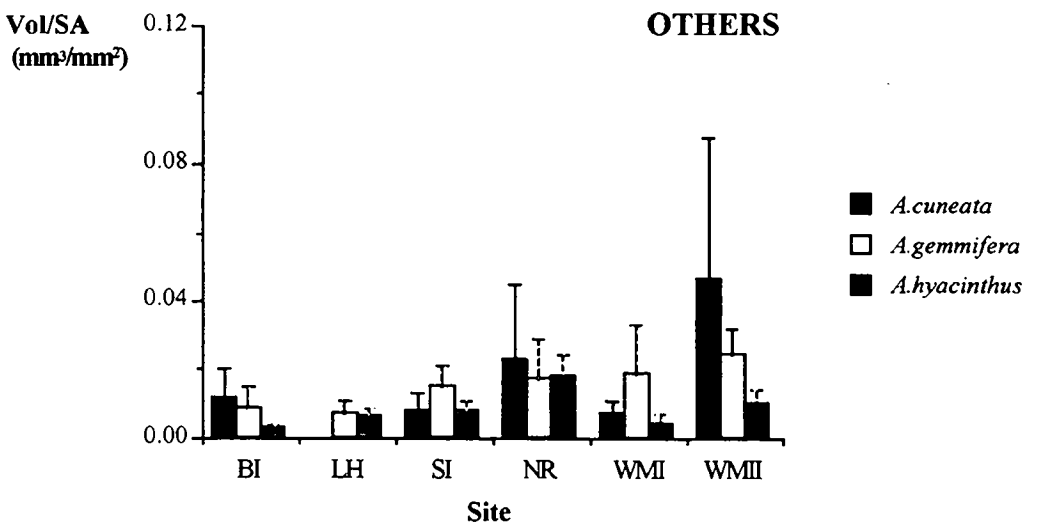


Figure 3.18: Mean volume (mm^3) removed per unit of surface area (mm^2) by others from A.hyacinthus, A.gemmifera *and* A.cuneata *at Bird Island (BI), Lizard Head (LH), South Island (SI), North Reef (NR), Washing Machine I (WMI) and Washing Machine II (WMII). Data are untransformed. Error bars are standard errors.*

3.3.9 Comparison of the dead and living colonies

Total bioerosion per unit of colony surface area was significantly greater in the colonies killed *in situ* than in the living colonies (F_s=52.9, $F_{0.05;1,2}$=18.51; p=0.018; Table A25, Figure 3.19). This was true for all three species, i.e. the interaction between species and status was not significant (power of the test was ϕ=1.43, ν_1=2 ν_2=4). Effect of species was significant (F_s=64.22, $F_{0.05;2,4}$=6.94; p=0.0009), with *A.cuneata* being more eroded than both *A.gemmifera* and *A.hyacinthus*.

Bioerosion by sponges per unit of surface area was not significantly different in living versus dead colonies at the corrected significance level (α=0.01), although F was high (F_s=55.95; $F_{0.01;1,2}$=98.50, p=0.017; Figure 3.20) and colony 'status' accounted for more than 25% of the overall variance. There was a significant effect of species (F_s=82.38; $F_{0.01;2,4}$=18, p=0.0006) and a high interaction between colony 'status' and species (F_s=8.23; $F_{0.01;2,4}$=18, p=0.03), indicating that after 21 months there was a tendency for the three species to be differentially excavated by sponges. In *A.cuneata* bioerosion by sponges was higher at the SE sites (Figure 3.20), although the overall location effect across the species was not significant.

Bioerosion by worms was significantly higher in the dead colonies than the living ones (F_s=349.6; $F_{0.01;1,2}$=98.50, p=0.002; Figure 3.21). The interaction between colony 'status' and species was significant also (F_s=24.71; $F_{0.01;2,4}$=18, p=0.005), with the descendent order for the living colonies being *A.gemmifera* > *A.hyacinthus* > *A.cuneata* and for the dead, experimental colonies being *A.hyacinthus* > *A.gemmifera* > *A.cuneata* (Figure 3.22).

Dead colonies had a larger extent of bioerosion by bivalves than the living ones (F_s=242.46; $F_{0.01;1,2}$=98.50, p=0.004). The factor species accounted for most of the total variation, due to the large difference of bioerosion by *L.cf.lessepsiana* in *A.cuneata* compared to the other two species. When bioerosion by bivalves in living versus dead colonies was analysed in *A.hyacinthus* and *A.gemmifera* only (where data were not overridden by *L.cf.lessepsiana*), the effect of species was not significant and the factor 'status' accounted for most of the variation not due to residual error. Furthermore, the

effect of location was significant, with the colonies at the SE sites experiencing greatest bioerosion by bivalves (Figure 3.23).

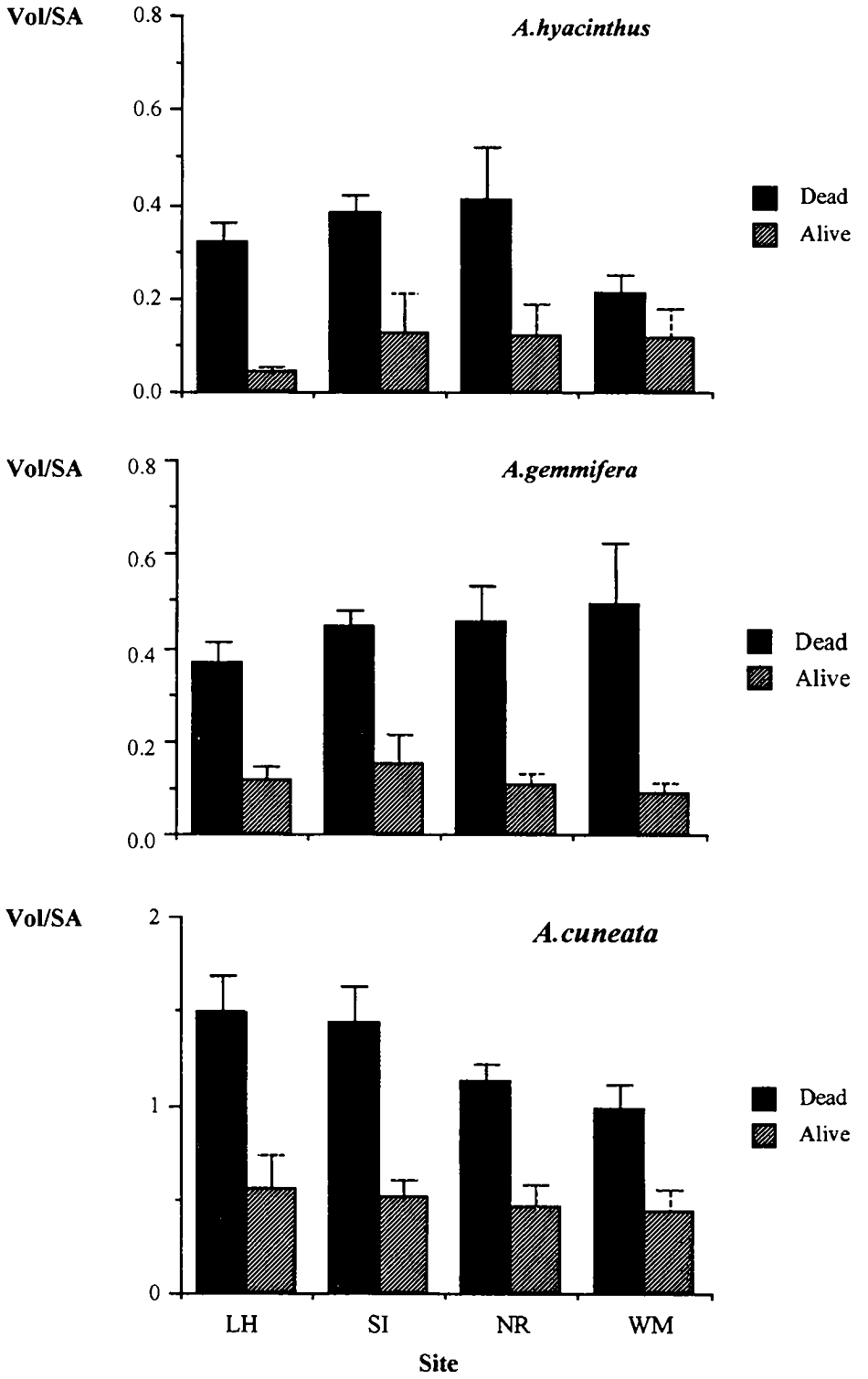


Figure 3.19: Mean volume of skeleton removed per unit of surface area (mm^3/mm^2) by all taxa in living and dead (experimental) colonies of A.hyacinthus, A.gemmifera *and* A.cuneata, *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Data are untransformed. Error bars are standard errors.*

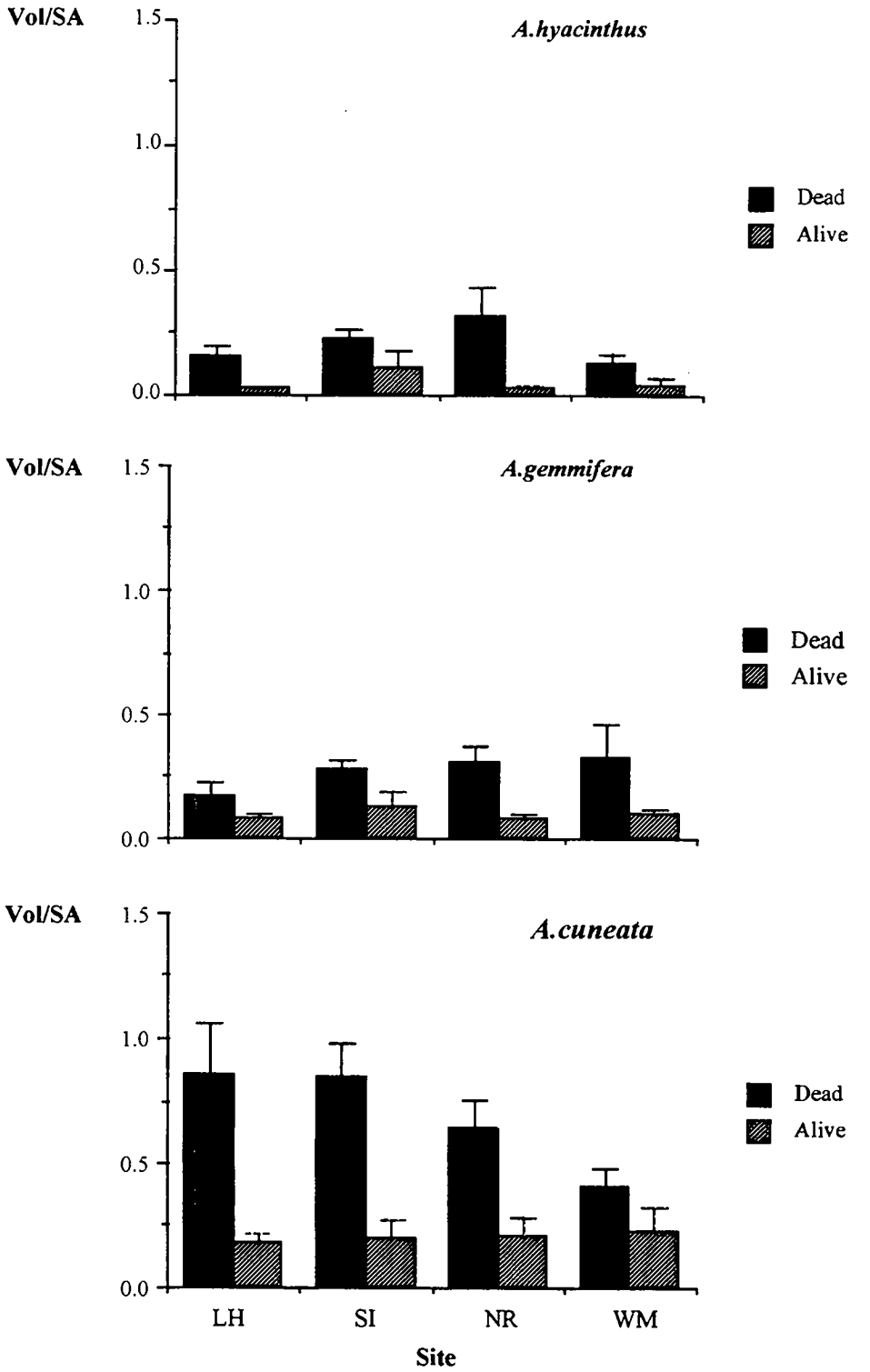


Figure 3.20: Mean volume of skeleton removed per unit of surface area (mm^3/mm^2) by sponges in living and dead (experimental) colonies of A.hyacinthus, A.gemmifera *and* A.cuneata, *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Data are untransformed. Error bars are standard errors.*

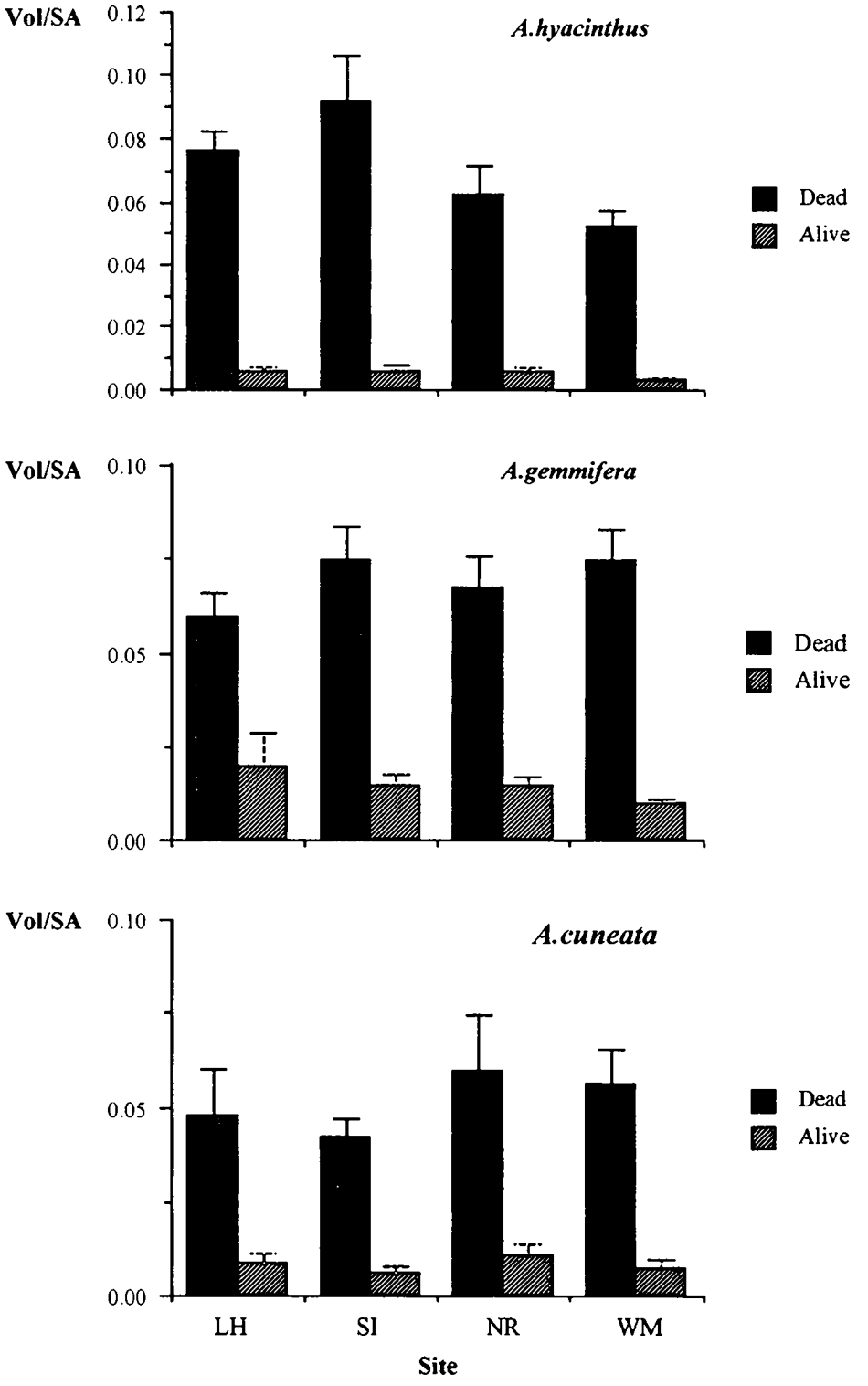


Figure 3.21: Mean volume of skeleton removed per unit of surface area (mm^3/mm^2) by WORMS in living and dead (experimental) colonies of A.hyacinthus, A.gemmifera *and* A.cuneata, *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Data are untransformed. Error bars are standard errors.*

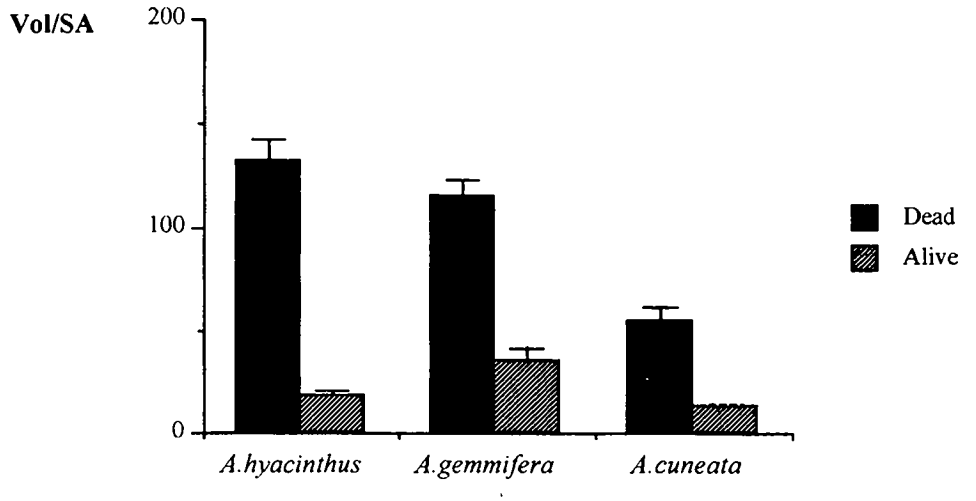


Figure 3.22: Bioerosion by WORMS per unit of surface area in dead (experimental) and live colonies of A.hyacinthus, A.gemmifera *and* A.cuneata.

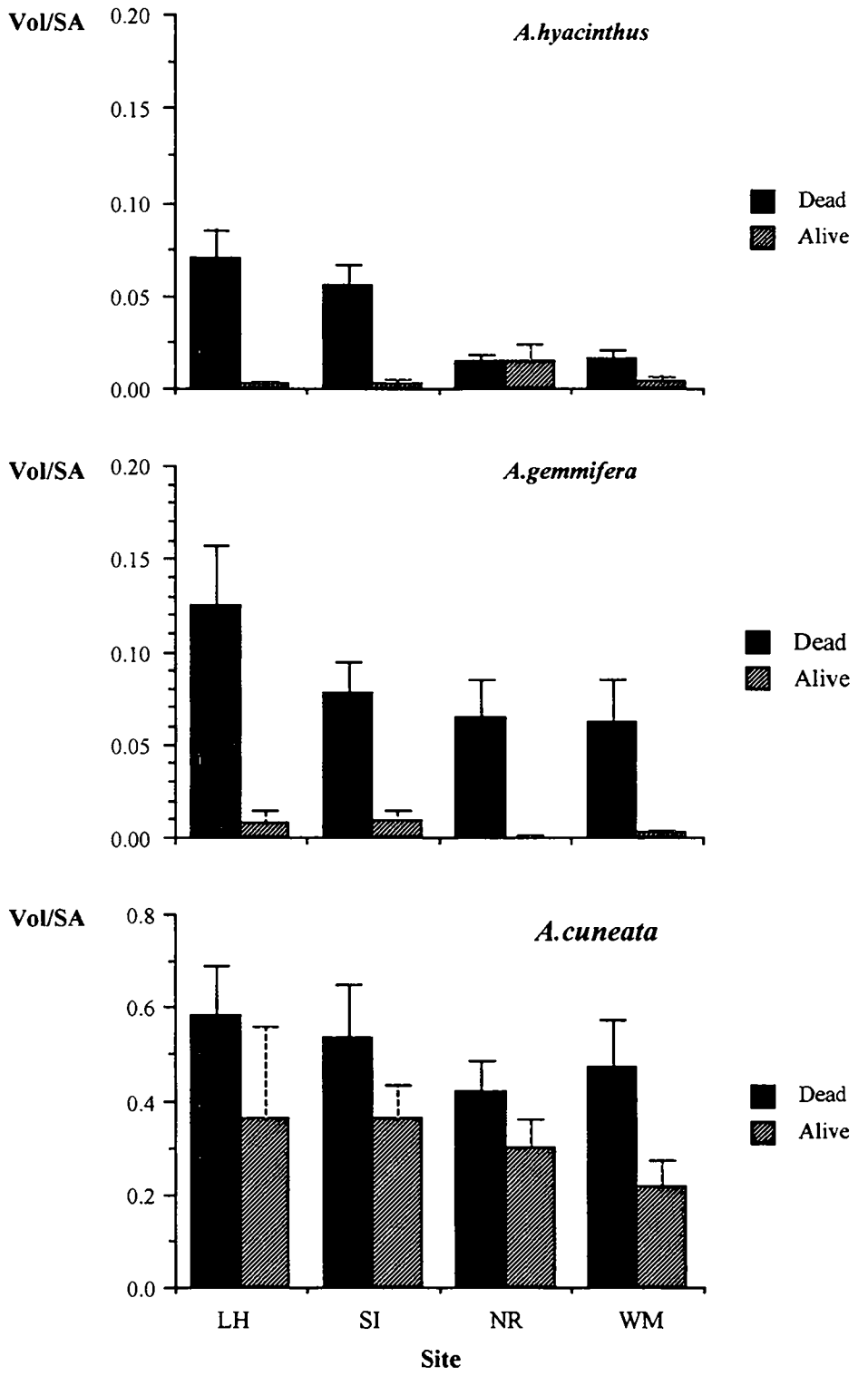


Figure 3.23: Mean volume of skeleton removed per unit of surface area (mm^3/mm^2) by bivalves in living and dead (experimental) colonies of A.hyacinthus, A.gemmifera *and* A.cuneata, *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM). Data are untransformed. Error bars are standard errors.*

3.3.10 Rates of reworking of $CaCO_3$ by macroborers in dead Acropora *corals*

Estimated rates of removal of calcium carbonate per unit of surface area per year for the three coral species and the five groups of borers considered in this study are provided in Table 3.13. Rates were calculated using the mean differences between bioerosion in experimental and living colonies (Table A32). The rates have been pooled across the sites within locations, as no significant site effect was detected for any boring taxa. However, the rates for the two locations were considered separately as location was found to have a significant effect on the rates of bioerosion by bivalves in *A.hyacinthus* and *A.gemmifera.*

Rates of removal of $CaCO_3$ by macroborers varied considerably in the three species (Figure 3.24). The rates were the highest for *A.cuneata*, ranging from 225.4g (± 39) to 1038.5g (± 164.3) $CaCO_3$ m^{-2} y^{-1}. This was due to the fact that *A.cuneata* had both the greatest volumes of skeleton excavated by borers and the densest skeleton of the three species (Table 3.3).

	sponges	WORMS	bivalves	barnacles	OTHERS	TOTAL
SE						
A.hyacinthus	103.70	65.99	51.42	2.57	0.08	225.39
	36.44	*6.57*	*8.01*	*2.23*	*2.14*	*39.03*
A.gemmifera	129.83	53.65	97.64	0.43	5.36	288.64
	36.74	*6.13*	*15.67*	*0.78*	*3.47*	*38.19*
A.cuneata	766.10	56.79	226.60	0.23	-	1038.46
	123.55	*10.065*	*136.47*	*2.70*	*5.42*	*164.27*
NE						
A.hyacinthus	162.83	45.42	4.28	0.85	10.28	226.25
	68.84	*5.58*	*5.91*	*1.35*	*3.86*	*69.57*
A.gemmifera	246.79	62.23	65.45	1.07	8.58	385.20
	80.285	*7.12*	*17.37*	*2.24*	*9.34*	*82.66*
A.cuneata	329.16	49.84	219.05	4.64	27.82	633.97
	107.22	*6.95*	*88.35*	*3.90*	*28.61*	*127.54*

Table 3.13: Mean values and standard errors of internal bioerosion rates (g $CaCO_3$ x m^{-2} x y^{-1}) for each group of borers, in the three species and at the two locations. Rates are calculated over a 21 months period, with the assumption they are constant through time. Rates refer to a m^2 of colony surface area.

WORMS displayed very similar rates in the three species and across sites ranging from 45.4 ± 5.5 to 66 ± 6.5 g $CaCO_3$ m^{-2} y^{-1}. sponges and bivalves had the highest rates of bioerosion, but were also the most variable. Rates of bioerosion for sponges ranged from 103.7 ± 36.4 up to 766.1 ± 123.6 g $CaCO_3$ m^{-2} y^{-1}, with the rates being higher in *A.cuneata* and lower in *A.hyacinthus.* bivalves also had the highest rates in *A.cuneata*

(up to 226.6 ± 136.5 g $CaCO_3$ m^{-2} y^{-1}), and the lowest in *A.hyacinthus*, with the rate being as low as 4.3 ± 5.9 g $CaCO_3$ m^{-2} y^{-1} at the NE location.

	Total	sponges	WORMS	bivalves	barnacles	OTHERS
A.cuneata						
LH	1897.00	1387.03	80.33	451.60	3.44	-
	210.06	*153.09*	*9.14*	*191.20*	*1.83*	-
SI	1746.08	1296.53	99.63	352.14	-	1.03
	164.27	*133.31*	*12.92*	*114.20*	-	*5.30*
NR	1211.68	875.92	71.91	246.90	-	16.94
	96.62	*100.49*	*4.42*	*68.88*	-	*16.90*
WM	1084.20	368.69	99.14	515.91	17.45	83.02
	125.06	*87.82*	*7.44*	*86.23*	*4.68*	*32.49*
A.gemmifera						
LH	466.19	167.62	74.96	217.82	4.45	1.34
	38.55	*35.35*	*7.43*	*21.85*	*1.03*	*3.81*
SI	545.66	287.77	113.89	127.31	-	19.36
	47.74	*45.31*	*6.34*	*11.39*	-	*4.10*
NR	657.58	434.18	98.80	119.35	1.86	3.39
	55.02	*45.91*	*6.41*	*15.39*	*2.33*	*9.65*
WM	697.33	431.88	121.12	111.51	3.88	28.94
	103.63	*106.01*	*6.99*	*18.10*	*1.58*	*6.62*
A.hyacinthus						
LH	415.99	202.39	105.57	100.11	9.33	-
	22.17	*18.90*	*3.55*	*7.97*	*2.63*	-
SI	384.73	174.75	129.19	78.67	-	2.12
	41.51	*39.39*	*7.54*	*6.02*	-	*2.04*
NR	535.30	422.17	85.40	0.29	3.49	23.95
	59.68	*60.96*	*4.76*	*5.10*	*1.21*	*3.09*
WM	238.09	132.22	73.33	16.50	2.33	13.70
	25.34	*21.62*	*2.82*	*2.95*	*0.62*	*2.33*

Table 3.14: Mean values and standard errors of internal bioerosion rates (g $CaCO_3$ x m^{-2} x y^{-1}) for each group of borers, in the three species at the four sites. Rates are calculated over a 21 months period, with the assumption they are constant through time. Rates refer to a m^2 of colony surface area.

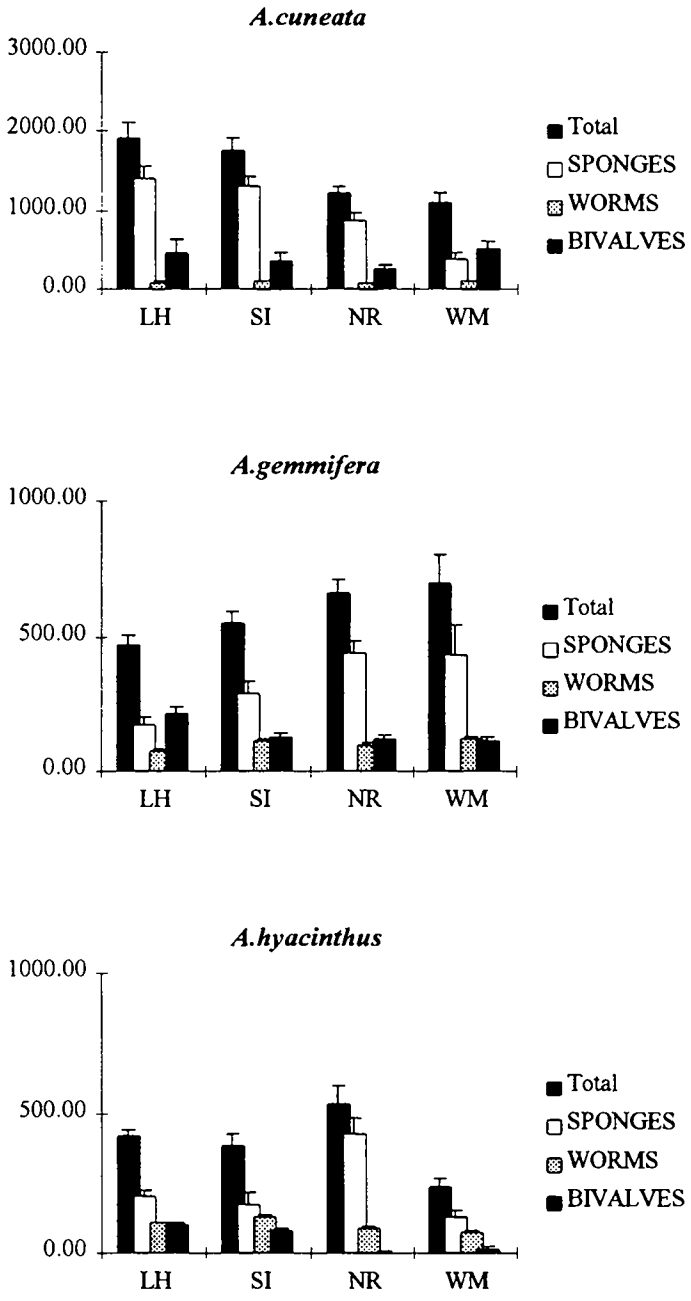


Figure 3.24: Rates of internal bioerosion (g $CaCO_3$ m^{-2} y^{-1}) for the three coral species at the four sites (SE sites: LH, Lizard Head and SI, South Island; NE sites: NR, North Reef and WM, Washing Machine II, see Figure 3.1). Error bars are Standard Errors (see 3.2.7). Notice: the diagrams are not in the same scale.

3.4 Discussion

The results from this field experiment demonstrate that: 1) The extent of internal bioerosion in dead colonies differs greatly among coral species. 2) The interspecific variation in the extent of bioerosion by WORMS is entirely explained by the extent of colony surface area available for settlement in the three coral species. 3) On the contrary, factors other than availability of substrate for settlement must account for the different extent of bioerosion by sponges in the three species. It is suggested that newly available substrates on the reef surface are readily excavated by the boring sponges already established in the adjacent substrates. 4) Bioerosion by newly settled bivalves was greater at the sites directly exposed to the trade winds. 5) No effect of location for other individual groups of borers was detected, but *A.cuneata* had a greater extent of total bioerosion by all taxa at the SE sites. 6) The majority of the variability encountered was due to variation at small spatial scales (within-site variation for all groups and within-colony variation for WORMS and bivalves in *A.hyacinthus* and *A.gemmifera*). However, a small proportion of variability was explained at the spatial scale of site (hundreds of meters) for bioerosion by both WORMS and sponges. 7) Total bioerosion was not correlated with any of the colony parameters considered. However, when bioerosion was considered for each group separately, there was a high correlation between colony surface area and bioerosion by WORMS, while bioerosion by sponges and bivalves was positively correlated with colony volume. Bioerosion by WORMS was positively correlated to rugosity, while bioerosion by sponges was negatively correlated with rugosity. 8) Rates of total bioerosion varied from approximately 225 ± 39 g $CaCO_3$ per m^2 per year in *A.hyacinthus* at both locations, to 1038 ± 164 g $CaCO_3$ per m^2 per year in *A.cuneata* at the SE sites.

3.4.1 Effect of coral species and spatial scale on the extent of internal bioerosion

The three species of coral differed in the extent of colony excavation by boring organisms following a period of 21 months after death. *A.cuneata* was generally more eroded than the other two species, but bioerosion by individual taxa displayed different patterns in the three species. The differences in the extent of internal bioerosion in the three species reflect the interspecific differences already found in the living colonies of

the same coral species. In the living colonies the interspecific pattern was mainly determined by the group bivalves, *Lithophaga cf. lessepsiana* in particular, which extensively bores in *A.cuneata*. To establish whether the specific patterns observed in the dead colonies were still dominated by the presence of *L.cf.lessepsiana* borings, the bioerosion by all groups excluding bivalves was considered. The results showed that *A.cuneata* was more extensively bioeroded by all groups independently of the group bivalves. This may be explained by considering that, as a result of the extent of excavation by *L.cf.lessepsiana* in living colonies of *A.cuneata,* and that most of these bivalves were killed with the coral tissue, the area available for settlement of borers includes the internal surface of the *Lithophaga* borings also. This is supported by the fact that during the analysis of the slices cut from colonies of *A.cuneata*, many excavations, mainly by sponges, were observed adjacent to large bivalve borings. Some species of boring sponges settle in cryptic microhabitats, such as those represented by empty bivalves borings (Figure 3.25). In this study, the pattern of bioerosion by sponges in the dead experiemtnal colonies paralleled the pattern of bioerosion by live-coral boring bivalves found in the living colonies (Figure 3.26).

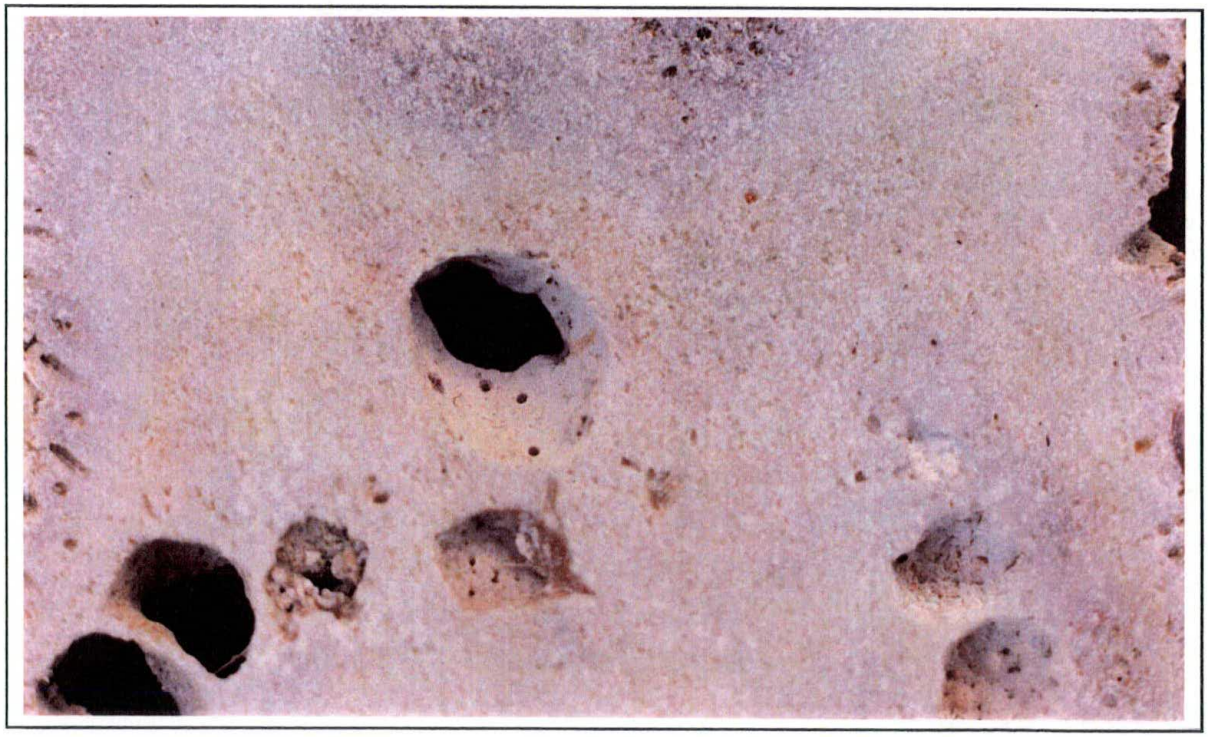


Figure 3.25: *Close-up of a section of* Acropora cuneata. *Notice the sponge perforations inside the large bivalve boring in the centre of the photograph.*

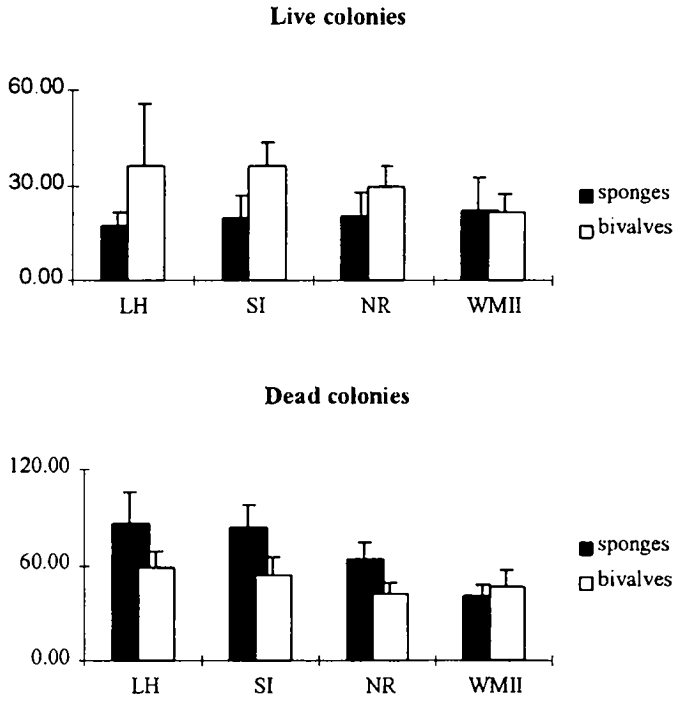


Figure 3.26: Means and Standard Errors of volume (mm^3) removed by sponges and bivalves per unit of surface area (cm^2), from living and dead colonies of A.cuneata. *Note: the two diagrams are not in the same scale.*

This habit of boring sponges to infest and enlarge relic bivalve borings and form 'composite borings', was previously documented by Scoffin and Garrett (1974). This suggests that live-coral borers may play an important role in providing microhabitats for other bioeroders. Also, the rate of bioerosion in coral colonies following death may be increased by the occurrence of live-coral borers in that species.

It is clear from this study that the major groups of borers display different patterns of distribution and responses to the colony features considered in this experiment. The present study, which focused on a single habitat, the reef crest, suggests that settlement of boring WORMS is relatively uniform at larger spatial scales such as locations (kilometres) and sites (hundred of meters). The majority of the variation occurs at scales of centimetres (within-colony) and a few meters (within-site). These results corroborate the suggestion by Hutchings and Murray (1982) that small-scale local disturbances (e.g. predation by grazers, occurrence of fish territories) are important in determining patterns of post-settlement survival of polychaetes. Hutchings (1985) found high levels of variability in recruitment of polychaetes at a scale of tens of centimetres and metres (adjacent grids). Similar patterns of variability have been demonstrated for

reef fish also, possibly due to very specific habitat requirements for settlement of many species (Doherty and Williams 1988). Factors responsible for patchy distribution of recruits are likely to include pre- and post-settlement processes. Hierarchical experiments with high replication at small spatial scales are required to determine whether the distribution of variability observed in this and the above mentioned studies is determined by post-settlement processes or reflects recruitment densities.

The finding that sponges caused the majority of internal bioerosion at all sites and in all coral species, parallels the situation described by several authors for both the Caribbean and the Pacific (Scoffin *et al.* 1980; Sammarco *et al.* 1987; Sammarco and Risk 1990) but it is in contrast to previous studies at Lizard Island. Davies and Hutchings (1983) and Kiene (1985) reported that in reef environments at Lizard Island, polychaetes dominate the boring communities during the initial period after the substrate becomes available. They found that in unbored coral blocks exposed for known time intervals to borers, sponges and bivalves became established only after 2-3 years. In their experiment the only mechanism of colonisation of the experimental substrate by borers was via recruitment of pelagic larvae, as the blocks were suspended on grids above the substrate. Some sponges observed in this study had almost certainly settled from larval stage (small sponge colonies adjacent to bivalve borings). However, it is suggested that the large extent of excavation by sponges in the present study after only 21 months was mostly due to the growth and movement (see Acker and Risk 1985) of sponges that were already present in the base of the colonies or in the adjacent reef matrix.

Freshly dead coral colonies would be readily invaded by sponge colonies which were previously restrained from excavating by the presence of living coral tissue. Few species of boring sponges can compete with living corals and outgrow them. Species belonging to the genus *Siphonodictyon* (fam. Adocidae) actively compete with corals by killing coral tissue around their protruding oscula (Rutzler 1971; Sullivan *et al.* 1983). Some *Cliona* spp. are known to occasionally overgrow corals with an encrusting (β form) or massive (γ form) growth (Hartman 1958; Rosell and Uriz 1992). This is the case in *C.viridis* on the Great Barrier Reef (Bergman 1983), although rarely encountered in this study, and more common in the related Caribbean species

C.caribbea (Acker and Risk 1985). However, apart from these few exceptions, the vast majority of boring sponges are unable to compete with corals. Their papillae cannot grow amid living polyps and this generally restricts their distribution to dead coral substrates. Although not as abundant as worms and bivalves, sponges are extremely destructive, and in several instances in this study a single sponge colony had bored through most of the coral colony (Figures 3.3 and 3.5). This suggests that bioerosion by sponges following the death of a coral colony depends less on availability of surface area and more on availability of volume, which may indicate that they do not settle but they move in from adjacent substrates. This is substantiated by previous studies in the same area, that found very little bioerosion by sponges in coral blocks which were set on a grid and were not in contact with the reef substrate (Davies and Hutchings 1983; Hutchings and Bamber 1985). Also, a recent preliminary study has shown that colonies of *Cliona* sp. from inner shelf habitats of the GBR, readily infested neighbour substrates in controlled aquarium experiments (Christine Schoenberg, AIMS, pers.comm.). The implication is that the extent and rate of sponge bioerosion in a coral colony may be controlled by the occurrence and extent of sponges in the adjacent reef substrates and the temporal dynamics of coral mortality.

Bioerosion by bivalves differed both among species and between the locations considered in this study. *A.cuneata* was significantly more bioeroded by bivalves than the other two species. However, this was due to the presence of large borings produced by *L.cf.lessepsiana* while the colonies were alive. Bioerosion by bivalves in *A.gemmifera* and *A.hyacinthus*, where most of the excavation by this group of borers occurred after death of the coral (Figure 3.23), did not differ in the two species. However, both species were significantly more eroded by bivalves at the SE location. During the study the species *Lithophaga lima, L.teres, L.hanleyana, L.malaccana* and one *Gastrochaena* sp. were identified from the experimental colonies. A finer taxonomic resolution may be necessary to reveal differences in the composition of molluscs boring within dead corals. Such differences in composition could explain the location effect observed. Alternatively, the pattern observed could result from differential growth rates and/or size structure of a same group of species at the two locations. However, in this study, borings by *L.cf.lessepsiana* in *A.cuneata* could not be

separated by borings by other bivalves. The lack of a location effect for bioerosion by bivalves in *A.cuneata,* and the low power to detect one, is probably due to the fact that in this species bioerosion by bivalves is dominated by the large *L.cf.lessepsiana* borings, which do not seem to be affected by location (see Chapter 2) and occur exclusively in living colonies. It is likely that the large effect of *L.cf.lessepsiana* overrides spatial patterns of other species of bivalves in *A.cuneata.*

There was a significant interaction between coral species and location for total bioerosion , as a result of *A.cuneata* being more extensively eroded at the SE sites. The effect for total bioerosion is likely to be due to the cumulative effect of bioerosion by sponges and bivalves, which are both higher, although not significantly, at the SE sites. The sum of the effects of both taxa is evident in *A.cuneata* due to the greater extent of excavation in this species. Hutchings and Bamber (1985) and Kiene (1985) suggested that patterns of internal bioerosion across reef environments cannot be detected before 3-4 years of exposure of the substrate to bioeroders, when the extent of excavation becomes considerable. The results of this experimental study suggest that this varies with the species of coral. *A.cuneata* was extensively eroded after only 21 months of exposure and it is possible that environmental patterns are already discernible, although analysis of individual taxa does not reveal a significant effect.

A consequence of the differential response of the taxonomic groups to colony parameters and spatial scales, is that total internal bioerosion does not appropriately represent the ecological patterns of boring organisms. Sammarco *et al.* (1987) found that total bioerosion displayed no clear patterns in response to different grazing pressure regimes and that data were highly variable, while definite patterns emerged when the major groups of borers were considered individually. In this study, total bioerosion varied with species, but did not display the spatial patterns evident when analysing the boring groups separately. In the same way, total bioerosion was not correlated to any of the coral colony features to which individual taxonomic groups showed differential responses. The extent to which an analysis of boring communities at a finer taxonomic level may resolve some of the large unexplained variation and reveal predictable ecological patterns is unknown.

3.4.2 Rates of bioerosion of $CaCO_3$ by borers

This study measured bioerosion in coral colonies following death. The observed bioerosion was due both to the growth and continued excavation of borers already present in the basal portion of the colony, and to the excavation of borers that settled on the surface of the colony following death. It is possible that this growth might have continued in the colonies even if they had not been killed. It is an assumption of this study that the difference in the extent of bioerosion between dead and living colonies is actually due to the death of the corals (see 3.2.6). However, this assumption is well supported by numerous previous studies that show that living coral tissue inhibits excavation of the underlying skeleton (MacGeachy and Stearn 1976; Highsmith 1981a; Hutchings 1986). Furthermore, for the three species used for the experiment, the sampling study described in Chapter 2 showed that excavation is concentrated in the dead basal area, with the exception of a live coral boring bivalve, which is found only in one of the three species.

This study has shown that within 21 months following the death of a coral colony on the reef crest, macroboring organisms can rework coral skeleton at a rate of up to 1038 $\pm$ 164 g $CaCO_3$ m^{-2} y^{-1}. The rates estimated from this study (Table 3.14) compare well to previous rates obtained from studies of internal bioerosion on both Pacific and Atlantic reefs (Scoffin *et al.* 1980; Hutchings and Bamber 1985; Hubbard *et al.* 1990; Hutchings *et al.* 1992; Table 3.15). Because these studies were conducted on a variety of carbonate substrates and reef environments, and used considerably different methods (from volume of borings to size of borers to sediment production; see Table 3.15), it may be said that rates ranging from 10^{-2} to 10^{3} g $CaCO_3$ m^{-2} y^{-1} are representative of internal bioerosion on modern coral reefs. Within this range, variation of one to two orders of magnitude was observed in this study among the most important groups of borers (several orders of magnitude when including the less important borers). Different substrates (in this case dead colonies of different species, but homogeneous in terms of duration of exposure to borers) displayed a range of rates of bioerosion that were generally within the same order of magnitude (the only exception being bivalves which spanned two orders of magnitude across the three species).

Type	Agent	Region/habitat	Rate	Method	Author
Overall erosion	-	Atlantic/exposed shore	0.45 mm y^{-1}	Surface lowering (micrometer)	Spencer 1985
"	-	Atlantic/protected shore	2.77 mm y^{-1}	"	"
Overall bioerosion	Sponges, scarids, echinoids	Atlantic	0.58-1.34 cm (?y^{-1})	Coral growth increments	Hudson 1977
"	Sponges, grazers	Atlantic/various	1.3 mm y^{-1}	Surface lowering	Bromley 1978
"	Borers, grazers	W.Pacific/reef slope	1.26-2.71 kg m^{-2} y^{-1} *1	Volume of borings	Kiene 1985
"	"	W.Pacific/reef flat	0.22-041 kg m^{-2} y^{-1} *1	"	"
"	"	W.Pacific/lagoon	0.44-1.95 kg m^{-2} y^{-1} *1	"	"
"	Borers, non-echinoids grazers	E.Pacific,Panama	23.84 g m^{-2} d^{-1}	Sediment production	Glynn 1988
"	"	E.Pacific,Galapagos	20.90 g m^{-2} d^{-1}	"	"
"	Borers, grazers	W. Pacific/reef slope	0.11-3.43 kg m^{-2} y^{-1} *2	Volume of bites and borings	Kiene 1988
"	"	W.Pacific/reef flat	0.71-1.71 kg m^{-2} y^{-1} *2	"	"
"	"	W.Pacific/lagoon	0.83-9.11 kg m^{-2} y^{-1} *2	"	"
External bioerosion	*Sparisoma viride*	Atlantic	40-168 g m^{-2} y^{-1}	Gut contents turnover	Frydl and Stearn 1978
"	Echinoids	Pacific	80-325 g m^{-2} y^{-1}	"	Russo 1980
"	*Diadema antillarum*	Atlantic	5.3±0.3 kg m^{-2} y^{-1}	"	Scoffin *et al.* 1980
"	*Sparisoma viride*	"	34±5 g m^{-2} y^{-1}	"	"
"	Echinoids	E.Pacific,Panama/upper reef slope	4.2 g m^{-2} d^{-1}	Sediment production	Glynn 1988
"	"	E.Pacific,Galapagos/ reef edge	16.2 g m^{-2} d^{-1}	"	"
"	Echinoids	Pacific	4.55 kg m^{-2} y^{-1}	Gut contents	Bak 1990
"	Echinoids	Atlantic	0.17 kg m^{-2} y^{-1}	Sediment production	Hubbard *et al.* 1990
"	Scarids	"	0.02 kg m^{-2} y^{-1}	"	"
"	Echinoids	Pacific	1.26 g m^{-2} d^{-1} *3	$CaCO_3$ dissolution	Le-Campion *et al.* 1993

Table 3.15: To be continued next page....

...*Continued from previous page*

Type	Agent	Region/habitat	Rate	Method	Author
Internal bioerosion	*Cliona lampa*	Atlantic/Bermuda	22-25 kg m^{-2} y^{-1}	-	Neumann 1966
"	Clionids	Atlantic	0.25-3 kg m^{-2} y^{-1}	-	Rutzler 1975
"	*Cliona peponaca*	Atlantic/Curaçao	2.5-3.3 kg m^{-2} y^{-1}	-	Bak 1976
"	Clionids	Atlantic/St.Croix	0.19-3.29 kg m^{-2} y^{-1}	Volume of borings	Moore and Shedd 1977
Internal bioerosion	Clionids	Atlantic/Jamaica	0.28-1.80 kg m^{-2} y^{-1}	Sedimentation of clionid silt	Moore and Shedd 1977
"	Macroborers	Atlantic	200±33 g m^{-2} y^{-1}	Volume of borings	Scoffin *et al.* 1980
"	Polychaetes	W.Pacific/reef front	0.69 kg m^{-2} y^{-1}	Volume of borers	Davies and Hutchings 1983
"	"	W.Pacific/reef flat	0.84 kg m^{-2} y^{-1}	Volume of borers	Davies and Hutchings 1983
"	"	W.Pacific/lagoon	1.78 kg m^{-2} y^{-1}	"	"
"	Polychaetes	W.Pacific	0.33-4.81 kg m^{-2} y^{-1} *4	"	Hutchings and Bamber 1985
"	*Cliona caribbea*	Atlantic	8 kg m^{-2} y^{-1}	Sponge growth rate	Acker and Risk 1985
"	*Lithotrya dorsalis*	Atlantic	2.72-5.11 kg m^{-2} y^{-1} *5	Volume of borings	Dineen 1990
"	*Tridacna crocea*	W.Pacific/leeward	140 g m^{-2} y^{-1}	Clam growth rate	Hamner and Jones 1976
"	Borers	Atlantic	0.05 kg m^{-2} y^{-1}	Sediment production	Hubbard *et al.* 1990

***Table 3.15:** Published rates of erosion by various agents in reef carbonate substrates.*

**1 The two rates reported were obtained in two different years.*

**2 The two rates reported here are the smallest and the largest of three rates obtained from three reefs.*

**3 The rate refers only to the dissolved calcium carbonate resulting from bioerosion by echinoids.*

**4 The two rates reported here are the smallest and the largest of the rates obtained at six sites.*

**5 The two rates reported refer to the smallest and the largest size class of Lithotrya dorsalis.*

Smaller variations, usually within the same order of magnitude, were observed for individual groups of borers at different sites and locations within a reef. This may be considered a descriptive model of natural variability in the rates of internal bioerosion for the substrates and location considered in the study.

When rates of excavation by individual groups of borers are compared among studies, there have been contradicting results. The present study showed that the rates of excavation by boring sponges ranged between 103.7 ± 36.4 to 766 ± 123 g $CaCO_3$ m^{-2} y^{-1}. Previously reported rates for boring sponges are much higher, ranging from 2.5-3.3 kg m^{-2} y^{-1} (Bak 1976) up to 25 kg m^{-2} y^{-1} (Nuemann 1966). Intermediate estimates include 8 kg m^{-2} y^{-1} (Acker and Risk 1985) and 3-13.4 kg m^{-2} y^{-1} (Hudson 1977, as calculated by Davies, 1983). Some of these studies however measured the 'potential' rates of bioerosion, by calculating unrestricted growth rates of the sponges, rather than actual rates. Actual rates must consider not only the abundance of the sponges on the reef, but also the fact that boring activity may be limited by the type of substrate and other controlling factors. Thus, estimates based on unrestrained growth are likely to substantially overestimate actual rates of erosion by sponges. Rutzler (1975) combined laboratory experiments with measurements of sponge biomass in the field and concluded that in Bermuda rates of bioerosion by sponges were approximately 256 g m^{-2} y^{-1}. The present study, using freshly killed coral *in situ*, provides rates that are representative of actual sponge bioerosion. Recently Kiene and Hutchings (1992) reported a maximum sponge bioerosion rate of 140 ± 10 g m^{-2} y^{-1} from the deep leeward site at Lizard Island over a 9 year period. This value is slightly lower than the rates found during the present study. However, Kiene and Hutchings (1992) used blocks of coral substrate that are limited in the amount of excavation they can experience. Over a 9 year period, this may lead to a saturation effect and ultimately to an underestimate of the bioerosion rates (see also Chapter 5). This is supported by the limiting effect of colony volume on sponge bioerosion as observed by this study (Table 3.4).

The estimated rates of bioerosion by worms (which in this study were represented mostly by polychaetes) were relatively uniform across the three coral substrates studied and the spatial scales investigated. Values ranging from 45.4 ± 5.6 and 65.9 ± 6.5 g

$CaCO_3$ $m^{-2}y^{-1}$ are much lower than those found by Davies and Hutchings (1983) on six environments at Lizard Island and calculated over a similar time frame (18 months). In fact, using the volume of the organisms extracted from coral blocks, they estimated rates that varied among environments, and ranged between 694 and 1788 g m^{-2} y^{-1} at the reef front and lagoonal patch reef, respectively. Hutchings and Bamber (1985) reported even higher rates of polychaete bioerosion of up to 4.8 ± 1.6 kg m^{-2} y^{-1} at the leeward site. The significance of the discrepancy between previous studies and the present one is difficult to evaluate. Davies and Hutchings (1983) used two replicates per site while Hutchings and Bamber (1985) did not provide the sample size used. Neither of these studies, included replication within sites, which also makes it impossible to interpret their results in terms of habitat related patterns of bioerosion. Kiene and Hutchings (1992), in reporting the long term results of the Lizard Island experiment, estimated rates of bioerosion by worms which compare very well to the ones found during this study (from 20 ± 10 g m^{-2} y^{-1} on the patch reef to 70 ± 10 g m^{-2} y^{-1} on the deep leeward site; Kiene and Hutchigns 1992). Contrary to the method employed by Davies and Hutchings (1983) and Hutchings and Bamber (1985), Kiene and Hutchings (1992) estimated internal bioerosion from the volume excavated by borers.

The method employed to measure internal bioerosion in this study does not take into account the borings in the portions of the colony that have been removed by external erosion (biological or other). However, this bias is likely to be small. In fact, as shown in Chapter 4, external erosion was high only for *A.hyacinthus*, and the most of it occurred soon after death of the coral, which would not have allowed much time for the borers to settle and excavate. The rates reported in Table 3.13 have been estimated from point estimates of bioerosion following a period of 21 month exposure. As demonstrated by previous authors there is a considerable variability in time of bioerosion rates (Hutchings and Bamber 1985; Hutchings et al. 1992; see also this study, Chapter 5). No allowance for temporal variation of the rates is made in this study, nor for inter-year variations in the recruitment of borers, which has been reported to be high (Davies and Hutchings 1983; Hutchings and Murray 1985). Therefore caution should be taken when considering these estimates in larger temporal frames.

3.4.3 Conclusions

The marked differences in rates of bioerosion among the coral species highlights the need for studies on bioerosion to include a wide range of *in situ* coral substrates and suggest that overall reef bioerosion may be influenced to a large extent by the population dynamics and community structure of corals. In situations of coral mass mortality where colonies are left standing *in situ*, e.g. following Crown-of-Thorns outbreaks, coral species will contribute differently to the reef degradation and sediment production. Coral community composition should be considered also in the context of specific relationships between certain coral species and live coral borers. Not only such relationships are important for the population dynamics of the coral species involved (through enhancing fragmentation and possibly mortality rates), but this study suggests that they also may be increasing considerably the extent of bioerosion of the colonies following death, by providing microhabitats that are suitable for settlement of boring sponges.

The results from this study emphasise the importance of small spatial scales for reef internal bioerosion. Internal bioerosion is a patchy process, its patchiness being determined both by the dynamics of mortality of coral colonies, and by the population dynamics of borers. Recruitment rates, reproductive strategies and dispersal modes appear to differ widely among the three most important groups of borers, as indicated by the spatial patterns and responses to substrate parameters of borers observed in this study. However, very little is known of the population dynamics of boring organisms. I suggest that a priority area of study for bioerosion research should concern the life history of individual important and common borers.

Chapter 4

External degradation in coral colonies of three *Acropora* species following death

4.1 Introduction

Standing dead coral skeletons on the reef surface are subjected to several processes of external degradation. They are broken down by the activity of grazing fishes and echinoderms which feed on their algae-covered surfaces and, at the same time, are excavated and weakened by boring organisms which settle on them or which are already in the skeleton at the time of death. Aside from biological destruction, colonies on the reef crest are eroded by physical agents such as water turbulence, breaking waves and other forms of mechanical abrasion.

Few workers have assessed the relative importance of physical and biological erosion in the reworking of coral reef substrates. Spencer (1985) and Trudgill (1976) established that, in non cyclonic conditions, biological erosion on a reef is greater than physical erosion by wave impact and mechanical abrasion. However, according to Spencer (1985), the relative importance of the two processes will vary within a reef, depending on the extent of exposure and the intensity of wave energy.

On the Great Barrier Reef, external bioerosion is predominantly due to the grazing activity of fish in the family Scaridae (Kiene 1988; Bellwood and Choat 1990). This contrasts to Eastern Pacific and Caribbean reefs, where grazing by echinoderms constitutes the major component of external bioerosion (Glynn 1988; Sammarco 1987; Bak 1990). Scoffin *et al.* (1980) found that sea urchins, and in particular *Diadema antillarum,* were responsible for reworking 5.3 ± 0.3 kg $CaCO_3$ $m^{-2}y^{-1}$, while, from the same area, scarids removed only 34 ± 5 g $m^{-2}y^{-1}$. Frydl and Stearn (1978) report comparable rates of up to 168 g $CaCO_3$ $m^{-2}y^{-1}$, from the gut contents of *Sparisoma viride*, one of the few scarids in the Caribbean to be able of excavating the substrate on which it grazes (Bellwood and Choat 1990). In the Western Pacific however, the relative importance of different agents of external bioerosion appears to be different, mainly due to the low densities of echinoids (Sammarco 1987; Sammarco *et al.* 1987), and the presence of many large species of functionally excavating scarids (Bellwood and Choat 1990).

On the Great Barrier Reef, erosion by scarids appears also to be quantitatively more important than bioerosion by boring organisms (Kiene 1988). Sammarco *et al.* (1986) found that dead colonies of the encrusting plate coral *Pachyseris speciosa*, were eroded down to 40-50% of their initial surface area after 18-24 months of exposure, and they attributed this degradation to scarids. In view of these findings, it is apparent that when studying bioerosion on coral reef it is essential to include the role of external bioeroders, such as scarids, in order to understand the relative importance of the different categories of bioerosion.

The external degradation to which standing coral skeletons are subject, not only results in the turn-over of the carbonate components, but it is also accompanied by a decrease in the structural complexity of the reef surface. Both physical erosion and erosion by scarids decrease the overall structural complexity of the reef surface. Scarids seem to preferentially graze on convex substrates which would result in an overall reduction in rugosity of the reef surface (Bellwood and Choat 1990). Presently it is not know how rapidly this process occurs or what environmental factors may affect it. Structural complexity of the reef surface is believed to be of fundamental importance to many ecological processes and groups (Moran and Reaka 1988; Sano *et al.* 1984; Kaufman and Ebersole 1984). Consequently, knowledge of the dynamics of the processes which affect structural complexity will increase our understanding of the reef ecological structure.

This chapter reports on the rates at which the skeletons of three species of *Acropora* corals are degraded by external biotic or abiotic erosive agents following death of a colony. Preliminary results of this study, after nine months of exposure, have been presented previously (Musso 1992, appendix B). In this chapter the results are extended to 21 months of monitoring, which include two additional surveys. Furthermore, data from the photographic monitoring of the colonies have been integrated with data on changes in colony rugosity over the same period of time. This provides an estimate of the decrease in structural complexity following death of three common coral species. Thus the effect of coral species, site and location on colony rugosity is examined also.

4.2 Methods

4.2.1 Sampling sites and sampling design

This study used of the same experimental setup as described in Chapter 3. For a description of the study sites and materials see 3.2.1 and 3.2.2. The design follows a three-way, mixed model, nested ANOVA, with species and location as crossed, fixed factors, and site (three sites per location) as a random factor nested within location, and 10 colonies per species at each site.

4.2.2 Monitoring procedure

The experimental colonies were photographed with a Nikonos camera fitted with a 35 mm lens, before, immediately after death, and at 3 monthly intervals for a period of 21 months. Table 4.1 provides the dates of the photographic sampling. Data from censuses 2 and 5 were not used in the analysis due to the poor quality of some of the slides.

Colonies were photographed from above at a distance of approximately 1 m. A 35 cm long bar was held close to the colony by a diver to provide a scale (Figure 4.1). It was no possible to use a rigid frame to ensure consistency of focal distance and angle, because of the difficulty of handling such equipment in high wave-energy environments.

The slides of the colonies obtained from the censuses were projected onto a digitising tablet and the outline of the colonies was digitised to obtain an estimate of the planimetric area. The use of the term 'planimetric area' is here emphasised, to avoid confusion with the term 'surface area' (total, living, dead, exposed), which is used in the previous and the following Chapters to indicate the coral colony surface area. An estimate of the precision, which includes precision of the technique for variation of parallax among censuses and precision of the digitising technique, was made by comparing the measurements of the areas of 5 colonies per species from 4 replicate photos of each colony. Precision was estimated as the mean coefficient of variation of the measurements for each species (Table 4.2). It estimates the minimum percent change in planimetric area of the colony which can be detected.

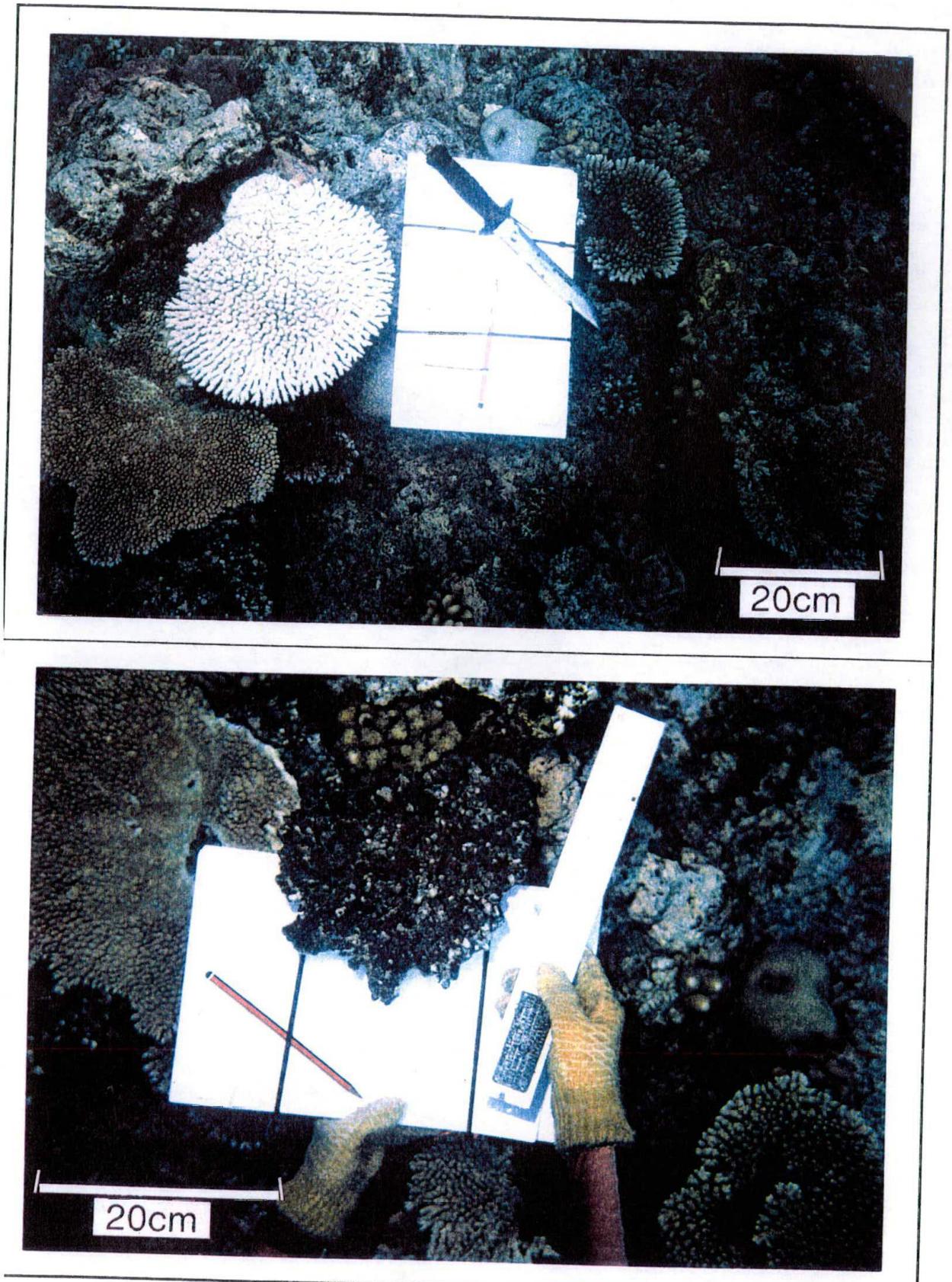


Figure 4.1: *A colony of* Acropora hyacinthus *photographed immediately following death (February 1991) and after 34 weeks exposure to external degradation agents (November 1991)*

Photographic survey	1	*2*	3	4	*5*	6
Date	May 91	*Jul 91*	Nov 91	Feb 92	*Jul 92*	Nov 92
Duration of exposure	11	*21*	34	52	*75*	90

Table 4.1: *Schedule of the photographic surveys of the experimental colonies killed in situ in February 1991. Data from censuses 2 and 5 could not be used in the analysis.*

A.hyacinthus	*A.gemmifera*	*A.cuneata*
4.56	5.40	5.76
(1.01)	*(0.74)*	*(0.63)*

Table 4.2: *Coefficients of variation of the measurement of colony size taken from 4 photos of 5 colonies for each species (Standard errors in brackets).*

4.2.3 Converting planimetric areas into $CaCO_3$ weight

To convert observed changes in planimetric area in *A. hyacinthus* into changes in weight of calcium carbonate, 20 recently dead colonies were photographed before and after removing the margins of the plate. Fragments were removed, collected and taken back to the laboratory, where they were bleached in order to remove epiphytes and encrusting organisms, dried for 24 hours at 80o C, and weighed. A linear regression of planimetric area on weight was estimated (viz. $W=axSA_p$; Equation 4.1, where 'a' is the regression coefficient and Sa_p is the planimetric area). Skeletal density was estimated as described in 2.2.3 (Table 4.3)

	A.hyacinthus	*A.gemmifera*	*A.cuneata*
Skeletal density	1.50 ± 0.10	1.88 ± 0.08	2.03 ± 0.12
Sample size	*10*	*10*	*10*

Table 4.3: *Skeletal bulk densities (g x cm^{-3}) of the three coral species* Acropora hyacinthus, A.gemmifera *and* A.cuneata *(errors are Standard Errors).*

Rates of loss of calcium carbonate from colonies of *A.hyacinthus* for each census for each site, were estimated using the following equation obtained from equation 4.1,

$$W_{ki} = a\, x \Sigma_{jk} (A_{j0} - A_{ji})/n_k \qquad \text{(Equation 4.2)}$$

where W_{ki} is the weight of $CaCO_3$ lost per colony at site k and at census i; A_{j0} is the initial (at census 0) planimetric area of colony j at site k and A_{ji} was the planimetric area of the same colony at census 1 and n_k is the number of colonies at each site. Equation 4.2 provides an estimate of $CaCO_3$ removed per colony. In order to express the rate of loss of $CaCO_3$ as grams per unit of surface area, the weight of $CaCO_3$ lost per colony was divided by the mean initial colony area. This was converted to an

annual rate by dividing by the number of weeks of exposure and multiplying by 52. An estimate of grams of $CaCO_3$ lost per m^2 per year was obtained after each census.

4.2.4 Data analysis

Data relative to changes in size were expressed both as absolute change in planimetric area (mm^2) and percent of the initial colony area removed at each census. Data for *A.gemmifera* and *A.cuneata* were from 2 censuses only (34 and 90 weeks), while data for *A.hyacinthus* were from four censuses (11, 34, 52 and 90 weeks). Data were tested for univariate and multivariate normality respectively with D'Agostino's test and graphical methods.

Data from all three species at 34 and 90 weeks were analysed with a Repeated Measures Multivariate ANOVA to account for the non-independence of observations on the same experimental units over time. Main effects included in the analysis were time (2 levels), species (3 levels), location (2 levels) and site as nested within location (3 levels per location). Interaction effects included the interaction between species and location and between species and site. Data were tested for homogeneity of variance-covariance matrices using Levene's test. None of the three species at 34 and 90 weeks had homogeneous variance-covariance matrices, either when untransformed or following angular transformation. To increase robustness of the multivariate test, equal numbers of replicates were obtained by randomly eliminating experimental units from the analysis. Balanced data displayed slight heterogeneity of variance-covariance matrices (Pillai's Trace=0.88; $F_{4,162}$=2.49, p=0.045). However robustness of the test was ensured by 1) equal number of replicates; 2) low number of variables (DVs=2) and 3) use of Pillai's Trace to assess significance of effects. Univariate ANOVAs were used to determine the contribution of the individual censuses to the effects observed. *A posteriori* comparisons of effect levels were done using Tukey's test.

Data relative to four censuses for *A.hyacinthus* were analysed with Repeated Measures MANOVA which included the factor time (with 4 levels: 11, 34, 52 and 90 weeks), and the factor location with site nested in location. Untransformed data from each of the four variables (percent size decrease at each census) were normal and homoscedastic when grouped in treatments. Untransformed data of the four variables

were multivariate normal and displayed homogeneity of variance-covariance matrices (Levene's test; Pillai's Trace for site effect=0.294, $F_{16,148}$=0.735, p=0.754).

Rugosity index in this study is the colony surface area to volume ratio (see 2.2.3). Rugosity indexes were measured in living colonies (Chapter 2) and in the dead colonies exposed for 21 months (Chapter 3). Living and dead colonies constituted the two levels of the factor 'colony status'. The changes in rugosity index following death and exposure to erosive agents were analysed with a 4-way, mixed model nested ANOVA, with factors colony status (2 levels), species (3 levels) and location (2 levels) being orthogonal and site being nested within location, with 3 sites per location.

4.3 Results

4.3.1 Size changes over time following death - Species comparison

The initial colony sizes did not differ within species across sites or locations (location F_s=0.02; $F_{0.05;1,4}$=7.71, p=0.89; site F_s=1.64; $F_{0.05,4,106}$=2.50, p=0.17). However, as expected, mean size of the experimental colonies of *A.hyacinthus* and *A.gemmifera* decreased with time since death (Table 4.4; Figure 4.2).

		t_0-t_1 (11 weeks)	t_0-t_3 (34 weeks)	t_0-t_4 (52 weeks)	t_0-t_6 (90 weeks)
A.hyacinthus	Mean	35.97	47.42	63.69	72.07
	SE	2.14	2.58	2.78	2.56
	n	43	43	43	43
A.gemmifera	Mean	4.72	6.06	7.37	13.30
	SE	2.79	1.92	3.06	3.16
	n	26	46	23	46
A.cuneata	Mean	-1.89	-0.08	3.65	0.15
	SE	4.65	1.06	5.56	3.82
	n	22	35	27	35

Table 4.4: Means, Standard Errors and sample sizes of the percent decrease in colony planimetric area for the three coral species. Data were pooled across sites and locations.

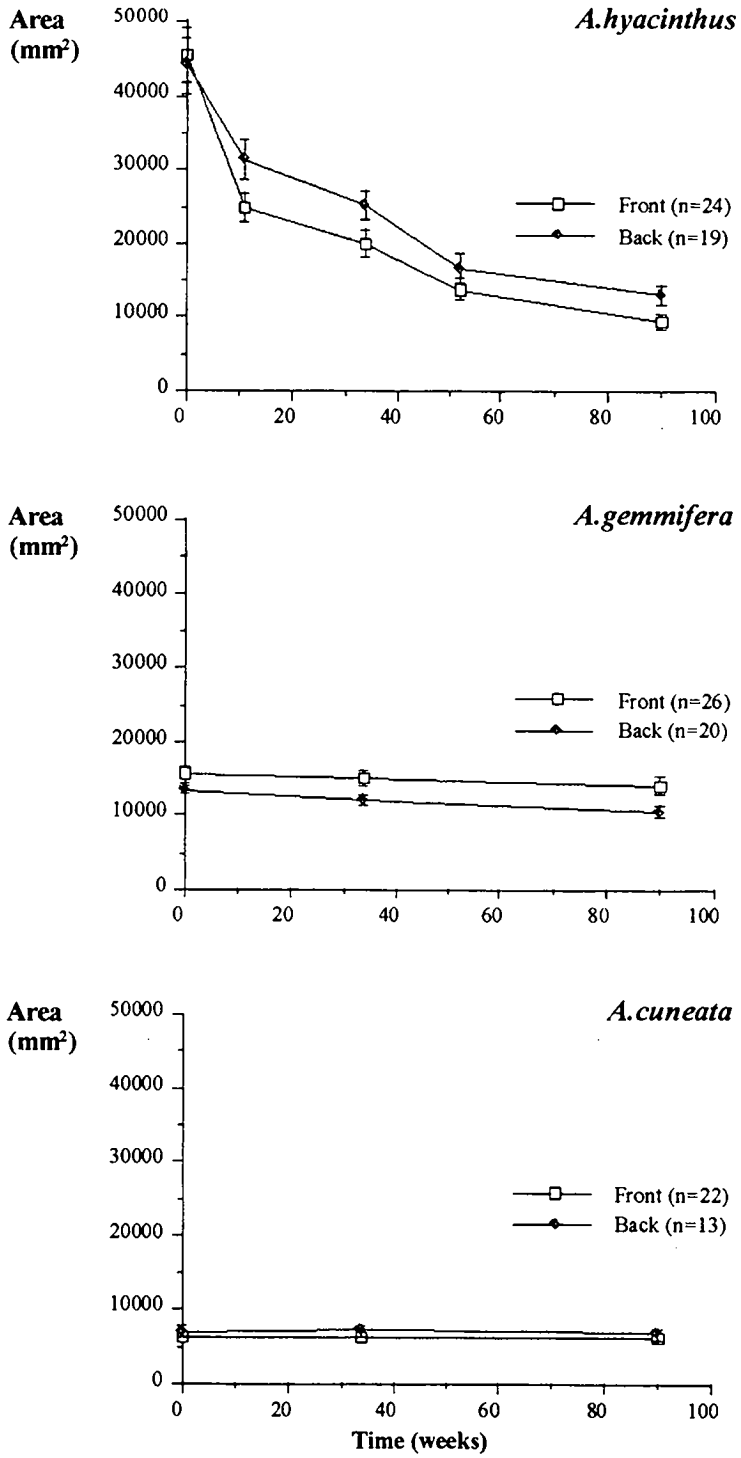


Figure 4.2: Mean planimetric area of colonies killed in situ at the two locations, measured after 11, 34, 52 and 90 weeks following death for A.hyacinthus, *and 34 and 90 weeks for* A.gemmifera *and* A.cuneata. *Error bars are standard errors.*

The mean size of colonies of *A.cuneata* did show random change (Tables 4.2 and 4.4), with the mean percent change in size being not larger than the minimum detectable

change (see 4.2.2) at any one census. For *A.gemmifera* the percent decrease in size was smaller than the minimum detectable size difference only after 11 weeks (Tables 4.2, 4.4).

Time had a highly significant effect on on the percent decrease in area of the individual colonies, from time 0, after 34 and 90 weeks (Pillai's Trace=0.388; $F_{1,72}$= 45.65, p=0.0001) (Table A33). The interaction between time and species was significant also (Pillai's Trace=0.262; $F_{2,72}$=12.84, p=0.0001), indicating that the three species were subject to differential rates of degradation (Figure 4.3). A significant interaction among time, species and site (Pillai's Trace=0.217; $F_{8,72}$=2.49, p=0.018) indicated that the rates of degradation were different for the three species at different sites.

Both species and location significantly affected the size decrease of the colonies (F_s=72.78; $F_{0.05,2,8}$=4.46, p<0.01 and F_s=7.74; $F_{0.05,1,4}$=7.71, p<0.05 respectively; Table A34). The percent size decrease was significantly different among the species after both periods (Tables A35 and A36). However, after 34 weeks only *A.hyacinthus* was different from the other two species at a α=0.05. With increasing time (90 weeks) the difference between *A.gemmifera* and *A.cuneata* also became significant (Tukey test, α=0.05, df=72). In contrast, location effect was significant only after 90 weeks (F_s=8.06; $F_{0.05,1,4}$=7.71, p=0.04), although the F value after 34 weeks was relatively high (F_s=4.71; $F_{0.05,1,4}$=7.71, p=0.09). The location effect was due to the percent decrease in size of the experimental colonies of *A.hyacinthus* being higher at the SE sites (Figures 4.2 and 4.3).

4.3.2 Size changes in A.hyacinthus

A.hyacinthus colonies decreased rapidly in size following death. After ninety weeks of exposure to eroding agents, colonies with an initial mean size of approximately 560 cm^2 were reduced of an average 444 cm^2, at the site that experienced the greatest erosion rates (Table 4.5; Figure 4.1).

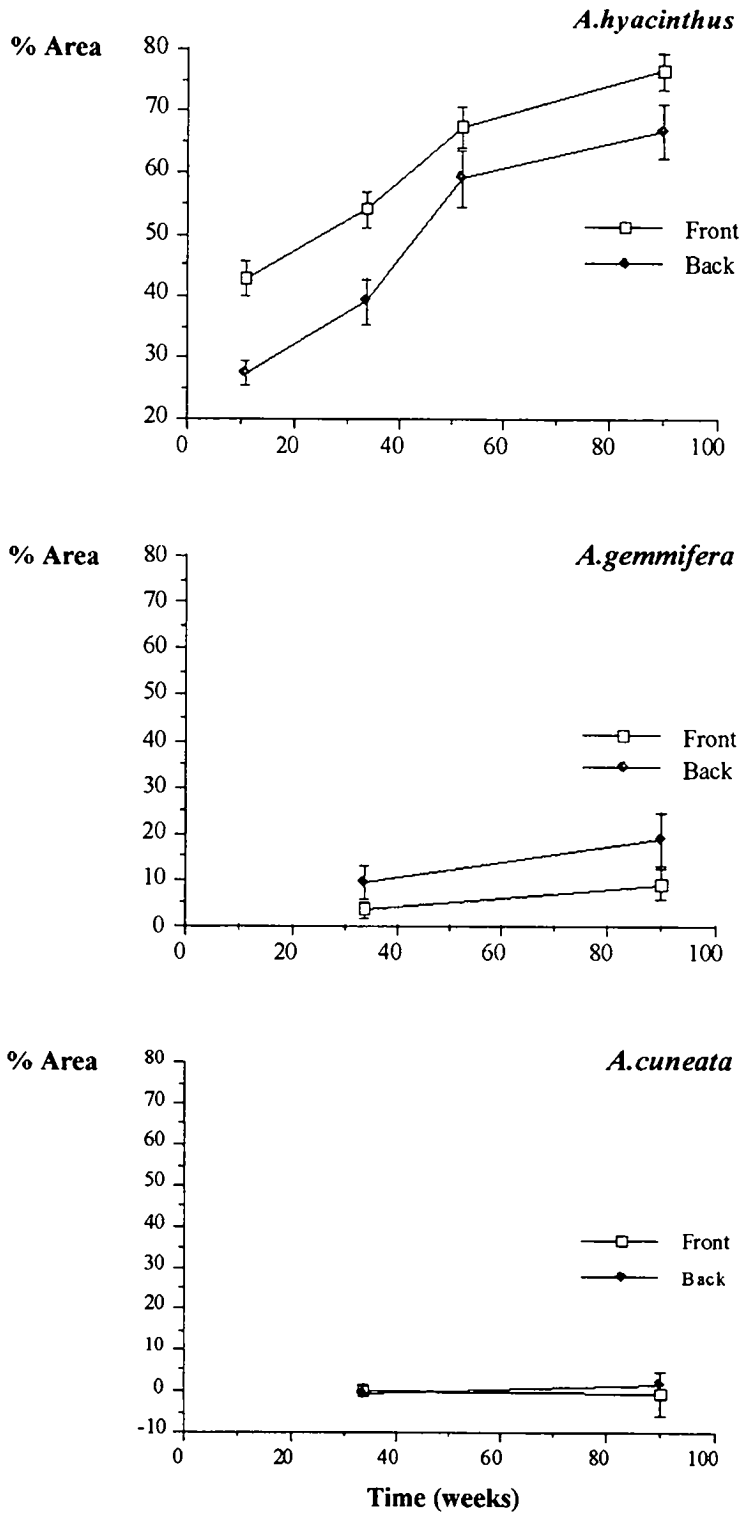


Figure 4.3: Mean percent of planimetric surface area removed per colony from colonies killed in situ at the two locations; measured after 11, 34, 52 and 90 weeks following death for A.hyacinthus, *and 34 and 90 weeks for* A.gemmifera *and* A.cuneata.

Site	Initial size	11 weeks	34 weeks	52 weeks	90 weeks
BI (10)	55968.52	27872.23	31570.16	41735.98	44355.96
	3634.3	*2716.43*	*1853.87*	*4070.95*	*4162.44*
LH (8)	39087.17	15465.57	20620.34	22526.54	32188.13
	4680.1	*2889.2*	*4464.96*	*4203.06*	*4898.91*
SI (6)	36246.59	14975.22	21204.68	26540.14	26724.39
	9656.52	*5655.19*	*7116.37*	*8058.82*	*8106.92*
NR (8)	39578.4	12424.41	15410.44	27113.63	27642.96
	4788.5	*2857.56*	*3429.39*	*4129.92*	*4371.26*
WMI (7)	49914.08	15095.57	25381.16	30274.96	37161.16
	6092.09	*3551.9*	*5378.67*	*6831.89*	*7088.39*
WMII (5)	42295.2	8949.16	13824.6	22229.66	26554.93
	11430.3	*2646.32*	*7677.85*	*9733.64*	*9808.87*

Table 4.5: Means (mm^2), standard errors and sample size of initail colony planimetric area and planimetric area lost from A.hyacinthus *colonies at each census from the six sites.*

Time and the interaction between time and site were significant for both absolute and relative change (Tables A37 and A38), indicating that different rates of degradation occurred at different sites. None of the between-subject effects was significant (Tables A39 and A40). Location and site accounted for 21.8% and 13.7% respectively of the total between-subject variability for data expressed as percent decrease in size. The within-subjects comparison did not show a significant interaction between time and site (Tables A41 and A42). The effect of site was large although not significant at the first and third censuses (11 and 52 weeks), which probably determined the significant interaction between site and time (Table A43).

The size decrease expressed as percent loss had a high, but not significant, effect of location, with colonies at the SE sites shrinking more than at NE sites (Table A40). The effect of location was larger at the beginning of the experiment (11 and 34 weeks), but became small at the later censuses (52 and 90 weeks; Table 4.1), determining the lack of effect for location in the Repeated Measures MANOVAs (Tables A39 and A40). After the first census the difference in the percent shrinkage between SE and NE sites was more than 15% (Table 4.6) *A.hyacinthus* colonies decreased down to almost 75% of their initial size during the course of the experiment (Tables 4.4 and 4.7).

	Lower 95 % C.L.	Mean	Upper 95% C.L.
t_0-t_1 (11 weeks)	*8.26*	15.29	*22.31*
t_0-t_3 (34 weeks)	*5.67*	14.85	*24.03*
t_0-t_4 (52 weeks)	*-2.15*	8.26	*18.65*
t_0-t_6 (90 weeks)	*-0.28*	9.82	*19.92*

Table 4.6: Mean differences of percent decrease in colony size for A.hyacinthus *between SE and NE sites.*

	t_0-t_1 (11weeks)	t_0-t_3 (34 weeks)	t_0-t_4 (52 weeks)	t_0-t_6 (90 weeks)
Mean	35.97	47.42	63.69	72.07
Standard Error	*1.72*	*2.25*	*2.54*	*2.47*

Table 4.7: Mean values and standard errors of the percent decrease in size of the experimental colonies of A.hyacinthus *at each census. Sample size is n=43.*

4.3.3 Decrease in rugosity following death and after 21 months exposure

Living colonies of all three species had significantly higher mean values of rugosity index (2.2.3) than dead colonies (F_s=30.28; $F_{0.05;1,2}$=18.51, p=0.03; Tables A44 and 4.8; Figure 4.4). Rugosity index was also significantly different among species (F_s=37.67; $F_{0.05;2,4}$=6.94, p=0.003), with *A.hyacinthus* having a significantly higher rugosity index than either *A.gemmifera* and *A.cuneata* (Tukey test; α=0.05 df=160).

	Location		*A.hyacinthus*	*A.gemmifera*	*A.cuneata*
Alive					
	SE sites	Mean	0.317	0.133	0.107
		SE	*0.059*	*0.005*	*0.007*
		n	*17*	*14*	*13*
	NE sites	Mean	0.254	0.128	0.113
		SE	*0.018*	*0.006*	*0.009*
		n	*16*	*13*	*15*
Dead					
	SE sites	Mean	0.102	0.090	0.064
		SE	*0.006*	*0.005*	*0.005*
		n	*17*	*16*	*11*
	NE sites	Mean	0.112	0.077	0.062
		SE	*0.005*	*0.004*	*0.003*
		n	*17*	*17*	*18*

Table 4.8: Means, standard errors and sample sizes of rugosity index in living and dead colonies of the three species at the two locations.

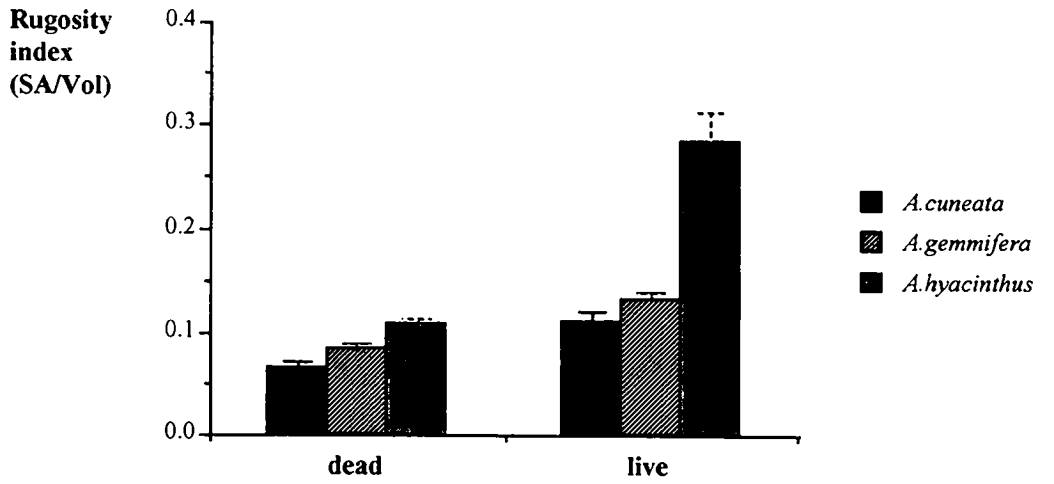


Figure 4.4: Untransformed rugosity index (ratio of colony surface area to colony volume) for living colonies and colonies killed in situ and left exposed for 21 months for A.hyacinthus, A.gemmifera *and* A.cuneata.

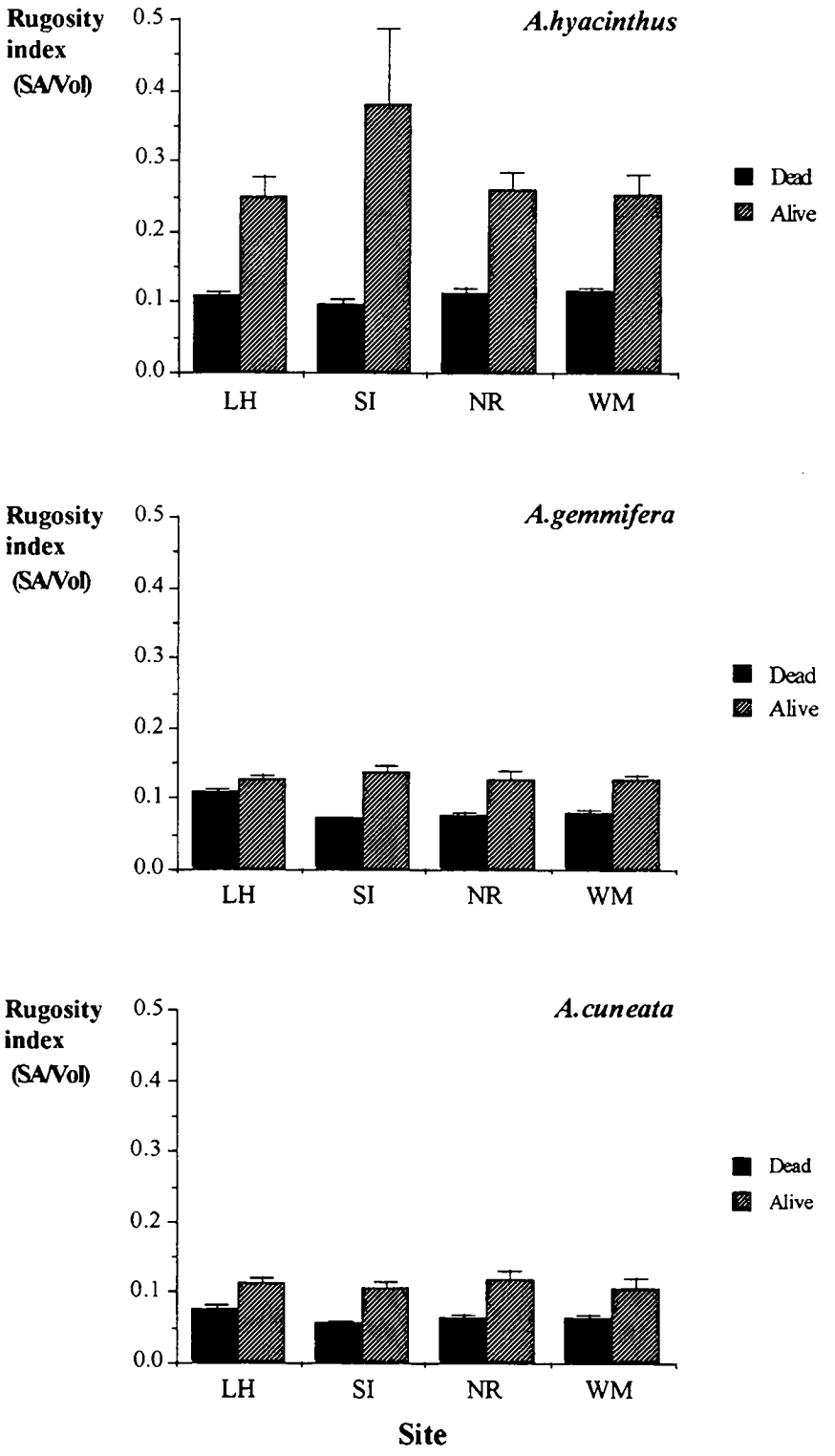


Figure 4.5: Untransformed rugosity index (ratio of colony surface area to colony volume) for living colonies and colonies killed in situ and left exposed for 21 months for A.hyacinthus, A.gemmifera *and* A.cuneata *at Lizard Head (LH), South Island (SI), North Reef (NR) and Washing Machine (WM).*

A.gemmifera and *A.cuneata* did not differ significantly in their rugosity indexes. The extent of the difference in rugosity index between living and dead colonies depended on the coral species (F_s=22.2; $F_{0.05;2,4}$=6.94, p=0.007; Table A44). This is evident from Figure 4.5 also, where the difference in rugosity index between living and dead colonies is much larger for *A.hyacinthus*. No effect of site or location was detected by the test or evident in the histograms for the individual species (Figure 4.5). Colony status and species accounted for 20.7% and 21.5% of the total variability in the data. Within-cell variation represented the 42.4% of the total variance (Table A44).

4.3.4 Rates of loss of $CaCO_3$ in A.hyacinthus

Planimetric surface areas and dry weight of the margins of recently dead plates of *A. hyacinthus*, were significantly correlated (r=0.81, 95% confidence limits: 0.57 and 0.92; n=20). The linear relation

$$W = (0.0136 \pm 0.001) \times SA \qquad \text{(Equation 4.3)}$$

was obtained by regressing the weight (=W) on the surface area (=SA; b'=0.01365, 95% confidence limits: 0.012 and 0.015; Bartlett's three groups method for Model II regression; Figure 4.6). Equation 4.3 was applied to the mean changes in surface area in colonies of *A.hyacinthus* (Table 4.5) in order to obtain estimates of weigth of $CaCO_3$ lost from the colonies over the period of the experiment for each site (Table 4.9).

Site	11 weeks	34 weeks	52 weeks	90 weeks
BI	379.06	429.35	567.60	603.24
	27.87	*31.57*	*41.73*	*44.35*
LH	210.33	280.43	306.36	437.75
	15.46	*20.62*	*22.52*	*32.18*
SI	203.66	288.38	360.94	363.45
	14.97	*21.20*	*26.54*	*26.72*
NR	168.97	209.58	368.74	375.94
	12.42	*15.41*	*27.11*	*27.64*
WMI	205.29	345.18	411.73	505.39
	15.09	*25.38*	*30.27*	*37.16*
WMII	121.70	188.01	302.32	361.14
	8.94	*13.82*	*22.22*	*26.55*

Table 4.9: Grams of calcium carbonate removed per colony in A.hyacinthus *at the six sites after each census. Stamdard Errors are in italics.*

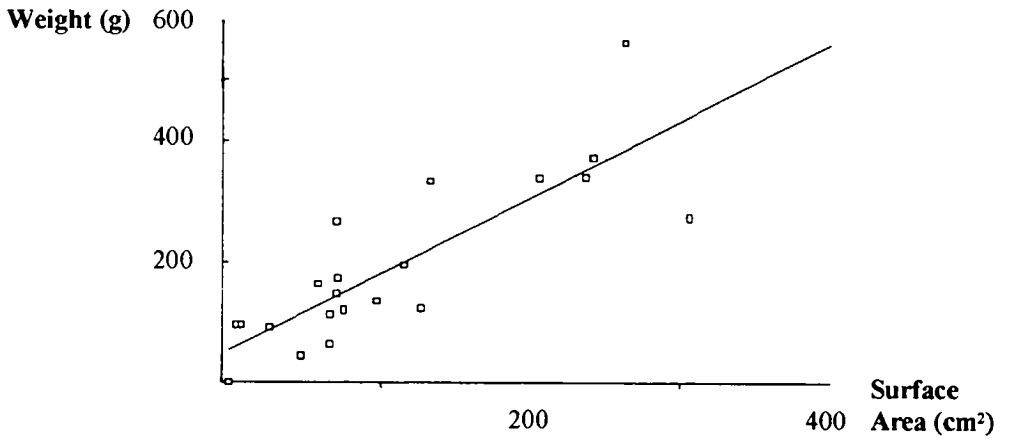


Figure 4.6: Regression of weight of $CaCO_3$ against colony surface area for A.hyacinthus *(r^2=0.687, n=20).*

Given the significant effect of location on skeletal degradation of *A.hyacinthus*, separate estimates of size decrease for each location were obtained (Table 4.10) by pooling the sites within location and considering mean colony area lost at each census. Instantaneous rates for each census are presented in Table 4.11.

	11 weeks	34 weeks	52 weeks	90 weeks
SE sites	20512.42	25328.85	31533.87	35892.12
	2339.17	*2558.71*	*3369.90*	*3352.85*
NE sites	12676.89	18750.00	27250.13	30920.61
	1798.91	*2918.62*	*3417.98*	*3634.89*

Table 4.10: Means and standard errors of the planimetric area (mm^2) lost per colony of A.hyacinthus *from the two locations.*

The rates of degradation decreased considerably with time at both locations, with the rates at first census (11 weeks) being 5 and 3 times higher than the last census (90 weeks) at the SE and NE locations respectively (Table 4.11).

	11 weeks	34 weeks	52 weeks	90 weeks
SE sites	29040.64	11601.62	9443.99	6210.67
	9609.54	*3838.97*	*3125.01*	*2055.11*
NE sites	17947.42	8588.24	8161.07	5350.41
	5938.80	*2841.84*	*2700.49*	*1770.45*

Table 4.11: Instantaneous rates of loss of $CaCO_3$ due to degradation of A.hyacinthus *colonies at each census. Rates are expressed as grams of $CaCO_3$ lost per unit of surface area (m^2) per year.*

After 90 weeks of exposure the rates of degradation for SE and NE sites were 6.2 and 5.4 kg of $CaCO_3$ m^{-2} y^{-1}, respectively. These rates refer to a m^2 with 100% cover of *A.hyacinthus*. The estimated percent cover of *A.hyacinthus* at the study sites is 19.3 ±

2.2 (S.E.) at the SE location and 7.6 ± 4.5 (S.E.) at the NE location (data from SI and WM sites respectively, obtained with 5 X 10m line transects, V.Nelson, unpubl. data). This yields potential rates for Lizard Island up to 1.19 and 0.41 kg of $CaCO_3$ lost per m^2 of reef surface per year at the SE and the NE sites respectively due to external degradation of dead colonies of *A.hyacinthus*.

4.4 Discussion

This study has shown that 1) both colony size and rugosity significantly decrease over time following the death of the coral. 2) The decrease in both size and rugosity varies considerably among the three species (*Acropora hyacinthus, A.gemmifera* and *A.cuneata*). 3) Rapid skeletal degradation occurs soon after death in plate colonies of *A.hyacinthus*. 4) The rate of external degradation in *A.hyacinthus* is not constant over time, being highest in the period soon after the death of the colony. 5) Rates of external degradation in *A.hyacinthus* differed between locations, possibly due to differences in wave energy, and this effect tends to decrease with time. 6) The external erosion of colonies of *A.hyacinthus* killed and left standing contributed a total of 0.41 and 1.19 kg of $CaCO_3$ per m^2 of reef surface per year at the SE and NE sites, respectively.

The decrease in colony size and colony rugosity following death varied considerably among the three species. After 21 months of erosion, the planimetric area of colonies of *A.hyacinthus* had decreased an average of 72 %, and their rugosity index had more than halved, with many of the colonies reduced to their basal stump. In contrast, colonies of *A.cuneata* did not undergo any detectable change in planimetric area, although their rugosity decreased slightly. Skeletal degradation in *A.gemmifera* was somehow intermediate between the other two species, with a significant decrease in planimetric area, but only a slight decrease in the rugosity index. A consequence of the different rates of degradation among species is that colonies of different species will remain *in situ* for different periods of time. Hence, *in situ* skeletal excavation by boring organisms is likely to be of greater relative importance in species which are eroded less by external bioeroders.

To correctly interpret the significance of the observed patterns, the limitations of the technique employed must be taken into account. In this study, the photographic monitoring involves analysis of two-dimensional images. This is more likely to detect size changes in plate colonies, such as *A.hyacinthus*, whose morphology develops predominantly in two dimensions, rather than three-dimensional morphologies of

A.cuneata and *A.gemmifera*. Consequently, the real extent of external erosion in *A.cuneata* and *A.gemmifera* may be greater than estimated by this technique.

Colonies of *A.hyacinthus* decreased in size rapidly following death (Figure 4.1). The rate of degradation decreases with time (Figure 4.2) and was higher at the SE sites. However, the difference between locations attenuated with time and was not significant after 52 and 90 weeks since death. This temporal pattern in both the rate of degradation and in the effect of location may be due to a shift in the relative importance of the agents responsible for the degradation in *A.hyacinthus*. Due to their finely branched morphology, the colonies are highly susceptible to breakage by the mechanical action of waves. This susceptibility decreases with time, as the less dense, weaker margins of the colony are eroded. At this point agents of bioerosion, such as grazing scarids, may become more important than physical erosion, and hence, the difference in the rates of external degradation between the differently exposed locations become similar.

Degradation in *A.gemmifera* became detectable with the technique employed only after the 3rd census (34 weeks since death). The rate of decrease in size was relatively constant through time (Figure 4.2). Although there was no effect of location for this species, the mean percent decrease in size shows a tendency to be larger at the NE sites than at the SE ones. The difference in rates and patterns between *A.hyacinthus* and *A.gemmifera* suggests that the relative importance of the agents acting on the two species may differ. Mechanical erosion may be important in the initial stages of the degradation of *A.hyacinthus*, to the extent that higher wave energy may result in higher rates of degradation. However, colonies of *A.gemmifera* are characterised by thick, short branches which are not likely to be very susceptible to mechanical breakdown by wave action. This suggests that external bioeroders contribute most to the degradation of colonies of this species.

The most likely agents for external bioerosion are scarids of the 'excavator' group cf. Bellwood and Choat (1990). Kiene (1985), found grazing to be the dominant bioerosive process in transplanted substrates which had been exposed for approximately three years at Lizard Island. Furthermore, Sammarco *et al.* (1986) used

a set of treatments which included caged colonies to exclude grazers to examine patterns of bioerosion. They established that grazers, mainly scarids, were responsible for the degradation of coral skeletons. In this study, visual inspection of the experimental colonies during and at the completion of the experiment, revealed that external damage to colonies of *A.gemmifera* consisted of breakage of the tips of the digitate branches which may be the results of the feeding activity of scarids.

The rates of loss of calcium carbonate obtained from this study must be taken with caution when considered in the context of overall reef bioerosion and of previously published rates of external bioerosion. Rates of 6.2 ± 3.3 and 5.4 ± 1.8 kg $CaCO_3$ m^{-2} y^{-1}, for the SE and NE locations respectively, refer to a m^2 of *A.hyacinthus* planimetric area, that is to say a m^2 of reef surface with a 100% cover of *A.hyacinthus*. However, it is likely that these rates are highly dependent on the colony age and/or size class. A large colony occupying a square metre of reef surface may shrink at a slower rates than the ones obtained from colonies in the size class considered in this study. The rates here reported for a square meter of reef surface, which account for the percent cover of *A.hyacinthus* at the study sites (0.41 and 1.19 kg for NE and SE, respectively) underestimate the overall rates of loss of $CaCO_3$ not due to borers. In fact, they do not account for external erosion and bioerosion of components of the reef framework other than *A.hyacinthus*.

The representativeness of the rates obtained during this study is difficult to assess also because there is little information on the rates of external bioerosion on coral reefs in the Western Pacific. Only three studies, as far as I am aware, have investigated external erosion. Two separate studies by Kiene (1985 and 1988) provided rates of total erosion (including internal, although negligible) over 2 and 4 years respectively. Erosion was estimated by the decrease in volume of blocks cut from colonies of *Porites* sp. and attached to a support structure above the reef surface. Rates estimated from these studies ranged from 0 to 9.11 kg m^{-2} y^{-1} (where square metre refers to unit of surface area of the blocks). Kiene (1985, 1988) attributed the external erosion to grazing by scarids, and interpreted the observed lower rates of erosion in reef flat environments, as a result of reduced access to grazers during low tide.

Sammarco *et al.* (1986) experimentally investigated the decrease in size of pieces of freshly killed corals and found that grazing undeterred by either caging or territorial fish caused a 50% decrease in planimetric area within a 18-24 month period. This decrease was also accompanied by a considerable change in microtopography which consisted in reduction of micro-relief. Unfortunately they do not provide estimates of the absolute decrease in size, from which it could be possible to estimate losses of $CaCO_3$. The agents of erosion in this study were identified through the use of time-lapse photography. It was clear that the major grazers were scarids and acanthurids and no echinoids were observed.

Rates of external bioerosion by both scarids and echinoids are available from regions other than the Western Pacific. Several estimates of bioerosion by the scarid *Sparisoma viride* are available in literature (see also Table 3.14). This scarid is the only relatively large species in the Caribbean that can be considered as functionally excavating the substrate on which it grazes (Bellwood and Choat 1990). Rates of 34 ± 5 $gCaCO_3m^{-2}y^{-1}$ and ranging from 40 to 168 $gCaCO_3\ m^{-2}y^{-1}$ have been estimated from gut contents of this species by Scoffin *et al.* (1980) and Frydl and Stearn (1978), respectively. However, estimating the erosion by grazers from the amount of sediment reworked does not account for the portion of substrate that is broken off during grazing. Depending on the type of substrate, and the mode of grazing, this may be high. As far as I am aware, no study has ever quantified external bioerosion in *in situ* substrates. The present study shows a considerable variation in the rate at which dead colonies of three different coral species are degraded and that at least one of the three species, *A.hyacinthus*, experiences very fast skeletal degradation following death. There is a clear need for furthering our understanding of the process of external bioerosion and how it impacts on the different components of the reef framework.

A.hyacinthus, with colonies reaching up to metres in diameter, is the most abundant coral in terms of cover, at all the reef crest sites (Nelson, pers. comm.), and in most of the reef crest environments on the GBR (Veron 1986). Therefore *A.hyacinthus* constitutes a major feature of the topography of the reef surface in this habitat. The results from this study show that plate corals on the reef crest are rapidly degraded following death. This has important ecological and geological implications in

situations of mass mortality of colonies of this species. Such mass mortality events occur as a result of *Acanthaster planci* outbreaks, as *Acropora* tables are the most affected corals by the starfish predation (Dea'th and Moran 1992).

The topographical changes resulting from disappearance of tabulate corals in such situations will potentially affect the coral community structure and recruitment patterns of the recovering reef. According to a study by Stimson (1985), the coral fauna living in the *A.hyacinthus* understory is characterised by low density and low diversity. By making patches of space available for colonisation, the high rates of degradation of *A.hyacinthus* colonies following death may increase coral diversity in areas of very high coral cover (Connell 1978).

Several authors have discussed the increased susceptibility of coral colonies to erosion following a COT outbreak (Endean and Stablum 1973; Sano *et al.* 1984). Fabricius and Fabricius (1992) found a high correlation between past sedimentation rates and abundance of COT skeletal elements. Although they could not conclude that the skeletal elements resulted from outbreak population densities, they discussed the potential for sedimentation rates to be increased following an outbreak. The present study suggests that in situations of mass mortality of plate *Acropora* the reworking of their skeletons is rapid, which is likely to result in increased rates of transfer of $CaCO_3$ from the framework to the rubble and sand compartments of the reef. Further studies specifically addressing the question of the carbonate by-products resulting from the degradation of standing dead coral colonies should be undertaken in order to fully understand the implications of mass mortality of corals on the morphological development of the reef.

The decrease in colony rugosity following death, although highest in *A.hyacinthus*, was considerable for all species. In *A.cuneata* the decrease in rugosity was not accompanied by a decrease in size. This may be explained by the effect of encrusting organisms, particularly coralline algae which are more abundant in this species (see 3.3.1 and Figure 3.3), and which cover the relative large corallites thus reducing the structural complexity of the colony surface, while maintaining its size.

Bellwood and Choat (1990) suggested that external bioerosion reduces the structural complexity of the reef surface, due to the preferential feeding by scarids on convex surfaces. The present study supports their observations and provide quantitative estimates of the reduction in rugosity in common coral substrates. For *A. hyacinthus* the mean colony rugosity more than halved its value after 21 months of exposure. For the other two species the reduction was less dramatic. The implications of such a decrease may be large, especially following episodes of mass coral mortality such as result from outbreaks of Crown-of-Thorns. Sano *et al.* (1984) examined experimentally the effect of decreased structural complexity of the coral colonies, as observed on reefs affected by heavy outbreaks of COTS. They suggested that this decrease was due to a higher susceptibility to physical and biological erosion of the dead coral colonies. The reduced structural complexity had a major effect on both the number of species and individual resident on coral colonies (Sano *et al.* 1984). However, whether such changes take place naturally was not tested. Moran and Reaka (1991) demonstrated that an increase in spatial complexity through the provision of rubble following a hurricane, had the effect of increasing diversity of motile cryptofauna. Further studies should assess the significance of reduction in structural complexity on other reef communities and processes, such as recruitment of benthic organisms.

Coral colonies of different species are degraded at different rates following death, and 'skeletal durability' (Brett 1990) varies in different species. Therefore, dead colonies of different species will remain *in situ* for varying periods and consequently will be available to boring organisms for different times. This suggests that the transfer of carbonate products from the reef framework to other carbonate compartments of coral reefs will vary in rate and composition depending on the dynamics and composition of coral community. Accordingly this should be taken into account when considering the implications of mass mortality events, such as COT outbreaks, on bioerosion of coral reefs.

Chapter 5

Long term rates of internal bioerosion in *Porites* substrates from four reefs on the GBR

5.1 Introduction

This chapter reports on a sampling survey conducted on four reefs in the Central and Cairns Sections of the Great Barrier Reef (GBR). Dead *Porites* colonies, which had been exposed to borers for known durations, were sampled in order to: 1) quantify the amount of coral skeleton removed by internal bioeroders; 2) estimate rates of internal bioerosion over periods from 1.5 to 100 years; 3) determine spatial patterns of bioerosion and composition of boring communities in dead *Porites*; and 4) investigate the potential effect of outbreaks of crown-of-thorns starfish (COTS) on the rates of internal bioerosion.

Bioerosion is a function of time, and the duration of exposure of a substrate to bioeroders is a major factor controlling the extent of excavation (MacGeachy and Stearn 1976; Davies and Hutchings 1983; Hutchings and Bamber 1985). Given that most internal bioeroders do not bore into living corals, the duration of exposure generally corresponds to the time elapsed since death of the living tissue (Hutchings and Peyrot-Clausade 1988). This makes coral substrates for which it is possible to determine the time of death ideal for studying short and long term rates of bioerosion. Dead coral substrates that can be dated have been previously used by Hudson (1977) in the Atlantic Ocean. He estimated the rate of bioerosion by sponges and grazers in *Montastrea annularis* over a six years period by matching skeletal "stress bands" on x-radiographs of coral sections. He found very high erosion rates (the height of a colony being reduced of 0.67 cm y^{-1}), mainly due to six species of boring sponges. However, there are no other studies that have applied this concept.

Ages of *Porites* colonies can be verified by using characteristic fluorescent bands which form as a result of incorporation of fulvic acids in the skeleton (Isdale 1984). The thickness of the bands depends on the intensity of the run-off in each wet season. Years with particularly high rainfall leave characteristically wide bands that may be used as references for dating (Isdale 1984; Susic *et al.* 1991). This study used dead substrates from large *Porites* colonies to estimate rates of bioerosion over periods of up to 100 years based on validated annual banding patterns. This made it possible to

examine spatial and temporal patterns of internal bioerosion over a range of temporal scales which would not be feasible to investigate with an experimental approach.

The pattern of colonisation of dead coral blocks by different taxonomic groups of non-colonial borers is strongly affected by temporal factors (Hutchings *et al.* 1992). In particular, the time of the year when the substrate becomes available, the duration of exposure to borers, and inter-year variations in recruitment appear to contribute substantially to the variation in numbers of polychaetes, sipunculans and bivalves that colonise artificial substrates during the initial stages of exposure (from a minimum of 3 months to 4 years; Hutchings 1985; Hutchings *et al.* 1992). However, it is not clear how these variations may influence the process of bioerosion within a reef on naturally occurring substrates over larger temporal scales. Internal bioerosion is a cumulative process which does not necessarily equate to the abundance of borers in a substrate at any point in time. The excavations we observe in eroded substrates are the result of numerous generations of borers. At present, it is not known whether the effect of short term variations in recruitment of borers may become swamped over longer periods of exposure, resulting in relatively uniform long term rates of bioerosion. Peyrot-Clausade *et al.* (1992) found that absolute and relative abundance of non-colonial borers in *Porites lobata* varied with the degree of colony degradation (from 100% live coral to colonies reduced to basal plates), while the overall boring community composition remained relatively uniform. Boring bivalves became increasingly important in the latter stages of colony degradation, while sipunculans dominated the half-dead and dead colonies (Peyrot-Clausade *et al.* 1992). Their results suggest that, if different agents are responsible for bioerosion at different stages, the rates of excavation of a substrate may vary with increasing length of exposure. The variation in rates of $CaCO_3$ loss with increasing time of exposure over long temporal scales has never been investigated before. The techniques used in this study allow these patterns to be examined.

In the present study, the potential to estimate the duration of exposure to borers of dead *Porites* surfaces also allows the long term effects of COTS outbreaks on the process of internal bioerosion to be investigated. The consequences of large outbreaks

of COTS on bioeroding organisms have never been investigated. A number of authors have recognised the potential of bioerosion to be altered following an outbreak (Price 1975; Hutchings 1986; Glynn 1988; Scoffin 1992). This is based on the fact that bioerosion acts primarily on dead coral substrates, and that there is a rapid increase in the availability of these substrates on the reef surface following COTS outbreaks. Fabricius and Fabricius (1992) reported a high correlation between sedimentation rates and abundance of COTS skeletal elements in subsurface sediment cores from two reefs on the GBR. Although they were unable to relate the relative abundance of skeletal elements in the sediment to absolute population sizes of COTS (i.e. outbreak population sizes), they discussed the potential increased susceptibility to erosion (and consequentely to sedimentation rates) of a reef surface that has experienced high levels of predation by *Acanthaster*.

The present study specifically addresses the effects of extensive coral mortality due to COTS feeding activity on bioerosion. The mechanism by which large outbreaks may potentially affect the processes of bioerosion on a reef is twofold. Firstly, a rapid and dramatic increase in dead coral cover would result in a linear increase of bioeroded substrate. This increase could be estimated from information on the rates of degradation of newly dead coral skeletons standing on the reef surface (see Chapters 3 and 4). The second mechanism through which an outbreak could affect the overall process of bioerosion consists of potential changes in the population dynamics of the organisms responsible for the erosion of the substrate (i.e. boring infauna and excavating grazers), which may result in a non-linear increase in the rates of bioerosion. This would happen if the availability of dead substrates triggered a cascading effect on recruitment of boring organisms. These potential shifts in the population dynamics of borers would be likely to manifest themselves over longer temporal scales. The aim of the study reported in this chapter was to investigate potential changes in the rates of bioerosion or taxonomic composition of boring communities in substrates that have been exposed for long periods of time (years to decades) and in areas of known past occurrence of COTS outbreaks and areas known to be unaffected by COTS over the same period.

5.2 Methods

5.2.1 Sampling sites and design.

Dead surfaces on large *Porites* colonies (see 5.2.2) were sampled on four reefs in the Cairns and Central Sections of the Great Barrier Reef, during field trips in July 1991, November 1991 and February 1993. The reefs sampled were: Green Island, John Brewer Reef, Centipede Reef and Low Isles (Figure 5.1).

Green Island and Low Isles are sand cay islands approximately 15-20 km offshore from Cairns and Port Douglas respectively. The reef around Green Island was affected by heavy outbreaks of the Crown-of-Thorns starfish *Acanthaster planci*, during the early 70's and early 80's (Moran 1986). Following these outbreaks the living coral cover was reduced by 90% of its original level (Endean 1982). Dead surfaces on *Porites* colonies are particularly abundant here because the second extensive COTS outbreak largely affected massive corals (COTS Study Team 1986). The reef coral community is presently (1993) showing evidence of recovery. Low Isles consist of a smaller, permanently exposed cay and of a larger cay which is submerged at high tide and on which an extensive mangrove growth has developed. The reef surrounding Low Isles has been monitored for over twenty years with a two to three years frequency (Peter Moran pers.comm.) and no COTS populations at outbreak densities have been reported.

John Brewer and Centipede Reefs are large lagoonal reefs in the Central Region of the GBR. Like Green Island, John Brewer was affected by two heavy outbreaks of *Acanthaster planci* in the early 70's and 80's, that greatly affected the coral communities (Done 1985; Moran *et al.* 1985). In contrast Centipede Reef is considered pristine with respect to COTS outbreaks (Peter Moran pers. comm.).

The study focused on the exposed side of each reef (Figure 5.1), on a fore-reef habitat characterised by *Porites* colonies sitting on a sandy bottom. The sampling design includes four reefs, two sites per reef, eight dead surfaces ('surface') per site with six replicates per dead surface. The factor 'COTS status' was considered orthogonal to

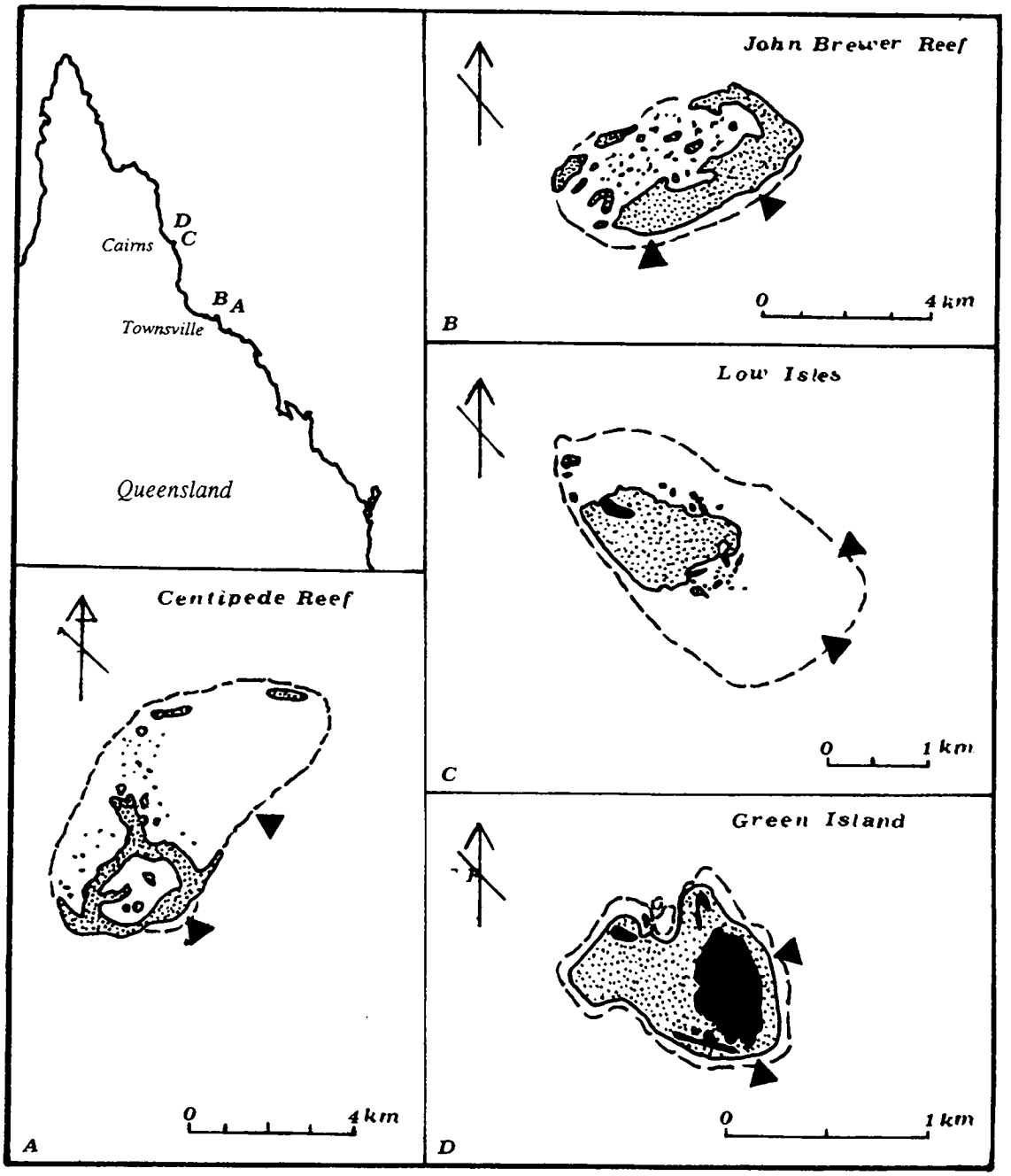


Figure 5.1: Position of the study sites on the four reefs (Centipede Reef and John Brewer Reef - Central Section of the Great Barrier Reef Marine Park; Green Island and Low Isles - Cairns Section of the GBRMP).

'reef'. The design for the pilot study conducted at Green Island included the factor 'colony' as well, with four colonies per site. In the pilot study, two or three dead surfaces were sampled on each colony for a total of 10 surfaces per site.

The author is aware of the potential confounding of the factor reef with both distance from shore (inner and middle shelf), tourist activity (the two inner shelf reefs, Green Island and Low Isles, are visited daily by tourists) and latitude (the two inner shelf reefs being in the Cairns section and the middle shelf in the Central section of the GBR - see Figure 5.1). However, these potentially confounding factors are equally represented within each of the 'COTS status' levels. In fact, for each level (pristine vs COTS affected) one reef is inner shelf, visited daily by tourists and in the Cairns section, and one is middle shelf, non visited by tourists and in the Central section. Although not an ideal situation, the author believes that this would minimise the confounding of the design. Moreover, following a thorough search of the literature, it was apparent that this was the only choice of reefs available for the purpose of this study. As far as the author is aware, Low Isles and Centipede Reefs are the only reefs for which ongoing, frequent and documented monitoring of Crown-of-Thorns populations has positively established that no outbreak has occurred in the last 25 years.

5.2.2 Porites *colonies and partial mortality*

In this study the word '*Porites* colony' refers to a colony of *Porites* spp. (no further identification has been attempted) which is at least one meter in diameter (Figure 5.2). Large *Porites* colonies are commonly found on Indo-Pacific reefs (Veron and Pichon 1982; Veron 1986; Done and Potts 1992). On the GBR they are found both in the deeper parts of lagoons or aggregated on terraces on the windward and leeward slopes. Some of these colonies are up to hundreds of years old (Isdale 1983).

Portions of bare skeleton on *Porites* colonies result from past events of partial mortality of the living tissue, such as episodes of predation by COTS (Done 1985). When part of the colony dies, the skeleton is colonised by algae, encrusting organisms and borers, while the surrounding living tissue continues to grow and to deposit

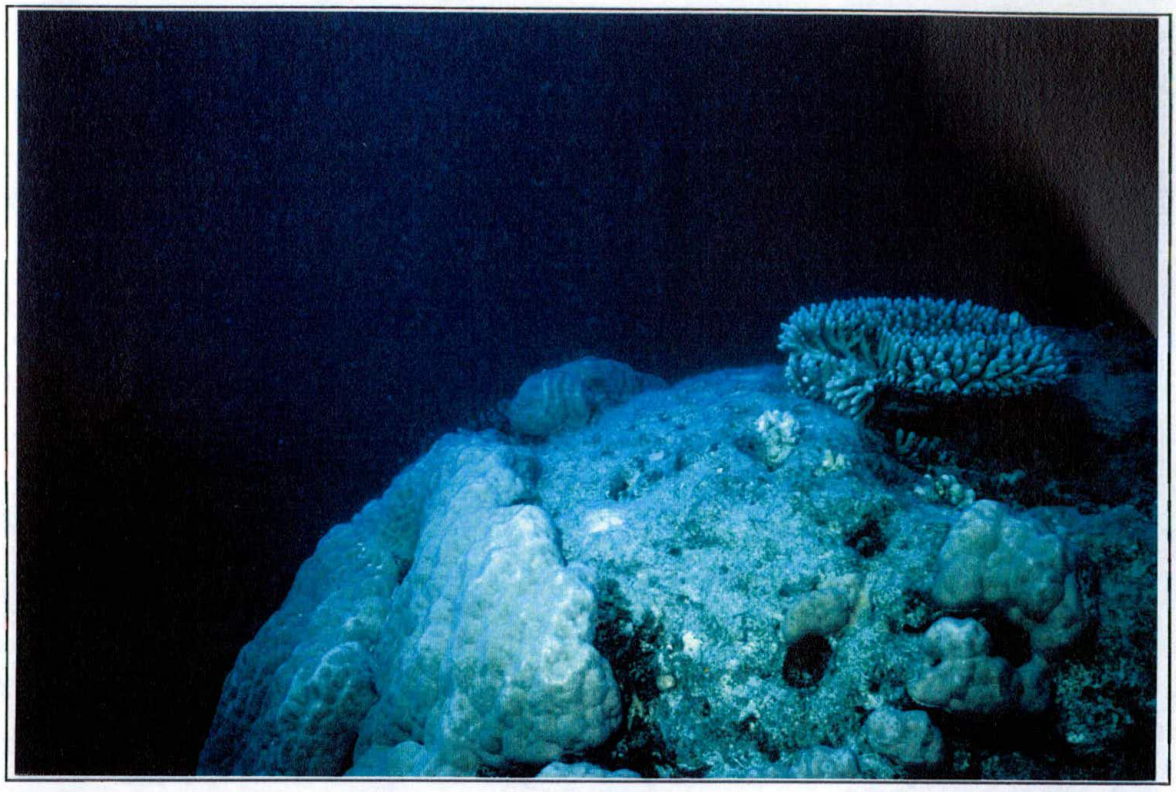


Figure 5.2: *Photograph of one of the* Porites *sp. colony sampled during the study.*

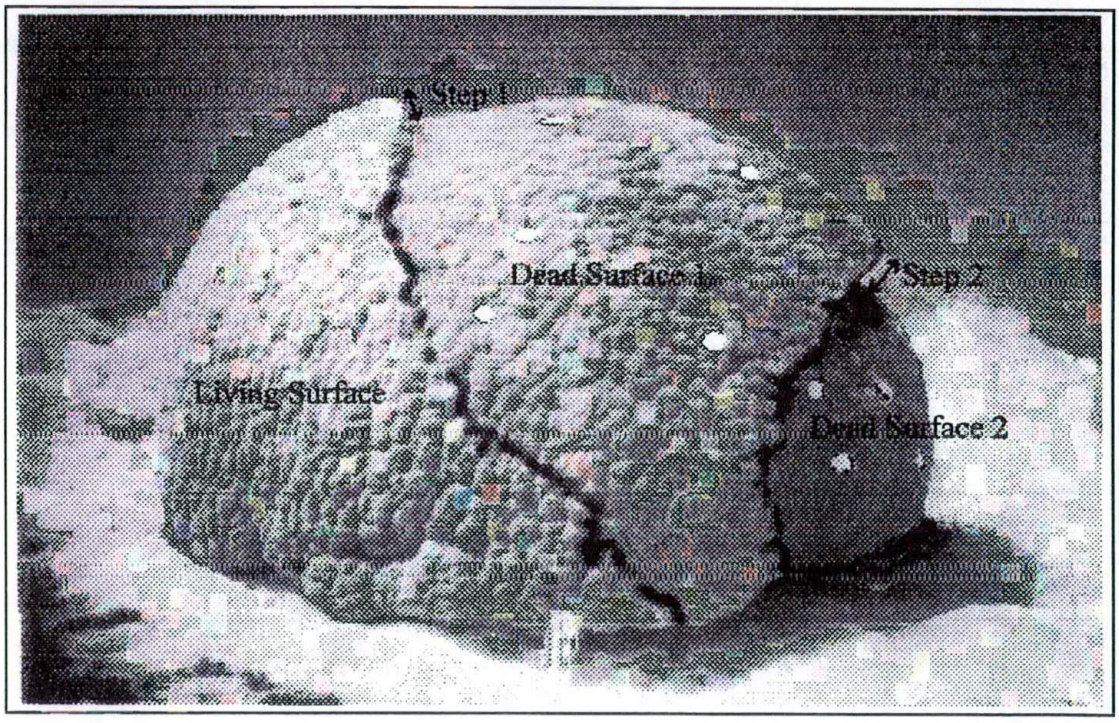


Figure 5.3: *Diagram of a* Porites *colony showing a 'living surface' and two 'dead surfaces' and the 'steps' that form between them (see 5.2.2). The white circles represent sampling cores.*

calcium carbonate. This results in a step (Figures 5.2 and 5.3) forming along the line between the living and the dead surfaces, which is an evidence of the skeletal continuity with the upper living portion (Done 1985). The height of the step is proportional to the time elapsed since the partial mortality occurred (COTS Study Team 1986).

Areas of dead skeleton on *Porites* colonies were sampled in this study. The terms 'dead surface', 'living surface' and 'step' refer to the corresponding features of a colony as shown in Figure 5.3. All the colonies sampled during the study had one or more dead surfaces as well as a living surface. In three instances, at Centipede and John Brewer reefs, the whole colony was dead but the step between the two dead surfaces was evident. On both Centipede and Low Isles reefs, the search time for appropriate *Porites* dead surfaces was much longer than at Green Island and John Brewer Reef, where the severe COTS outbreaks over the last twenty years had left many colonies with partial mortality as evidence of predation episodes (COTS Study Team 1986).

5.2.3 Sampling procedure

The dead surfaces were sampled by drilling 5cm in diameter cores, to a depth of 10-12cm in length. A pneumatic drill was powered by an air compressor on board a tender vessel. A 20m hose linked the drill to the compressor. This proved considerably more powerful and efficient than the use of SCUBA tanks to operate the drill. The cores were obtained by using cylindrical coring barrels, with either diamond coated or saw-toothed edges. Approximately 5 to 7 minutes were required to drill one core. Cores were extracted from the substrate by tapping a small chisel inserted in the cut produced by the blade. The length of the cores obtained in this way was approximately 8-10cm. Each core was stored in a sealed plastic bag and preserved in formalin for extraction of infaunal organisms. The distance among cores within a same dead surface was approximately 20-30 cm. In a few cases the distance was less, due to the limited size of the surface.

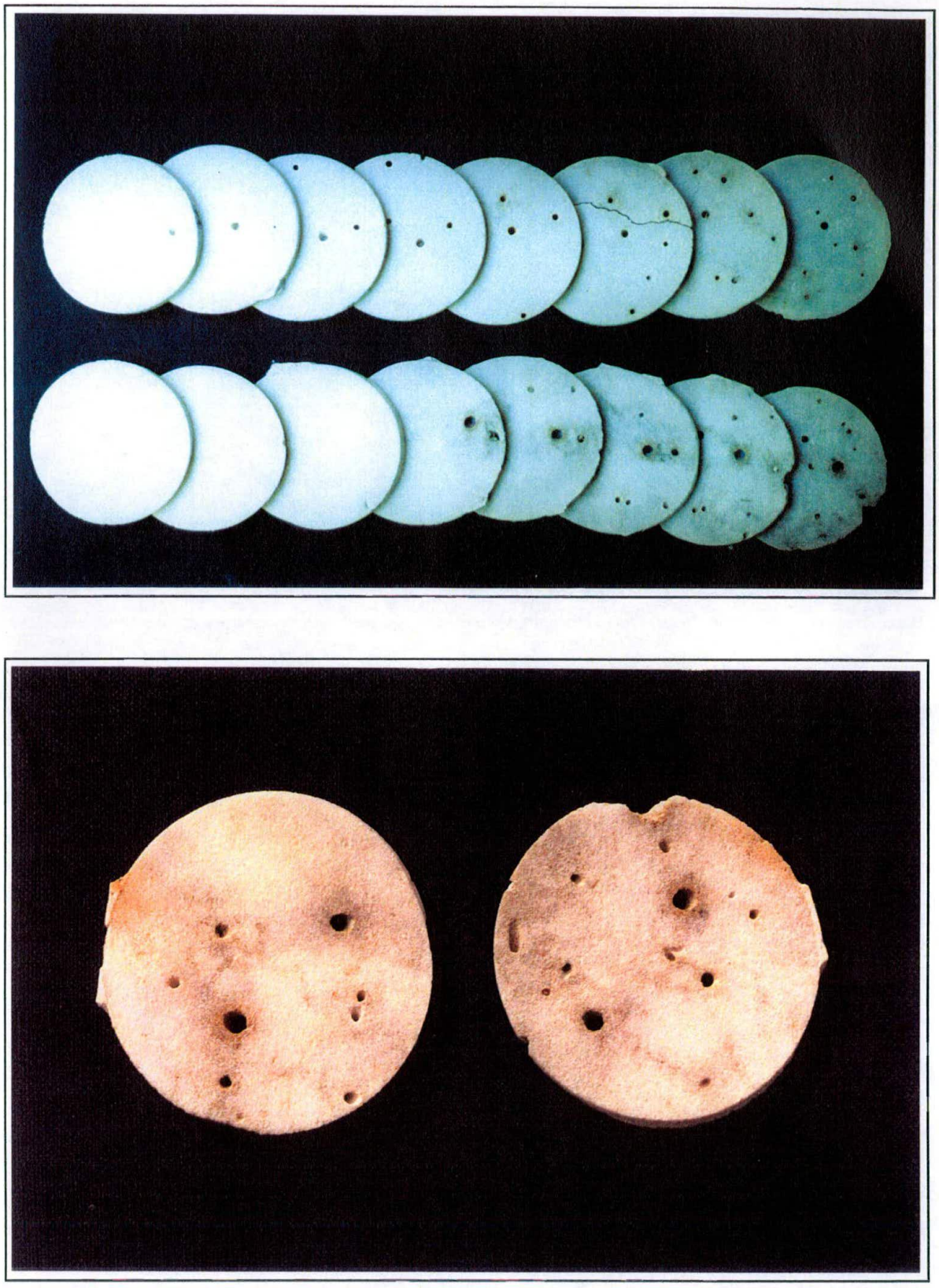


Figure 5.4: *Top: two cores sectioned in eight disks. The disks at the right end correspond to the top of the core. The area of the boreholes on the lower surface of each disk were estimated using a digitiser. Bottom: details of two disks showing boreholes produced by WORMS (mainly sipunculans).*

5.2.4 Estimating the extent of bioerosion

The cores were cut transversally parallel to the external surface of the core, into a series of 3mm thick disks (Figure 5.4). A rock saw with a 3 mm thick diamond coated blade was used. To facilitate the process, all the cores were cast in plaster. Each cast included several cores, which were cut simultaneously. The same sliding tablet described in the section 2.2.3 was used to ensure the cuts were parallel. A total of 8 disks were obtained from each core, which, accounting for the thickness of the blade, represented the top 4.8 cm of the core. Although some boreholes penetrated deeper than 5 cm into the substrate, an analysis of the samples collected during the pilot study demonstrated that more than the 94% of the total bioerosion occurs within the first 4-5 cm of skeleton. Therefore it was decided to analyse the top 8 disks only from each core.

The lower surfaces of the 8 disks from each core were photo-copied on a A4 sheet. The photocopied image of each disk was then compared to the original and the boreholes assigned to one of five categories of boring agents (see 2.2.4). The area of the boreholes was estimated by digitising the outlines on the photocopy. The area of boreholes within each category was summed across the disks from each core. For the analysis of patterns of bioerosion, data did not need to be standardised for surface area, as the cores were of equal size. Estimates of bioerosion rates as g $CaCO_3$ m^{-2} y^{-1} was obtained as follows:

$$Rate_{ij}(gCaCO_3\ m^{-2}\ y^{-1}) = \Sigma SA_{ij} \times 3\ mm \times 2 \times (1.2 \times 10^{-3}\ g\ cm^{-3}) \times 666.67 \times {'time'}_j^{-1}$$

where ΣSA_{ij} is the sum of the area of all borings produced by group i in the surface j; 3mm is the thickness of each disk; 2 is a factor that accounts for the volume of the core that is destroyed by the blade; 1.2 g cm^{-3} is a conservative estimate of density of *Porites* sp. (Hughes 1987), and 10^{-3} converts mm^3 into cm^3; 666.67 is a factor to convert the unit of surface area to m^2 (given the surface of each core is 15 cm^2); ‘time’$_j$ is the estimated duration of exposure to borers of the surface j (see next section).

Rates of bioerosion were estimated also from regressions of volume removed on duration of exposure for individual colonies (see 5.2.6), whenever this was linear and significant. This was the case for rates measured from each of three colonies per site at

Green Island, and for rates measured at each site of the four reefs by including three surfaces per site (see 5.2.6). The estimated coefficients of regression were expressed in $mm^2 \times year^{-1}$ and referred to an exposed area of 15 cm^2 (area of the top surface of each core). They were converted to yield estimates of rates as g of $CaCO_3$ removed by all and/or individual taxa, per m^2 of surface area exposed per year. Volume of skeleton removed (surface area multiplied by 3mm) was converted to weight removed by using $1.2\ g \times cm^{-3}$ (Hughes 1987) as estimate of density for *Porites*.

5.2.5 Dating the substrates

From each dead surface, one or two long cores were taken for the dating of the substrate. A longer (30 cm), thinner (2.5 cm in diameter) barrel was used for these cores. The year in which the living tissue died and the *Porites* surfaces became exposed to bioeroders is referred to as T_0. Time of exposure to bioeroders is estimated as the difference between the year when the sampling took place (T_s) and T_0, and is hereafter referred to as 'time'. Two independent estimates of 'time' have been obtained for each surface (for a previous use of these dating methods, see COTS Study Team, 1986; Table 5.1). The first estimate was made by measuring the height of the step between the living surface of the *Porites* colony and the dead surface (Figure 5.3). For each surface, 3 measures were taken and averaged. The height was converted to time using an estimate of growth rate. This was calculated as the average distance between density bands for each long core.

The second estimate was obtained from the long cores taken from each substrate. The cores were cut in half longitudinally, to provide a flat, smooth surface. The surface of the section was analysed under UV light to highlight the fluorescent bands. The fluorescent bands where matched to bands on reference cores collected and dated by P.Isdale (Australian Institute of Marine Science, Townsville) (Figure 5.5). Fluorescent bands in *Porites* and other massive corals result from the inclusion of fulvic acids into the skeleton during growth (Isdale 1984, Susic *et al.* 1991). These acids come into coastal waters through runoff, and therefore their concentration is proportional to the level of the rainfall. During years of heavy rainfall, wide fluorescent bands form, while thin or no bands form during dry years. During a wet season characterised by two

periods of heavy rainfall, a characteristic double band will result. These particularly thick and/or double bands provide reference points for the dating of the cores. Using fluorescent bands in *Porites* skeletons, Isdale (1984) was able to backdate living colonies to hundreds years old. In this study reference cores dated by Isdale from John Brewer Reef (used for both John Brewer and Centipede reefs), Green Island and Low Isles were used to establish the year of death of the *Porites* living surface and 'time'.

The estimates of 'time' obtained with the two methods were compared (Table 5.1). The estimate obtained using the fluorescent bands was considered valid, whenever the two estimates disagreed. However, in some instances the estimates from the height of step were the only alternative, due to difficulty in reading the fluorescent bands (this happened predominantly at Centipede Reef probably due to the greater distance from shore and local hydrodynamic regime). In three instances, colonies did not have a living surface left. Only the step from the least recently dead to the most recently dead surface could be measured. In two of these cases the difference determined from the step corresponded to the difference between the fluorescent bands estimates (Table 5.1).

	Green Island		John Brewer R.		Centipede R.		Low Isles	
	Bands	*'Step'*	Bands	*'Step'*	Bands	*'Step'*	Bands	*'Step'*
Site 1	6	*5.5*	12	*10*	8	*4.5*	2.5	*2.5*
	11	*13*	20	*22*	17	*20*	4	*9.5*
	19	*18.5*	5.5	*6*	12	*11*	18	*14.5*
	12	*12*	19	*20.5*	11	*10*	8	*8*
	20	*21*	9	*8.5*	(10)	*7.5*	(11)	*2*
	7	*6.5*	27	*25*	5	*2.5*	3.5	*2.5*
	20	*14*	7.5	*11*	4	*6.5*	4.5	*4*
	12	*13*	19	*20*	12	*14*	13.5	*10.5*
	33	*26*						
	(65)	*50*						
Site 2	7	*6*	6	*4*	5	*5.5*	(5)	*2.5*
	20	*20*	9	*8*	7	*6*	(12)	*5*
	33	*35*	9	*8.5*	(17)	*c*	8.5	*8.5*
	13	*8.5*	23	*21.5*	(22)	*c+5*	14	*6*
	(65)	*47*	18	*a*	-	*22.5*	10.5	*10.5*
	(100)	*102*	24	*a+14*	-	*20*	8	*8*
	12	*8.5*	(9.5)	*b*	-	*10*	(11)	*6*
	33	*34.5*	(26)	*b+16*	1	*1*	(15)	*7*
	4	*5*						
	11	*16*						

Table 5.1: Estimates of duration of exposure to borers (years) of the dead surfaces on Porites ***colonies sampled at the four reefs, as obtained from fluorescent bands (normal font) and from the 'step' (italics). Estimates grouped within a cell refer to surfaces of a same colony.***

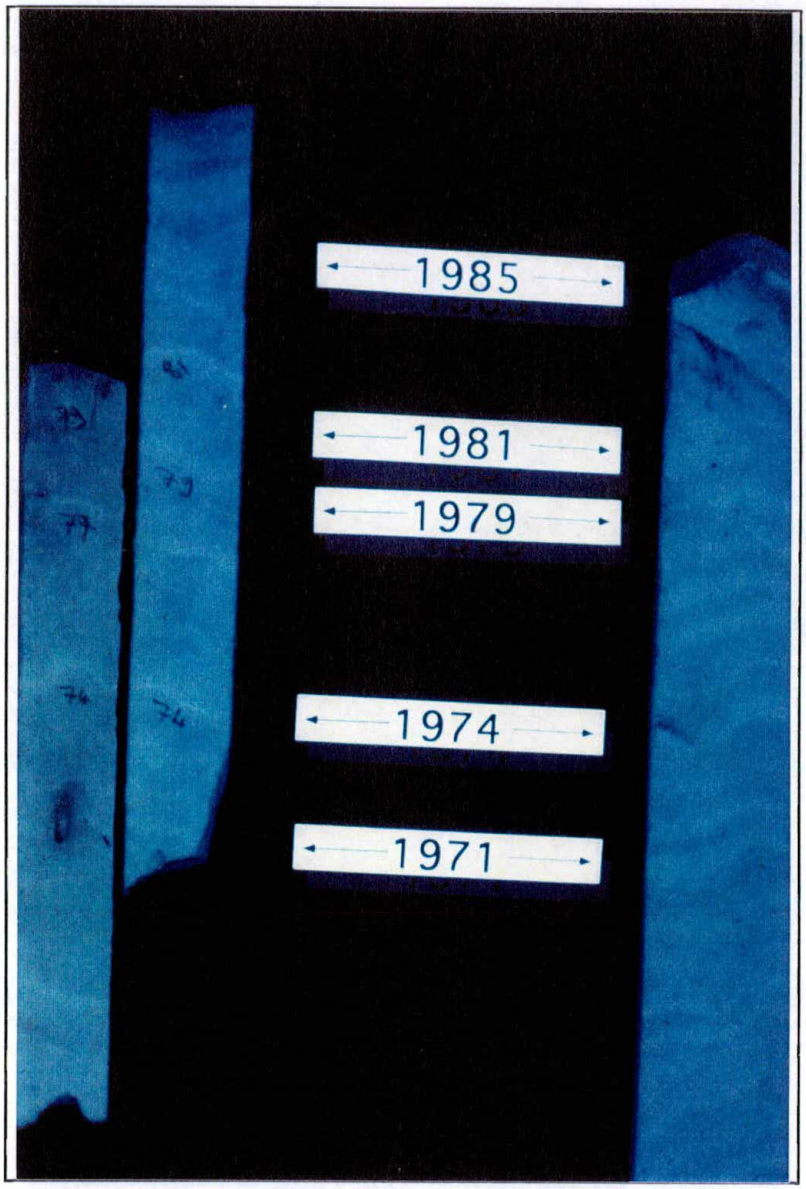


Figure 5.5: *Sample cores (left) and reference core (courtesy of P.Isdale, AIMS) used to date dead* Porites *surfaces. The fluorescent bands on the samle cores, which appear as pale horizontal stripes, were matched with the dated bands on the reference core.*

5.2.6 Data analysis

The sampling design aimed at testing for differences in the extent of bioerosion in substrates that occur on different reefs and sites within a reef, after partialling out the factor 'time'. The appropriate analysis in one dimension (total bioerosion) is the Analysis of Covariance. The covariate is the duration of exposure to bioeroders ('time'), the variate is total bioerosion or bioerosion by individual categories. The model followed a four-way, mixed model nested ANCOVA, with 'status' fixed, and reef, site and 'surface' nested. The model for the pilot study at Green Island included the spatial factors site, colony nested in site and 'surface' nested within colony.

	Site 1					Site 2		
Bombie	1	2	3	4	5	*(6)*	7	8
Surface 1	6	12	7	12	7	*13*	12	4
Surface 2	11	20	20	33	20	*65*	33	11
Surface 3	19			65	33	*100*		

Table 5.2: Duration of exposure ('time') in years of the dead surfaces sampled on the 8 colonies on Green Island. Colony 6 at site 2 was not used in the analysis because the regression of bioerosion on time was not linear.

Normality of the untransformed and transformed variables was tested using Shapiro and Wilk W statistic. Homogeneity of variances for grouped variables was tested with Levene's F ratio. Spatial patterns and the effect of duration of exposure were tested at Green Island by Analysis of Covariance (Zar 1984), including all the surfaces sampled at this reef (Table 5.2). Linearity and significance of regression of the extent of bioerosion on 'time' were tested for each colony. Regressions were forced through the origin as no bioerosion was found at T_0=0 (i.e. living surfaces). Colony 6 at site 2 on Green Island was discarded from the analysis of covariance as the regression was found to be significant but not linear. Analysis of covariance was used to test homogeneity of slopes among colonies and between sites. An estimate of the percent variance components for the spatial scales considered was obtained by partialling out the effect of 'time'.

Linearity of the relationship between extent of bioerosion and duration of exposure, at each site, was necessary for the use of ANCOVA to test the effect of the treatments.

Linearity and significance of the regression of volume eroded on 'time', was tested for each site. As a consequence of the lack of linearity in the regressions of the rates of bioerosion for 5 of the 8 sites, the effects of reef, site and the COTS 'status' could not be tested using an ANCOVA, as originally planned. Therefore reefs were compared in two ways :

1) For each site, surfaces were discarded from the regression analysis until the relationship of total bioerosion and time was linear. The surfaces retained for each site were three, and their values of 'time' (Table 5.3) were well distributed across the temporal range considered by the study (0-33 years). An Analysis of Covariance was performed on the reduced subset of data. The model included the covariate 'time', the factor COTS 'status' with two levels, the factor reef nested in 'status' and the factor site nested in reef.

	C1	C2	LI1	LI2	GI1	GI2	JB1	JB2
Surface 1	8	7	6	8	6	7	7.5	6
Surface 2	10	10	9	13.5	11	12	12	9
Surface 3	17	20	10.5	18	19	20	20	18

Table 5.3: Duration of exposure ('time') of the three dead surfaces per site used for ANCOVA at the four reefs.

2) Comparisons among sites, reefs and COTS 'status' were carried out with an ANOVA on data of samples from surfaces exposed for approximately 5 and approximately 12 years. These two values of 'time' constituted the fixed factor 'stage' with two levels, 'recent' (approx. 5 ys) and 'old' (approx. 10-13 ys). The exact value of 'time' of the surfaces included in the analysis for each reef and site is provided in Table 5.4. The model was a nested, 4-way ANOVA with 'status' as a fixed factor with two levels (pristine reefs and reefs that experienced heavy outbreaks), 'stage' as a fixed factor with two levels, recent and old, reef nested within 'COTS status' and site nested within each reef.

	C1	C2	LI1	LI2	GI1	GI2	JB1	JB2
'Recent'	5	5	4.5	5	6	4	5.5	6
'Old'	10	10	13.5	10.5	11	11	9	9.5

Table 5.4: Duration of exposure ('time') of the surfaces included in the levels 'recent' and 'old' for the factor 'stage', in the ANOVA which tests the effect of COTS 'status', reef, 'stage' and site on the extent of internal bioerosion.

5.3 Results

5.3.1 Bioerosion in Porites *colonies -Volume excavated and agents*

The total volume excavated by borers from the dead surfaces of *Porites* spp. at all reefs, ranged from a minimum of 3.4 ± 0.4 mm^3 per cm^2 for 2 years exposure, to a maximum of 515.1 ± 111.1 mm^3 per cm^2 for 100 years exposure (Table 5.5). The total volume excavated generally increased with time of exposure at all reefs (Figure 5.6). However, it was not a consistent monotonic trend, with some sites showing a multimodal function of volume removed with time (Figure 5.6). Sponges were patchily distributed in dead *Porites* colonies, and there was no evidence of excavation by sponges in 22 of the 68 surfaces sampled during the study. There was also large variation within individual surfaces. When sponges were present, the extent of excavation was high (Figure 5.7) and tended to obscure the trend of bioerosion by other groups, particularly WORMS, which tended to increase with time. In fact, sponges did not display a clear increase in bioerosion with time, with the exception of Green Island, where bioerosion by sponges was greater in older surfaces (Table 5.5; Figures 5.8). Sponges produced excavations resulting in a maximum of 425.6 ± 111.5 mm^3 of skeleton removed per cm^2 of surface area (100 year exposure; Table 5.5).

Worms were the most important borers (Figure 5.8) and were represented mainly by sipunculans, which were found excavating the *Porites* spp. surfaces at all sites and reefs. Some cores also had high numbers of small polychaetes of *Polydora* species. Bioerosion by worms ranged between 3.4 ± 0.4 to 117.8 ± 39.8 mm^3 per cm^2, for surfaces exposed for 2 and 33 years respectively (Table 5.5). Bioerosion by worms increased with time at all sites, and exhibited the lowest variation among cores (Figure 5.9). Bioerosion by bivalves was small, with the exception of Centipede Reef where they were relatively important (Figure 5.10). Bivalves also were patchy, not being found in 25 of the 68 surfaces. The volume excavated was small in comparison to the other groups (from less than a mm^3 per cm^2 to 96.7 ± 46.2 mm^3 per cm^2; Table 5.5). There was no pattern of increased bioerosion by bivalves with time at any of the sites (Figure 5.10).

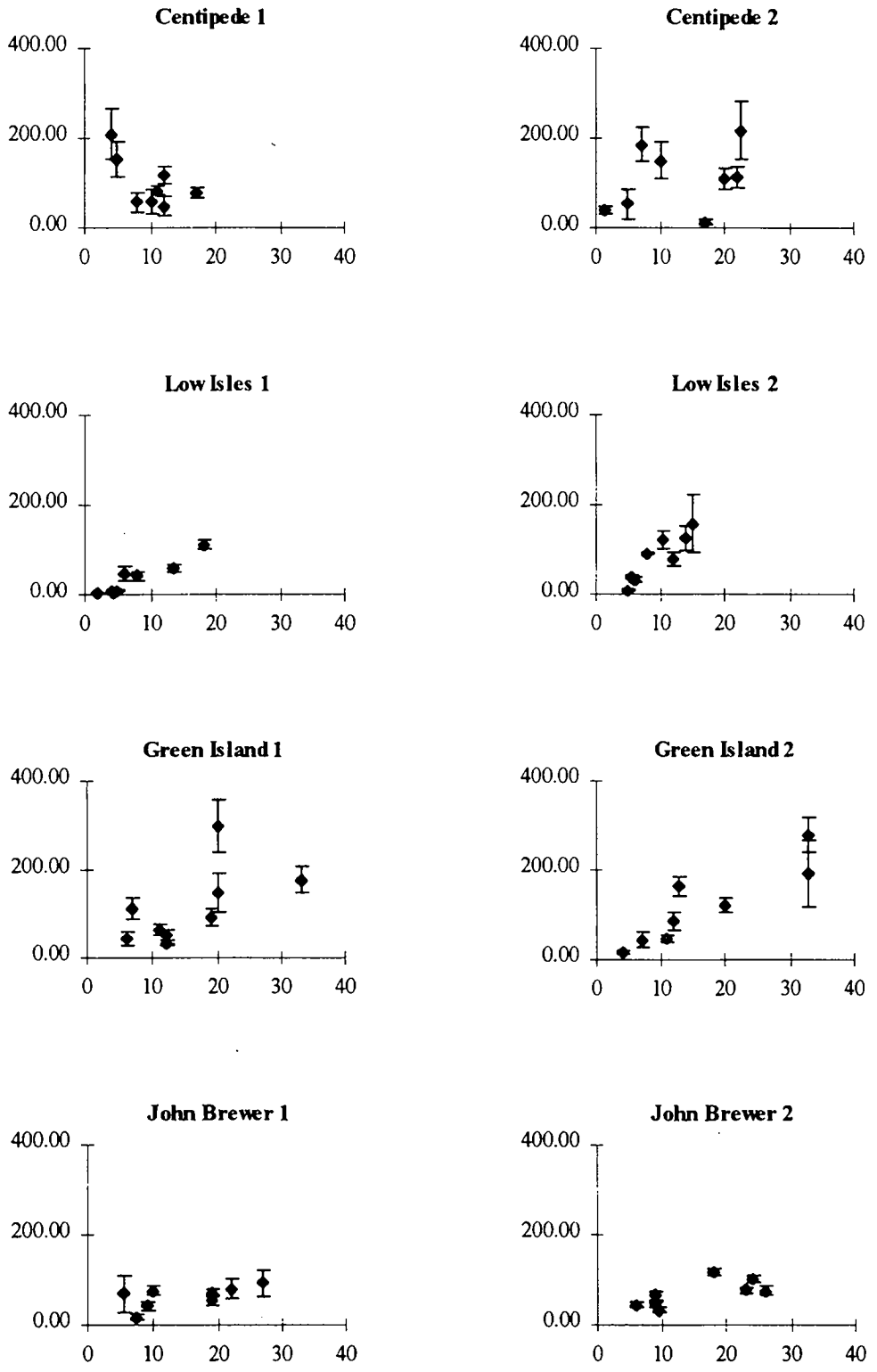


Figure 5.6: Mean volume removed by all taxa per unit of surface area (mm^3 cm^{-2}) from the surfaces with 'time' ≤ 33 years, plotted against 'time', for the two sites on the four reefs. Error bars are Standard Errors.

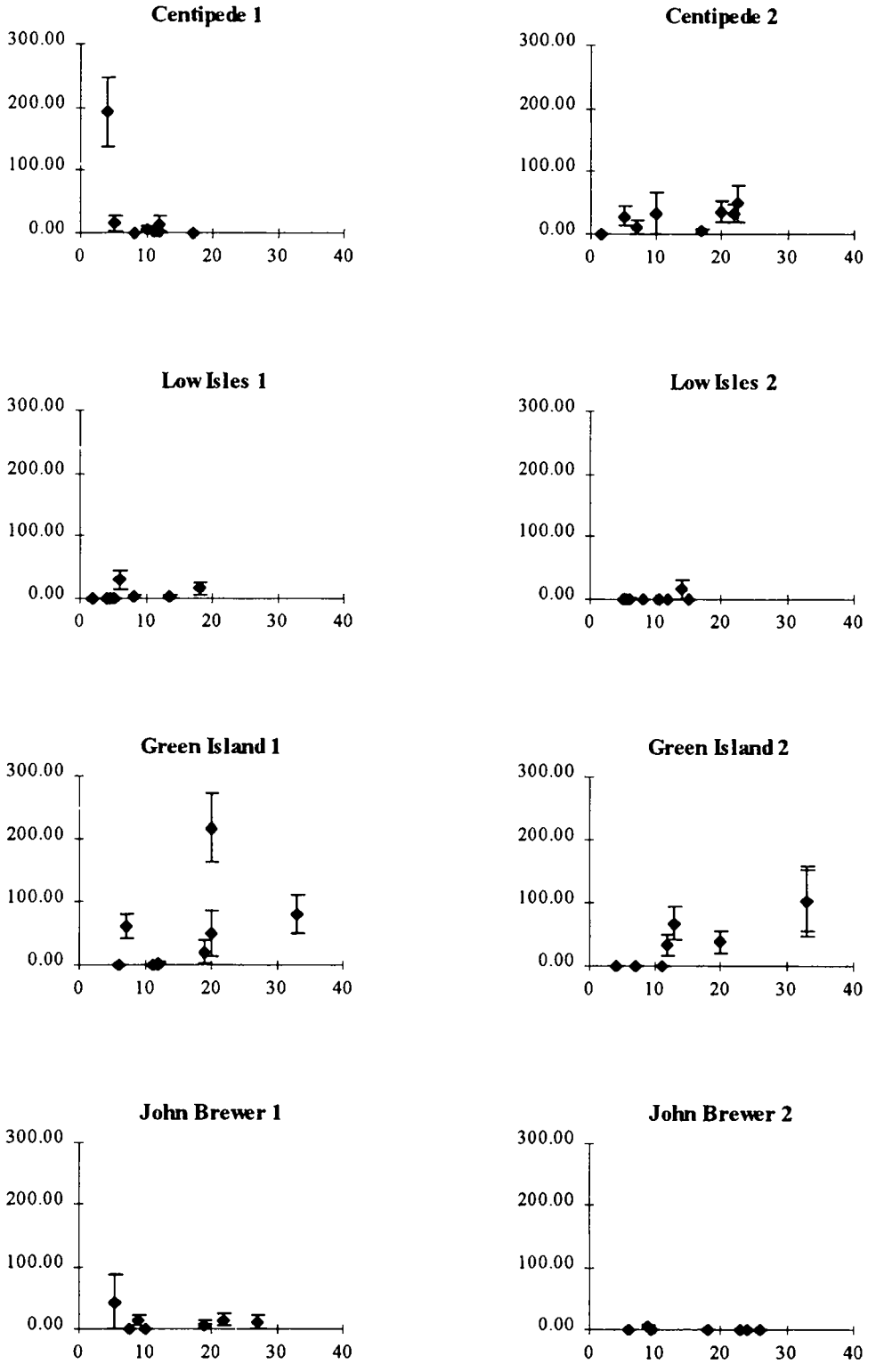


Figure 5.7: Mean volume removed by sponges per unit of surface area (mm^3 cm^{-2}) from the surfaces with 'time' ≤ 33 years, plotted against 'time', for the two sites on the four reefs. Error bars are Standard Errors.

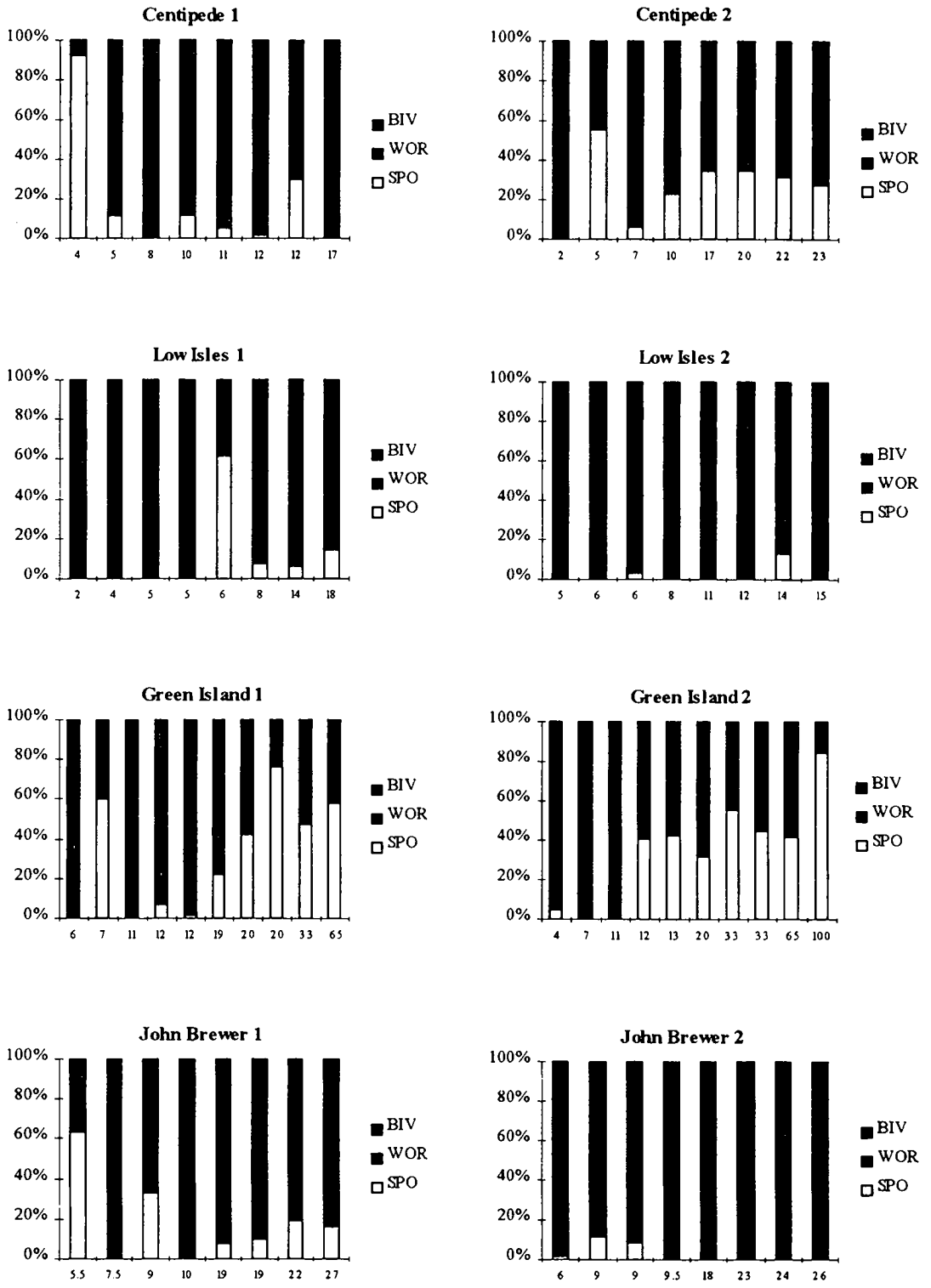


Figure 5.8: Percent of volume removed by each of the three major groups of borers plotted against 'time' (years).

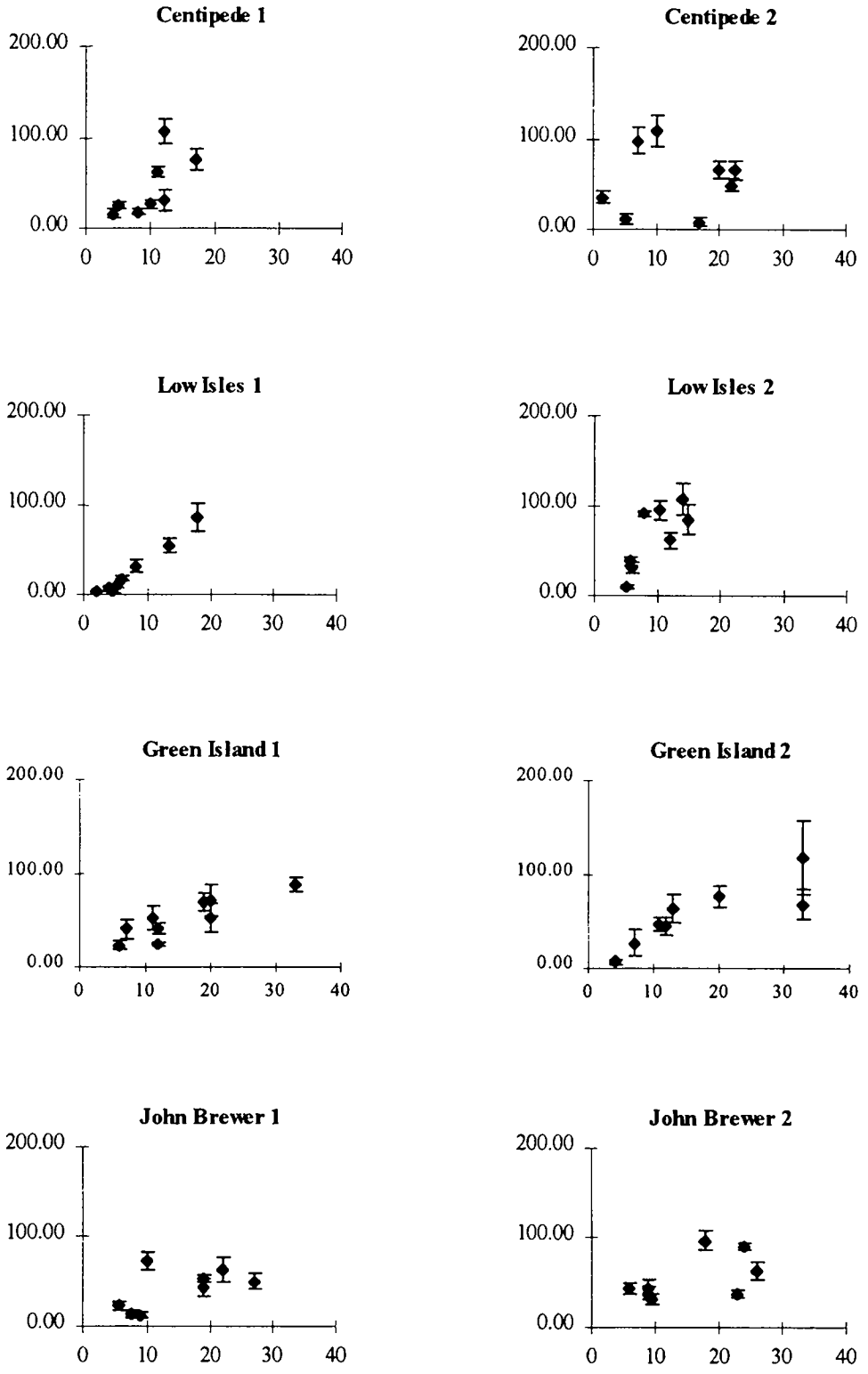


Figure 5.9 : Mean volume removed by WORMS per unit of surface area (mm^3 cm^{-2}) from the surfaces with 'time' ≤ 33 years, plotted against 'time', for the two sites on the four reefs. Error bars are Standard Errors.

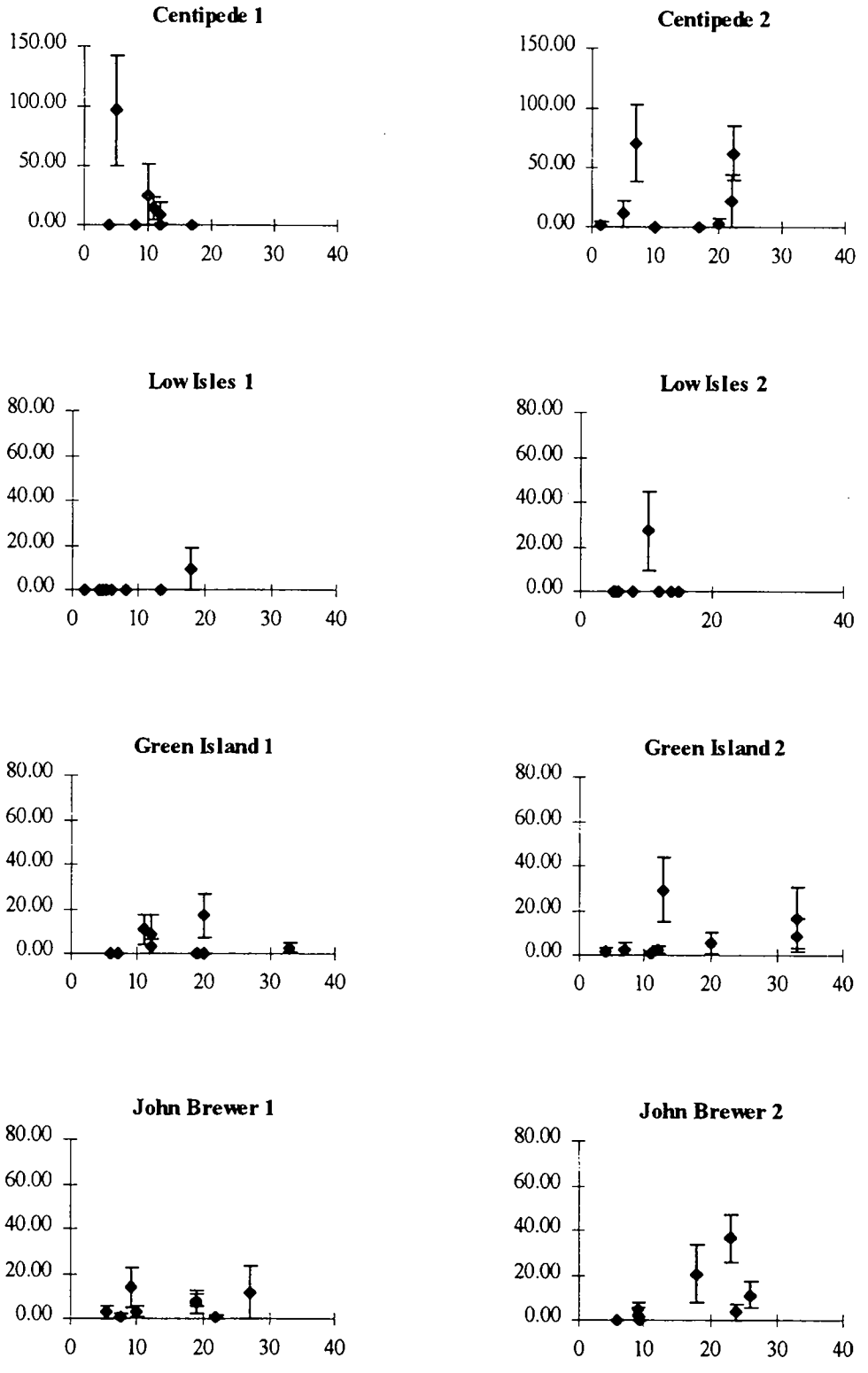


Figure 5.10: Mean volume removed by bivalves per unit of surface area (mm^3 cm^{-2}) from the surfaces with 'time' ≤ 33 years, plotted against 'time', for the two sites on the four reefs. Error bars are Standard Errors.

SITE	'time'	Total	SPONGES	WORMS	BIVALVES
C1	4	208.63	192.33	16.30	-
		56.93	*55.37*	*4.85*	-
	5	153.62	15.93	25.65	96.69
		38.47	*11.85*	*4.40*	*46.19*
	8	57.09	-	17.70	-
		23.08	-	*2.87*	-
	10	59.48	6.81	26.60	25.58
		26.32	*3.67*	*5.38*	*25.58*
	11	83.88	4.14	62.55	13.99
		8.58	*4.14*	*6.10*	*9.08*
	12	117.75	1.46	107.03	9.26
		19.90	*1.46*	*12.86*	*9.26*
	12	48.61	13.42	30.94	0.53
		20.16	*13.42*	*11.38*	*0.53*
	17	76.99	0.66	76.21	-
		12.22	*0.66*	*12.00*	-
C2	1.5	37.42	-	35.37	2.05
		7.89	-	*6.98*	*2.05*
	5	53.58	29.37	12.35	11.34
		32.65	*16.27*	*6.06*	*11.34*
	7	185.98	11.72	97.88	70.14
		38.41	*11.14*	*14.23*	*32.50*
	10	149.43	33.22	109.40	-
		41.19	*33.22*	*17.36*	-
	17	12.40	4.32	8.08	-
		5.61	*4.32*	*5.01*	-
	20	108.19	37.45	66.58	3.56
		23.26	*16.67*	*9.61*	*3.56*
	22	113.54	33.21	49.32	22.20
		24.49	*14.27*	*7.11*	*22.20*
	22.5	215.80	49.69	65.24	62.41
		64.70	*29.03*	*10.29*	*22.72*
LI1	2	3.43	-	3.43	-
		0.37	-	*0.37*	-
	4	6.90	-	6.90	-
		2.58	-	*2.58*	-
	4.5	3.55	-	3.55	-
		2.29	-	*2.29*	-
	5	9.66	-	9.66	-
		2.55	-	*2.55*	-
	6	47.97	29.64	18.33	-
		15.64	*15.63*	*3.06*	-
	8	42.10	2.61	32.18	-
		9.12	*2.61*	*7.21*	-
	13.5	58.82	3.76	55.06	-
		8.19	*2.51*	*8.65*	-
	18	111.09	15.79	85.85	9.45
		9.48	*9.00*	*15.16*	*9.45*

To be continued...

Table 5.5: *Means and standard errors of the volume (mm^3) per unit of surface area (cm^2) removed from the dead* Porites *sp. surfaces by the three major groups of borers. "Time" is an estimate of the duration of exposure of the surface to bioeroders. Sample size is n=6 cores for all sites but GI1 and GI2, where n=5, and C2 with 'time'=1.5, where n=4. Dashes represent zeroes.*

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SITE	'time'	Total	SPONGES	WORMS	BIVALVES
LI2	5	9.49	-	9.49	-
		1.38	-	*1.38*	-
	5.5	38.80	-	38.80	-
		4.73	-	*4.73*	-
	6	32.72	1.11	31.61	-
		5.61	*1.11*	*6.16*	-
	8	91.20	-	91.20	-
		2.94	-	*2.94*	-
	10.5	122.56	-	95.32	27.24
		20.38	-	*10.47*	*17.56*
	12	77.60	-	61.97	-
		16.42	-	*9.07*	-
	14	124.59	16.53	108.06	-
		28.27	*15.24*	*17.43*	-
	15	158.67	-	84.91	-
		63.94	-	*16.42*	-
JB1	5.5	69.20	43.71	22.60	2.89
		41.83	*43.71*	*5.53*	*2.89*
	7.5	17.53	-	14.61	1.16
		5.12	-	*3.99*	*1.16*
	9	41.60	13.11	12.63	13.82
		9.70	*8.29*	*2.40*	*8.85*
	10	76.44	-	73.20	3.24
		10.12	-	*9.87*	*2.15*
	19	54.59	6.40	52.91	7.36
		10.14	*6.40*	*3.49*	*4.87*
	19	71.64	4.29	42.32	7.99
		7.21	*2.94*	*9.89*	*2.74*
	22	78.99	15.33	62.99	0.67
		21.79	*11.06*	*13.18*	*0.67*
	27	93.70	11.94	49.99	11.91
		29.22	*11.94*	*9.07*	*11.91*
JB2	6	44.98	0.56	42.89	-
		6.20	*0.56*	*6.43*	-
	9	45.78	5.32	37.87	2.59
		5.19	*3.64*	*7.42*	*2.59*
	9	65.57	4.50	43.94	4.54
		8.98	*2.85*	*9.57*	*3.12*
	9.5	32.09	-	32.09	-
		5.73	-	*5.73*	-
	18	117.52	-	96.81	20.70
		9.04	-	*10.91*	*13.20*
	23	76.75	-	37.96	36.53
		6.45	-	*3.87*	*10.48*
	24	103.70	-	89.55	3.66
		7.89	-	*3.94*	*3.66*
	26	75.52	0.54	62.65	11.37
		9.87	*0.54*	*9.69*	*5.76*

To be continued...

***Table 5.5**: Means and standard errors of the volume (mm^3) per unit of surface area (cm^2) removed from the dead* Porites *sp. surfaces by the three major groups of borers. "Time" is an estimate of the duration of exposure of the surface to bioeroders. Sample size is n=6 cores for all sites but GI1 and GI2, where n=5, and C2 with 'time'=1.5, where n=4. Dashes represent zeroes.*

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SITE	'time'	Total	SPONGES	WORMS	BIVALVES
GI1	6	43.28	-	22.82	-
		14.82	-	*4.49*	-
	7	112.36	61.70	40.20	-
		23.73	*20.19*	*10.21*	-
	11	63.66	-	52.93	10.73
		12.54	-	*12.96*	*6.77*
	12	30.63	0.90	41.45	8.49
		2.92	*0.90*	*5.59*	*8.49*
	12	52.97	2.10	24.08	3.26
		11.73	*2.10*	*2.12*	*3.26*
	19	90.86	20.15	69.38	-
		19.31	*18.45*	*9.06*	-
	20	145.43	51.19	70.40	-
		44.21	*36.23*	*16.77*	-
	20	295.64	217.95	51.87	16.89
		59.87	*53.57*	*15.31*	*10.11*
	33	175.99	80.39	87.74	2.47
		28.75	*30.41*	*6.93*	*1.85*
	65	279.66	158.66	68.49	46.90
		59.18	*52.94*	*15.88*	*19.58*
GI2	4	14.12	0.43	6.68	1.59
		4.22	*0.43*	*2.26*	*1.59*
	7	45.05	-	26.87	2.63
		18.48	-	*13.51*	*2.63*
	11	48.39	-	47.12	0.59
		7.26	-	*6.98*	*0.59*
	12	86.40	32.44	44.74	2.29
		20.54	*16.95*	*8.55*	*1.47*
	13	163.65	68.01	62.93	29.39
		22.11	*27.17*	*14.99*	*14.86*
	20	122.32	38.23	76.74	5.52
		16.48	*17.63*	*11.90*	*4.67*
GI2	33	190.98	103.07	117.78	8.88
		74.01	*54.66*	*39.81*	*7.36*
	33	277.54	103.71	67.37	16.83
		39.51	*47.92*	*15.87*	*13.79*
	65	134.73	42.10	46.22	12.56
		30.23	*27.00*	*8.62*	*5.44*
	100	515.08	425.59	65.80	13.87
		111.07	*111.48*	*7.58*	*12.80*

***Table 5.5:** Means and standard errors of the volume (mm^3) per unit of surface area (cm^2) removed from the dead* Porites *sp. surfaces by the three major groups of borers. "Time" is an estimate of the duration of exposure of the surface to bioeroders. Sample size is n=6 cores for all sites but GI1 and GI2, where n=5, and C2 with 'time'=1.5, where n=4. Dashes represent zeroes.*

5.3.2 Spatial variability - Pilot study at Green Island

Data for total bioerosion at Green Island were normally distributed (W=0.96; p=0.07) and homoscedastic (Levene's test; F=0.76, ν_1=15, ν_2=76; p=0.71) when transformed as sqrt(X+1). The regression through the origin of bioerosion on 'time' of the surfaces

was significant and did not deviate from linearity in all colonies but colony 6 at site 2 (Table A45). This colony included the two oldest substrates sampled, 65 and 100 years old respectively (Table 5.2). Slopes at site 2 were not different (F_s=0.808; $F_{0.05;2,44}$=4.03, p>0.5), however at site 1 the slopes of the linear regressions (i.e. rates of bioerosion) were significantly different (F_s=8.29; $F_{0.05;3,62}$=3.33, p<0.001). The colony effect was due to colony 3 having a higher regression coefficient for bioerosion by all taxa and by sponges than the other colonies (Table 5.6; Figure 5.11).

	Total	SPONGES	WORMS	BIVALVES
Colony 1	13.25	1.84	9.83	0.56
	1.56	1.17	1.05	0.50
Colony 2	13.79	4.82	7.79	0.17
	3.44	2.90	1.41	0.26
Colony 3	37.71	26.67	7.34	1.88
	6.00	4.81	1.76	0.87
Colony 4	11.57	5.94	3.59	1.48
	1.35	1.17	0.60	0.44
Colony 5	15.21	6.80	6.41	1.11
	2.81	1.87	1.02	0.52
Colony 7	20.65	9.06	10.52	0.76
	2.29	3.24	2.04	0.44
Colony 8	11.31	0.03	9.94	0.23
	1.30	0.07	1.33	0.27

Table 5.6: Regression coefficients and standard errors for the regressions of the extent of bioerosion on 'time' of the surfaces, for each colony at the two sites on Green Island.

After partitioning out the effect of 'time', the majority of the variability in the extent of bioerosion was accounted for by differences among cores and surfaces. Variation due to differences among colonies was important, particularly for total bioerosion and sponges (Table 5.7).

	Total	SPONGES	WORMS	BIVALVES
between sites	0.12%	0.02%	0.45%	0.18%
between colonies	21.90%	18.22%	14.81%	7.36%
between surfaces	39.96%	29.42%	33.66%	20.75%
between cores	29.30%	40.74%	52.42%	63.09%

Table 5.7: Percent of the total variance in the extent of total bioerosion and bioerosion by SPONGES, WORMS and BIVALVES at Green Island., due to each of the four spatial factors considered after partitioning out the effect of 'time'.

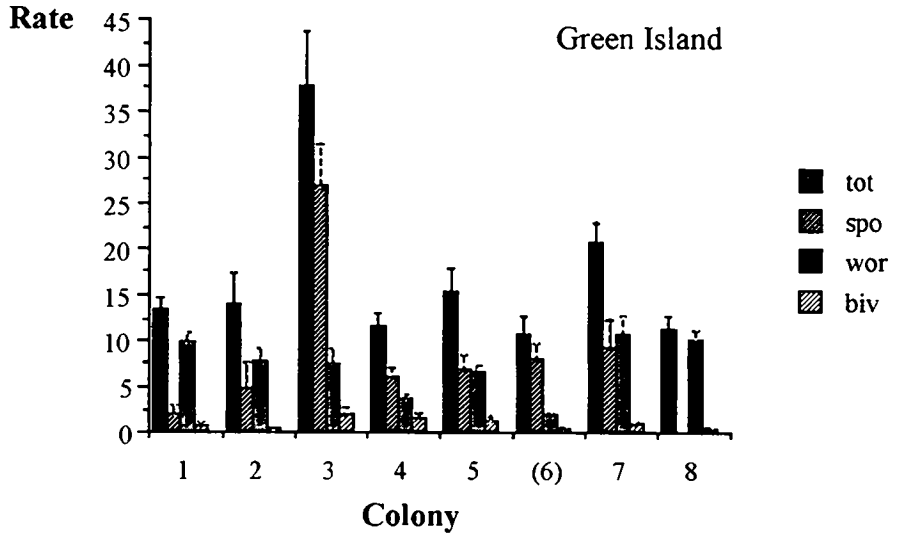


Figure 5.11: Mean rate of internal bioerosion (mm³/core/year) of Porites *substrates by all taxa (tot), sponges (spo), worms (wor) and bivalves (biv) at each of the eight* Porites *bombies sampled at Green Island. Bombie 6, in parentheses was not used in the ANOVA. Data are untransformed. Error bars are standard errors.*

5.3.3 Long term temporal patterns of bioerosion

When all surfaces at each site on the four reefs were considered, the regression of internal bioerosion versus duration of exposure was significant at all sites. However only at the two sites on Green Island (excluding the oldest surfaces) and one site at Low Isles, was the regression linear. All the sites on the remaining three reefs showed a significant deviation from linearity (Table A46). This indicates a non-linear relationship between the extent of internal bioerosion and the duration of exposure of the substrates to borers. The transformation $X_1=1x(X^4+1)^{-1}$ made the regressions linear at all sites (Table A46), but it flattened the relationship to such an extent that the regression coefficients were not different from zero.

To highlight the non-linear relationship of bioerosion with time, the instantaneous rates of bioerosion for each surface were plotted against time (Figures 5.12 to 5.15). Instantaneous rates of bioerosion were obtained by regressing the extent of excavation on the duration of exposure, and forcing the regression through zero. Rates of total bioerosion and bioerosion by worms decreased with time of exposure at all reefs, and approached a lower asymptote after approximately 18-20 years of exposure to borers.

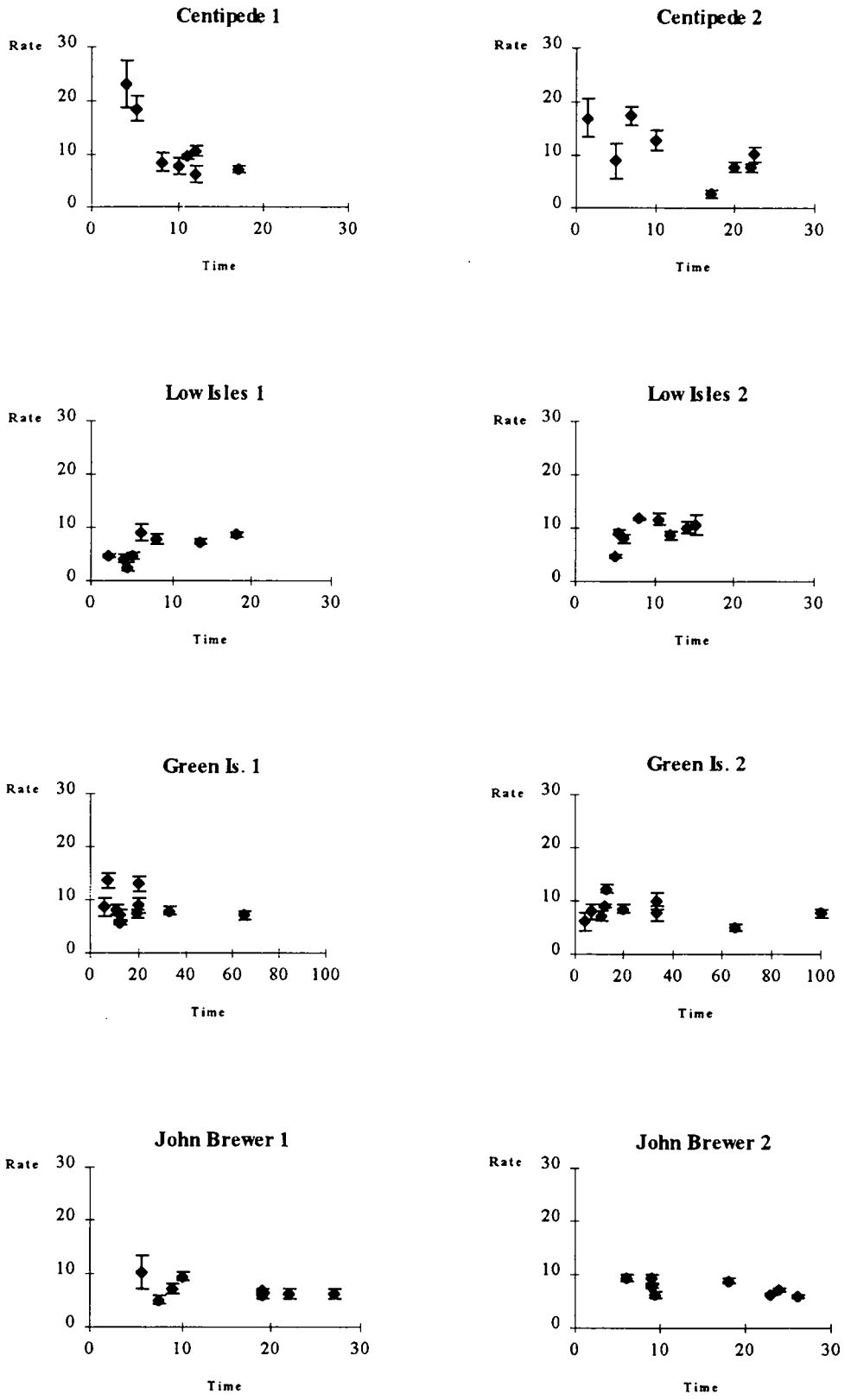


Figure 5.12: Rate of bioerosion by all taxa (gr $CaCO_3$ m^{-2} y^{-1}) plotted against duration of exposure to borers (years). Each point represents one Porites *surface. Data are transformed as x_1=sqrt(x+1)*

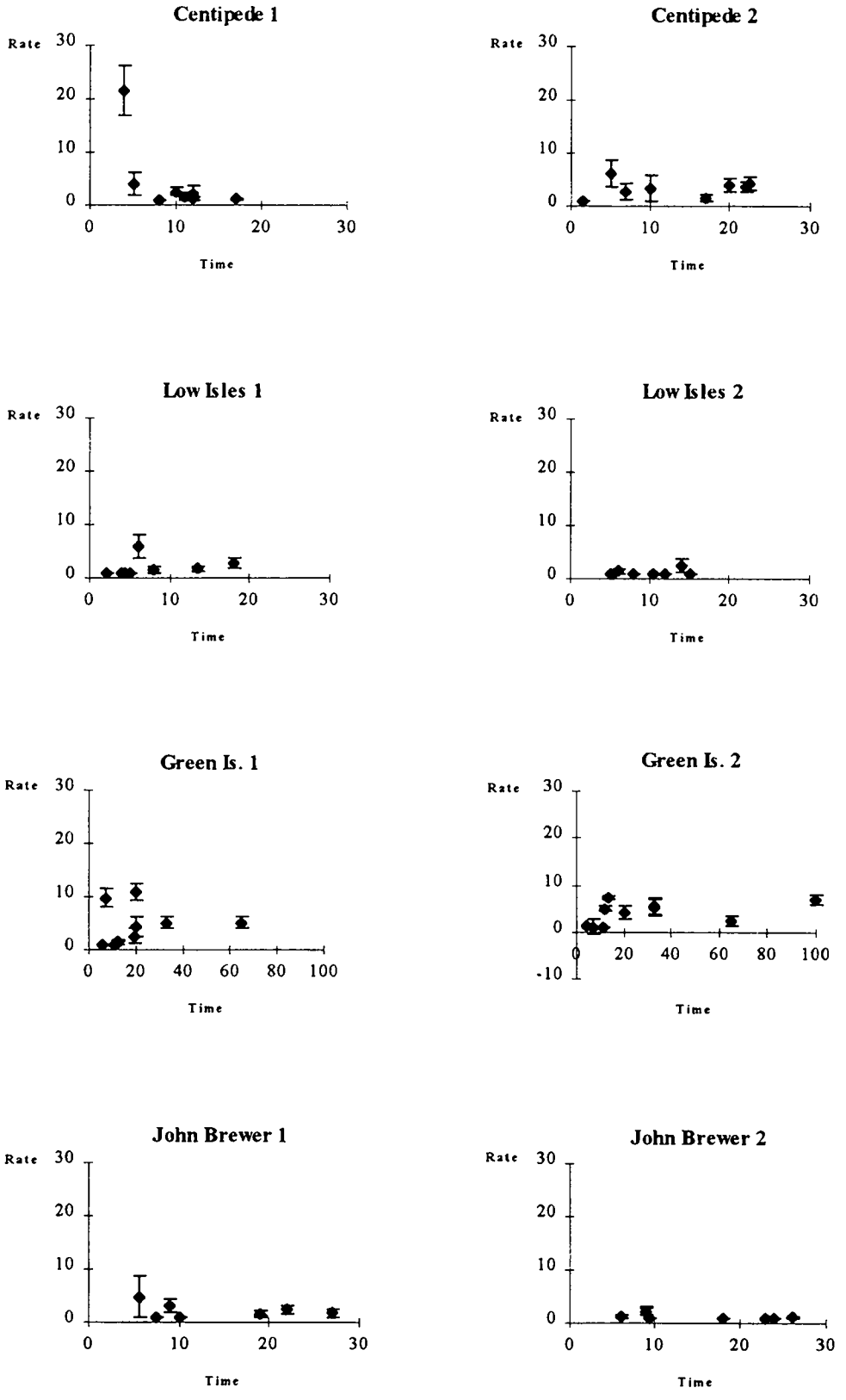


Figure 5.13: Rate of bioerosion by sponges (gr $CaCO_3$ m^{-2} y^{-1}) plotted against duration of exposure to borers (years). Each point represents one Porites *surface. Data are transformed as x_1=sqrt(x+1)*

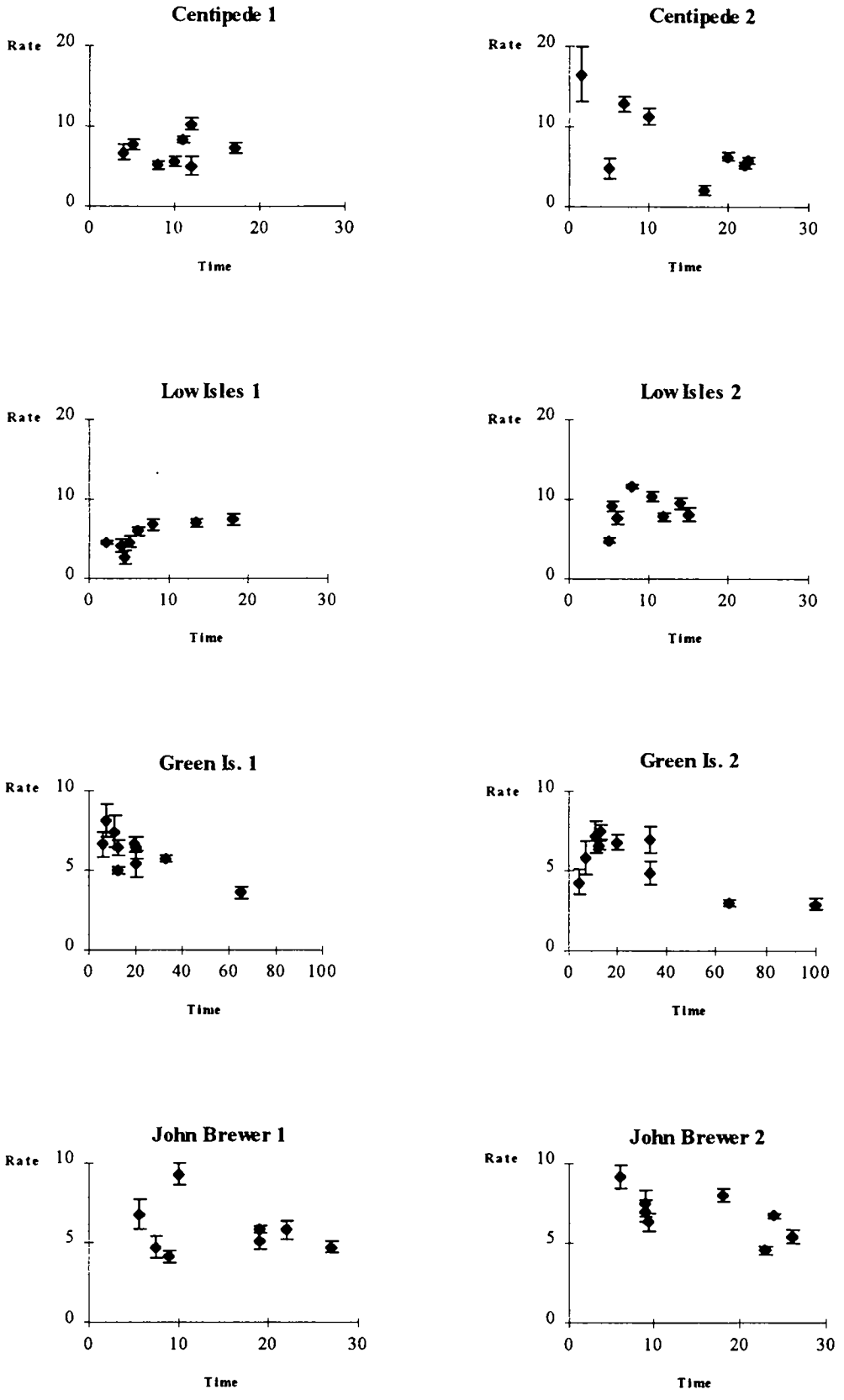


Figure 5.14: Rate of bioerosion by WORMS (gr $CaCO_3$ m^{-2} y^{-1}) plotted against duration of exposure to borers (years). Each point represents one Porites *surface. Data are transformed as x_1=sqrt(x+1)*

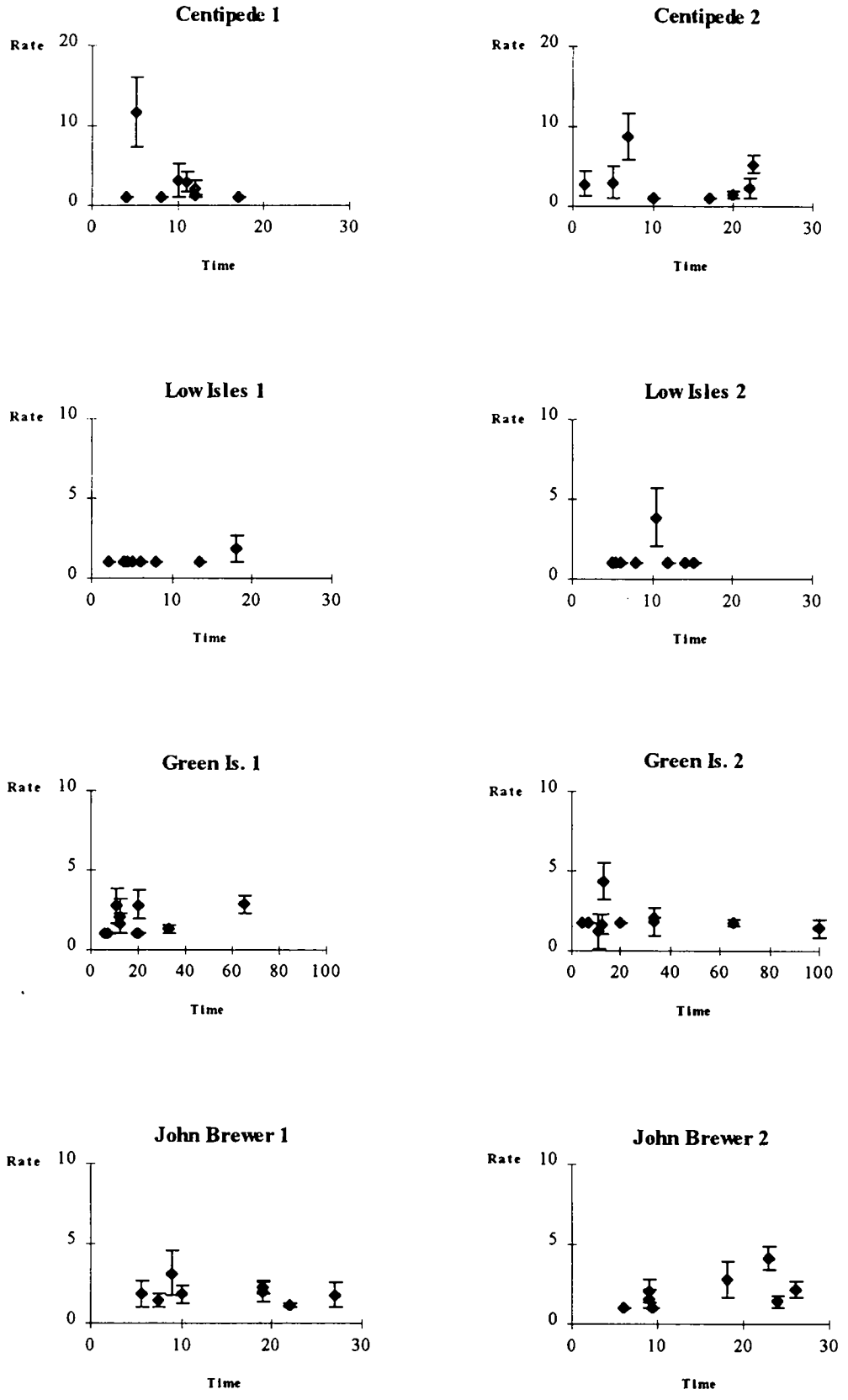


Figure 5.15: Rate of bioerosion by bivalves (gr $CaCO_3$ m^{-2} y^{-1}) plotted against duration of exposure to borers (years). Each point represents one Porites *surface. Data are transformed as* $x_1=sqrt(x+1)$

5.3.4 Reef comparison and COTS outbreak status

When only three surfaces per site were considered (Table 5.3; Figures 5.16 to 5.18), the relationship between extent of bioerosion and 'time' of the surface was highly significant (F_s=38.50; $F_{0.05;1,122}$=5.15, p=0.0001; Table A47). The effect of site was significant also (F_s=6.07; $F_{0.05;4,122}$=2.89, p=0.0002). The significance of the interaction between site and the covariate 'time' indicated that the slope of the regressions (i.e. rates of bioerosion) were different at different sites (Table A47). This effect was mainly due to site 2 at Centipede Reef and site 2 at Low Isles, which had higher rates of bioerosion (Table 5.8; Figures 5.16 and 5.19).

The ANOVA including the factor 'stage' with surfaces within sites classified as 'old' or 'recent' (see 5.2.6), showed approximately the same patterns as displayed by the previous analysis. Total bioerosion and bioerosion by worms (Tables A48 and A49) was not significantly different between the two 'stages' but the F ratio was high (F_s=20.46; $F_{0.05;1,2}$=38.5, p=0.08; Table A49). Bioerosion by worms was significantly different among sites (F_s=5.46; $F_{0.05;4,76}$=2.97, p<0.001; Table A49). The significant interaction between site and 'stage' was due to site 2 at John Brewer Reef, where the older surfaces was less eroded by worms than the younger ones (Figure 5.20).

	Total	Sponges	Worms	Bivalves
Centipede 1	12.60	-	*9.26*	-
	2.39	-	*1.11*	-
Centipede 2	22.58	5.29	14.16	-
	5.49	2.34	2.84	-
Low Isles 1	13.72	1.56	11.16	-
	1.04	0.59	1.12	-
Low Isles 2	28.65	-	*23.79*	-
	3.70	-	*2.42*	-
Green Is. 1	12.96	-	9.83	-
	1.73	-	1.05	-
Green Is. 2	16.01	4.86	9.52	-
	1.85	1.46	1.13	-
John Brewer 1	10.94	-	9.36	-
	1.59	-	1.28	-
John Brewer 2	12.70	-	*7.57*	3.95
	1.19	-	*1.29*	0.86

Table 5.8: Regression coefficients and standard errors for the regressions of extent of bioerosion (mm^3) on 'time' (y) for three surfaces per site on the four reefs (see 5.3.3). Missing cells represent non significant regressions. Regression coefficients in italics and underlined deviated significantly from linearity. Data are untransformed.

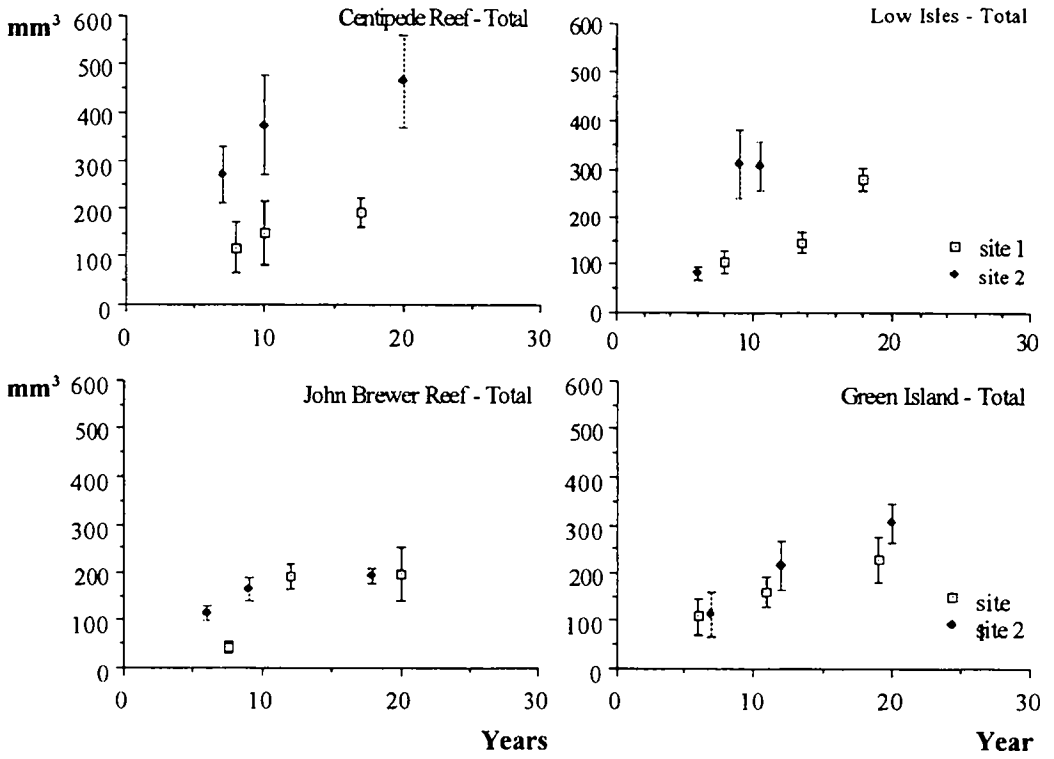


Figure 5.16: Untransformed mean volume removed per core by all taxa plotted against time for the three surfaces selected for the inter-reef comparison (see 5.3.4). Error bars are standard errors.

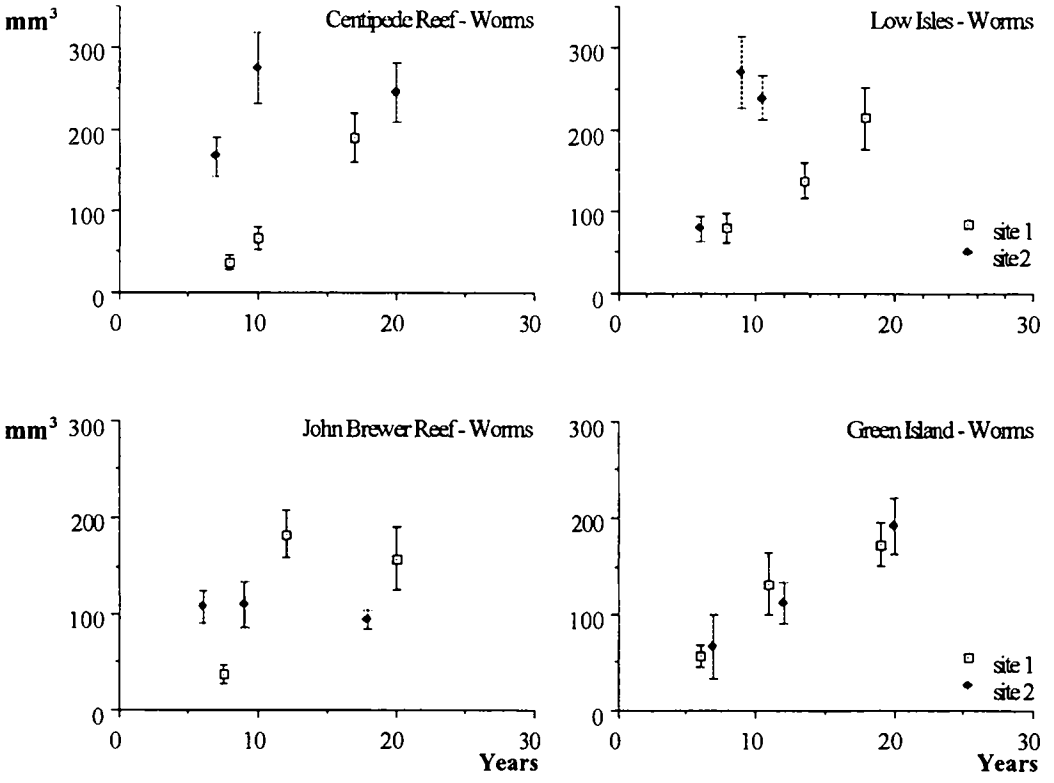


Figure 5.17: Untransformed mean volume removed per core by WORMS plotted against time for the three surfaces selected for the inter-reef comparison (see 5.3.4). Error bars are standard errors.

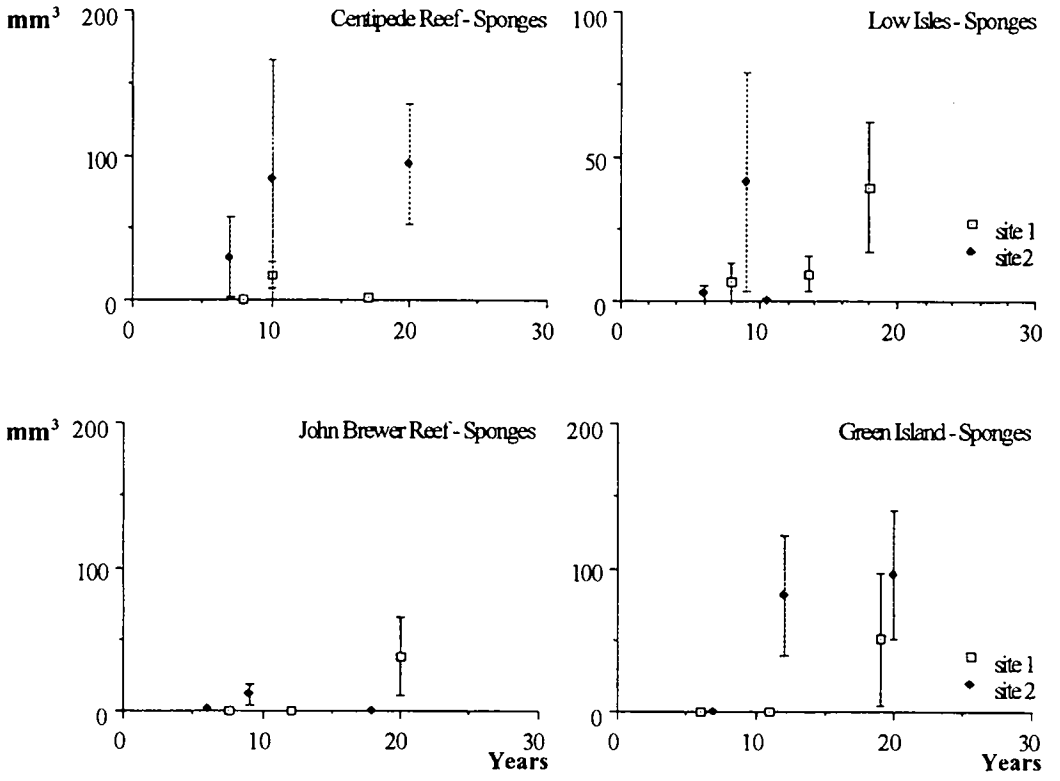


Figure 5.18: Untransformed mean volume removed per core by sponges plotted against time for the three surfaces selected for the inter-reef comparison (see 5.3.4). Error bars are standard errors.

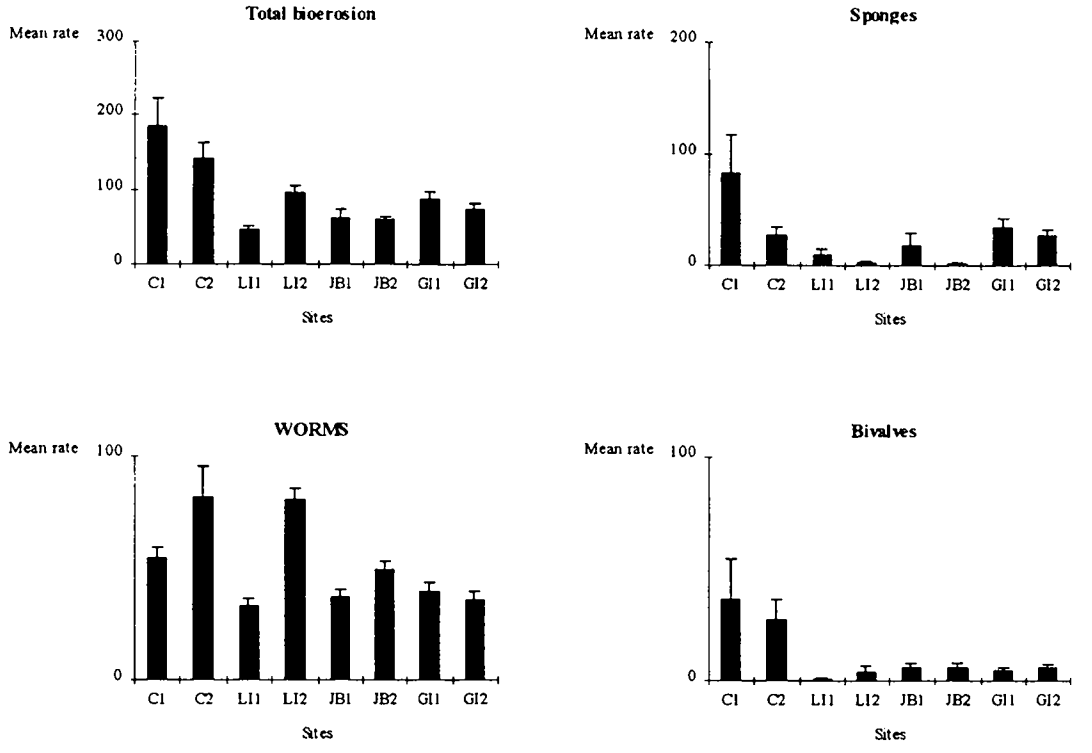
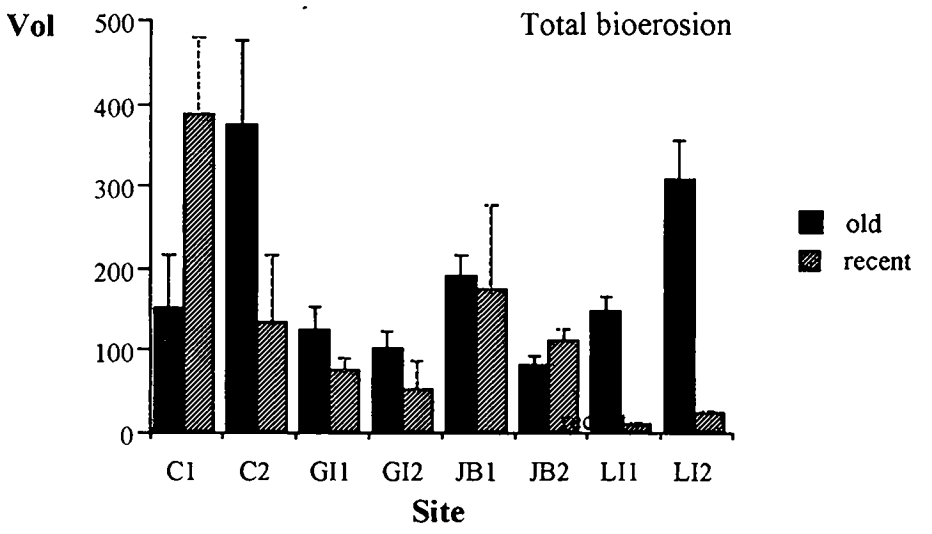


Figure 5.19: Mean rate (g $CaCO_3$ m^{-2} y^{-1}) of internal bioerosion by all taxa and by sponges, WORMS and bivalves at all reefs and sites. Data are untransformed. Error bars are Standard Errors (n=48 for C, LI and JB sites and n=50 for GI sites).



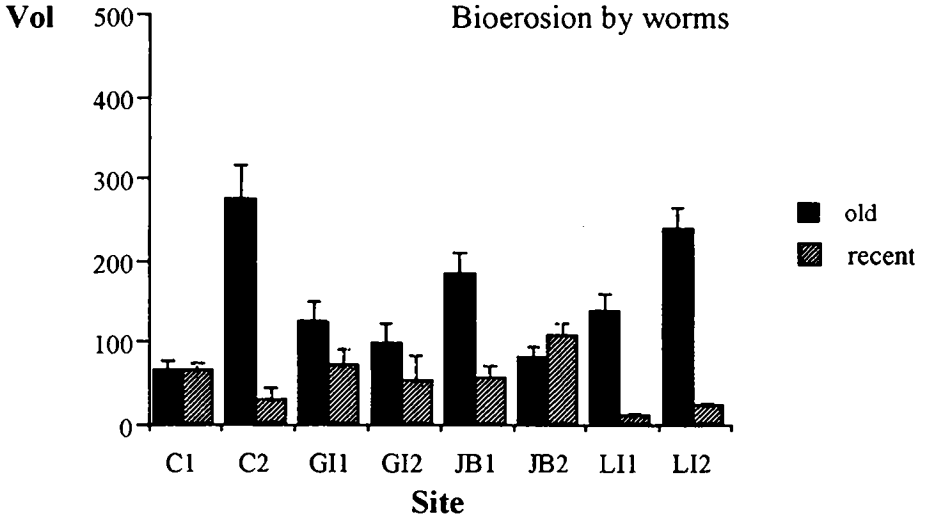


Figure 5.20: Mean volume (mm^3) removed per core by all taxa and by WORMS in "new" and "old" surfaces (see 5.3.4) at each site on Centipede Reef (C1&2), Green Island (GI1&2), John Brewer Reef (JB1&2) and Low Isles (LI1&2). Data are untransformed. Error bars are standard errors.

5.3.5 Long term rates of internal bioerosion in Porites

Two rates of internal bioerosion by all taxa were calculated for Green Is., using the common regression coefficients estimated at each site (Table 5.9). At the two sites, 6.8 ± 0.9 and 7.5 ± 1.2 g $CaCO_3$ respectively, were removed by internal bioeroders per m^2 per year, when all surfaces sampled are considered.

	Site 1	Site 2
Rate ($gCaCO_3\ m^{-2}\ y^{-1}$)	6.83	7.49
	0.99	*1.25*

Table 5.9: Mean rates of internal bioerosion expressed as g of $CaCO_3$ removed by internal bioeroders per m^2 per year from dead Porites *surfaces at the two sites on Green Island. Standard errors are in italics below estimates.*

These rates were similar, although slightly smaller, to the rates obtained by including only the three surfaces per site that had similar values of 'time' across the four reefs (Tables 5.8 and 5.10). The rates ranged from 8.7 ± 1.3 to 22.9 ± 2.9 g $CaCO_3$ per m^2 per year across the four reefs.

These rates were calculated assuming that they are linear over the period of time considered in the study (33 years). However, this assumption does not hold when all the surfaces sampled per site were considered. An instantaneous rate of bioerosion was therefore calculated for each surface sampled, as the average weight of calcium carbonate removed by each group divided the time of exposure. These estimates allow the variation in rate of bioerosion to be examined among a number of substrates that have been exposed for various durations. The instantaneous rates of total internal bioerosion varied from 8.8 ± 3.9 to 625.9 ± 170.8 g CaCO3 $m^{-2}\ y^{-1}$.

	Site 1	Site 2
Centipede Reef	10.08	18.06
	1.91	*4.39*
Low Isles	10.98	22.92
	0.83	*2.96*
Green Island	10.37	12.81
	1.38	*1.48*
John Brewer Reef	8.75	10.16
	1.27	*0.95*

Table 5.10: Mean rates of internal bioerosion expressed as g of $CaCO_3$ removed by all internal bioeroders per m^2 per year from dead Porites *surfaces at the two sites on the four reefs. Rates were obtained from regression coefficients of bioerosion in three surfaces per site at the four reefs (see 6.3.3). Standard errors are in italics below estimates.*

	'Time'	Total	SPONGES	WORMS	BIVALVES	BARNACLES	OTHERS
C1	4	625.88	576.98	48.90	-	-	-
		170.78	*166.12*	*14.54*	-	-	-
	5	368.68	38.23	61.56	232.05	25.85	10.99
		92.32	*28.44*	*10.56*	*110.84*	*10.40*	*7.77*
	8	85.64	-	26.56	-	-	59.08
		34.62	-	*4.30*	-	-	*36.61*
	10	71.38	8.17	31.92	30.70	-	0.59
		31.58	*4.41*	*6.46*	*30.70*	-	*0.59*
	11	91.50	4.51	68.24	15.26	-	3.48
		9.36	*4.51*	*6.65*	*9.90*	-	*2.57*
	12	48.61	13.42	30.94	0.53	-	3.73
		20.16	*13.42*	*11.38*	*0.53*	-	*3.73*
	12	117.75	1.46	107.03	9.26	-	-
		19.90	*1.46*	*12.86*	*9.26*	-	-
	17	54.35	0.47	53.80	-	-	0.08
		8.62	*0.47*	*8.47*	-	-	*0.08*
C2	1.5	299.35	-	282.93	16.42	-	-
		63.13	-	*55.84*	*16.42*	-	-
	5	128.59	70.50	29.63	27.21	-	1.25
		78.37	*39.05*	*14.54*	*27.21*	-	*1.25*
	7	318.83	20.10	167.80	120.24	6.98	3.71
		65.84	*19.10*	*24.39*	*55.71*	*6.98*	*3.71*
	10	179.31	39.86	131.28	-	-	8.17
		49.43	*39.86*	*20.83*	-	-	*5.25*
	17	8.75	3.05	5.70	-	-	-
		3.96	*3.05*	*3.53*	-	-	-
	20	64.91	22.47	39.95	2.13	-	0.36
		13.96	*10.00*	*5.77*	*2.13*	-	*0.36*
	22	61.93	18.11	26.90	12.11	3.81	1.00
		13.36	*7.78*	*3.88*	*12.11*	*3.81*	*1.00*
	22.5	115.09	26.50	34.79	33.29	-	20.51
		34.51	*15.48*	*5.49*	*12.12*	-	*13.69*
LI1	2	20.61	-	20.61	-	-	-
		2.24	-	*2.24*	-	-	-
	4	20.70	-	20.70	-	-	-
		7.73	-	*7.73*	-	-	-
	4.5	9.47	-	9.47	-	-	-
		6.11	-	*6.11*	-	-	-
	5	23.19	-	23.19	-	-	-
		6.11	-	*6.11*	-	-	-
	6	95.95	59.29	36.66	-	-	-
		31.28	*31.26*	*6.12*	-	-	-
	8	63.15	3.92	48.27	-	10.95	-
		13.68	*3.92*	*10.82*	-	*10.95*	-
	13.5	52.29	3.34	48.94	-	-	-
		7.28	*2.23*	*7.69*	-	-	-
	18	74.06	10.53	57.23	6.30	-	-
		6.32	*6.00*	*10.11*	*6.30*	-	-

To be continued...

Table 5.10: *Instantaneous rates of bioerosion (g $CaCO_3$ m^{-2} y^{-1}) for each* Porites *sp. surface sampled at each site. "Time" is an estimate of the duration of exposure of the surface to bioeroders. Sample size is n=6 cores for all sites but GI1 and GI2, where n=5, and C2 with 'time'=1.5, where n=4.*

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	'Time'	Total	SPONGES	WORMS	BIVALVES	BARNACLES	OTHERS
LI2	5	22.78	-	22.78	-	-	-
		3.30	-	*3.30*	-	-	-
	5.5	84.66	-	84.66	-	-	-
		10.33	-	*10.33*	-	-	-
	6	65.44	2.22	63.22	-	-	-
		11.22	*2.22*	*12.33*	-	-	-
	8	136.81	-	136.81	-	-	-
		4.40	-	*4.40*	-	-	-
	10.5	140.07	-	108.94	31.13	-	-
		23.29	-	*11.96*	*20.07*	-	-
	12	77.60	-	61.97	-	-	15.63
		16.42	-	*9.07*	-	-	*9.96*
	14	106.79	14.17	92.62	-	-	-
		24.23	*13.06*	*14.94*	-	-	-
-	15	126.93	-	67.93	-	-	59.01
-		*51.15*	-	*13.14*	-	-	*59.01*
JB1	5.5	150.98	95.36	49.31	6.31	-	-
		91.26	*95.36*	*12.06*	*6.31*	-	-
	7.5	28.05	-	23.38	1.86	-	2.82
		8.19	-	*6.38*	*1.86*	-	*2.82*
	9	55.47	17.48	16.83	18.43	-	2.73
		12.93	*11.06*	*3.20*	*11.80*	-	*1.98*
	10	91.72	-	87.84	3.88	-	-
		12.15	-	*11.84*	*2.58*	-	-
	19	45.24	4.04	33.42	4.65	-	3.14
		4.55	*4.04*	*2.20*	*3.08*	-	*2.49*
	19	34.48	2.71	26.73	5.04	-	-
		6.41	*1.86*	*6.25*	*1.73*	-	-
	22	43.08	8.36	34.36	0.36	-	-
		11.89	*6.03*	*7.19*	*0.36*	-	-
	27	41.64	5.31	22.22	5.29	0.67	8.16
		12.99	*5.31*	*4.03*	*5.29*	*0.67*	*6.11*
JB2	6	89.96	1.11	85.78	-	-	3.06
		12.41	*1.11*	*12.87*	-	-	*3.06*
	9	61.04	7.09	50.49	3.46	-	-
		6.92	*4.85*	*9.90*	*3.46*	-	-
	9	87.43	6.00	58.59	6.05	-	16.79
		11.98	*3.80*	*12.76*	*4.16*	-	*12.21*
	9.5	40.54	-	40.54	-	-	-
		7.24	-	*7.24*	-	-	-
	18	78.34	-	64.54	13.80	-	-
		6.03	-	*7.27*	*8.80*	-	-
	23	40.04	-	19.80	19.06	-	1.18
		3.36	-	*2.02*	*5.47*	-	*1.18*
	24	51.85	-	44.77	1.83	0.98	4.26
		3.95	-	*1.97*	*1.83*	*0.98*	*4.26*
	26	34.85	0.25	28.91	5.25	-	0.45
		4.56	*0.25*	*4.47*	*2.66*	-	*0.45*

To be continued...

Table 5.10: *Instantaneous rates of bioerosion (g $CaCO_3$ m^{-2} y^{-1}) for each* Porites *sp. surface sampled at each site. "Time" is an estimate of the duration of exposure of the surface to bioeroders. Sample size is n=6 cores for all sites but GI1 and GI2, where n=5, and C2 with 'time'=1.5, where n=4.*

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	'Time'	Total	SPONGES	WORMS	BIVALVES	BARNACLES	OTHERS
GI1	6	86.56	-	45.64	-	-	40.92
		29.64	-	*8.99*	-	-	*23.24*
	7	192.61	105.76	68.91	-	-	17.94
		40.68	*34.62*	*17.50*	-	-	*13.15*
	11	69.45	-	57.74	11.71	-	-
		13.68	-	*14.13*	*7.39*	-	-
	12	52.97	0.90	41.45	8.49	-	2.13
		11.73	*0.90*	*5.59*	*8.49*	-	*2.13*
	12	30.63	2.10	24.08	3.26	-	1.19
		2.92	*2.10*	*2.12*	*3.26*	-	*1.19*
	19	57.39	12.72	43.82	-	-	0.84
		12.20	*11.65*	*5.72*	-	-	*0.57*
	20	87.26	30.71	42.24	-	-	14.30
		26.52	*21.74*	*10.06*	-	-	*8.18*
	20	177.38	130.77	31.12	10.14	-	5.35
		35.92	*32.14*	*9.18*	*6.07*	-	*4.38*
	33	64.00	29.23	31.91	0.90	-	1.96
		10.45	*11.06*	*2.52*	*0.67*	-	*0.97*
	65	51.63	29.29	12.64	8.66	-	1.04
		10.93	*9.77*	*2.93*	*3.61*	-	*0.89*
GI2	4	42.37	1.30	20.04	4.78	-	16.25
		12.66	*1.30*	*6.79*	*4.78*	-	*9.96*
	7	77.23	-	46.06	4.50	-	26.66
		31.68	-	*23.15*	*4.50*	-	*9.30*
	11	52.79	-	51.41	0.65	-	0.74
		7.92	-	*7.61*	*0.65*	-	*0.74*
	12	86.40	32.44	44.74	2.29	-	6.93
		20.54	*16.95*	*8.55*	*1.47*	-	*3.34*
	13	151.06	62.78	58.09	27.12	-	3.07
		20.41	*25.08*	*13.84*	*13.71*	-	*2.35*
	20	73.39	22.94	46.05	3.31	-	1.09
		9.89	*10.58*	*7.14*	*2.80*	-	*0.67*
	33	100.92	44.98	51.28	3.88	-	0.79
		14.37	*22.55*	*14.40*	*3.18*	-	*0.79*
	33	69.45	37.71	24.50	6.12	-	1.12
		26.91	*17.42*	*5.77*	*5.02*	-	*1.02*
	65	24.87	7.77	8.53	2.32	-	6.25
		5.58	*4.99*	*1.59*	*1.00*	-	*2.89*
	100	61.81	51.07	7.90	1.66	-	1.18
		13.33	*13.38*	*0.91*	*1.54*	-	*0.54*

Table 5.10: *Instantaneous rates of bioerosion (g $CaCO_3$ m^{-2} y^{-1}) for each* Porites *sp. surface sampled at each site. "Time" is an estimate of the duration of exposure of the surface to bioeroders. Sample size is n=6 cores for all sites but GI1 and GI2, where n=5, and C2 with 'time'=1.5, where n=4.*

5.4 Discussion

The results of this study depend on the validity of the two assumptions underlying the methods used to estimate bioerosion. Firstly, the extent of excavation in the living surfaces on *Porites* colonies is assumed to be zero. This assumption was tested by sampling living surfaces on two of the four reefs, where the amount of excavation was in fact zero. It is further supported by previous studies that showed that internal borers in large living colonies of *Porites lobata* were restricted to two species of molluscs that occurred rarely (Peyrot-Clausade *et al.* 1992). The second assumption is that the effect of external degradation on the dating of the surfaces is negligible. That is to say the lowering of the dead surface by the action of grazers does not occur at such a rate that it biases the estimated date of death of the *Porites* tissue. It is apparent from published rates of bioerosion expressed as surface lowering (Table 3.13), that many years (20 years according to Spencer 1985, and approximately 7.5 years as for Bromley 1978) are necessary to lower a surface by 1 cm. Given the average rate of growth in *Porites,* such rate of external bioerosion would cause the dating of the substrate to be overestimated by only one year for every ten or twenty years of exposure. Hence, it is considered unlikely that this would have been a source of significant bias in this study.

5.4.1 Temporal and spatial patterns of internal bioerosion in dead Porites

The results of this study indicate that rates of bioerosion are not constant over time and that the temporal patterns of rates of bioerosion vary among the groups of borers considered. While volume excavated by worms consistently increased with time for all reefs, bioerosion by sponges and bivalves did not show a consistent pattern with increasing duration of exposure. Although bivalves and sponges tended to become more common with increasing time, this was not always the case, suggesting that recruitment for these two groups of borers is patchy at both spatial and temporal scales. The category WORMS in this study included almost exclusively sipunculans. These were found in all dead *Porites* surfaces sampled, and overall they were the most important borers of the substrates at all reefs (Figure 5.8). This parallels the findings of Hutchings (1974) and Peyrot-Clausade *et al.* (1992), who found that sipunculans were the most abundant borers in large dead colonies of *Porites* species.

At three of the four reefs sampled, the relationship between the extent of internal bioerosion and the duration of exposure of the substrate was not linear. At the reefs with surfaces exposed for more than 20 years, the rates appeared to approach an asymptote after approximately 20 years. The youngest surfaces sampled i.e. 1.5 years exposure at Centipede Reef, had an instantaneous rate of bioerosion more than 6 times higher than older surfaces, suggesting that bioerosion is much more rapid during the early stages of exposure and decreases with time. This suggests that temporal patterns in rates of bioerosion in *Porites* may best be described by a logistic curve.

Temporal variability in rates of bioerosion have previously been investigated in *Porites* substrates using an experimental approach, over a 4 years period (Hutchings and Bamber 1985; Hutchings *et al.* 1992). Their study demonstrated large inter-year variations in the numbers and composition of non-colonial borers (Hutchings *et al.* 1992). They clearly showed that within non-colonial borers, many species are short lived and their numbers decline after few months (12 to 25) since the substrate became available. They also found that within boring polychaetes, some species seem to recruit throughout the year and are usually pioneer species (e.g. *Polydora* spp. and Fabricinae), while some others have seasonal recruitment, e.g. eunicids. Sipunculans, bivalves and the polychaetes of the family Eunicidae appear to be long term species, which are present in substrates exposed for long periods, and whose number increases with duration of exposure (Hutchings *et al.* 1992). The present study confirms this pattern. However, it is not clear how the inter-year and seasonal variations in recruitment of individual groups of borers can affect the rates of bioerosion of the substrate, especially in the long term. Hutchings *et al.* (1992) suggest that pioneer, short lived polychaetes may be responsible for micro-modifications of the substrate, which facilitate bioerosion by other borers. This would result into a succession of macroborers in newly available substrates, from pioneer polychaetes to bivalves and sipunculans (after 12-15 months; Davies and Hutchings 1983) and finally boring sponges (after 2-3 years; Hutchings and Bamber 1985, Kiene 1985). Within this model, and for substrates where colonisation by borers is via recruitment of pelagic larvae, initial rates of bioerosion should be low, as most species of polychaetes are small sized and are responsible for small excavations (e.g. few millimetres for

Polydora spp. and Fabricinae). Rates of bioerosion should then increase dramatically when destructive borers such as sponges and bivalves, colonise the substrate. During the present study, however, the opposite trend was evident at some sites, where rates of bioerosion tended to decrease with increasing time of exposure. It is likely that the samples collected in this study had been exposed for too long a period to reveal any of the temporal patterns predicted by the model of succession described above. It remains to be known how such initial patterns may affect later borers, and ultimately rates of bioerosion. In this context, the large variations observed in this study in rates of bioerosion among substrates exposed for varying times, may be due to spatial effects (local conditions for recruitment) and/or to an interaction bewteen local and temporal factors, whereas substrates that initially have been colonised by certain borers due to local effects, follow a pattern which depends on those initial stages. However, the pattern of decreased rates of bioerosion with time of exposure, as observed in this study, suggests that variations due to initial patterns in boring community composition become overidden after long exposure periods. This overriding effect is likely to occur quickly, as initial rates of excavation, at least for sponges, are very high (Nuemann 1966; Rutzler 1975).

In Moorea, French Polynesia, Peyrot-Clausade *et al.* (1992), investigating internal bioerosion in dead *Porites* heads at four different stages of colony degradation, suggested that rates of bioerosion increase with time after the death of the colony. They attributed this increase to changes over time in the relative abundance of different boring agents, from bivalves to sipunculans. However, in that study, time elapsed since the death of the colony was only approximately estimated by the appearance of the coral head, and therefore it was not possible to obtain an estimate of the rate of bioerosion at each stage of degradation. Results from this study suggest that while the amount of skeleton removed by boring worms per unit of surface area increases with time after the death of the coral, the actual rates of bioerosion decrease. This may be explained by density dependent mechanisms which affect the recruitment of borers and/or physiological constraints of borers, which prevent them from excavating deeper than few centimetres into the substrate (Highsmith 1981a), Either of these mechanisms may result in "saturation" of the substrate. Further studies are

required to examine the dynamics of recruitment of borers to naturally occurring substrates and to determine the rate of growth and excavation by individual taxa (Hutchings 1986).

Spatial patterns investigated across the four reefs indicated that rates of total bioerosion were relatively uniform among the different sites and reefs (Figure 5.17). However, a few sites displayed unusually high values, which resulted in a significant effect for site. These high values may be either an artefact derived from incorrect dating of the substrates (they occurred at sites on Centipede Reef and Low Isles, Figure 5.17, for which dating was more difficult, see 5.2.5 and Table 5.1), or may reflect a local occurrence of genuinely higher rates of bioerosion. Spatial patterns in the extent of internal bioerosion were examined at multiple and finer scales on Green Island. After accounting for duration of exposure, which was the most important source of variation in the data, most of the variability was accounted for by differences among small spatial scales. The difference among sites (hundreds of meters) explained a negligible portion of the total variation, while the smaller spatial scales found within a site, accounted for most of the variability. These included, in descending order of importance, differences due to error, which include the between cores variation (centimetres), among surfaces within colonies (within 1-2 meters) and among colonies (approx. 2-20 meters). These patterns were the same for the three major taxa considered, worms, sponges and bivalves. This supports the results described in the previous chapters for internal bioerosion in living and dead colonies of *Acropora*. Processes operating at small spatial scales are most important in determining patterns of bioerosion. It also is in agreement with previous results by Sammarco and Risk (1990), who reported that up to the 56% of the variance in the extent of bioerosion in small *Porites* heads was due to variation among heads (a large portion of which may be due to failure to account for the extent of dead surface area; see Chapter 2), and a further 20% to variability within heads (although this is likely to be an underestimate, as it represents variation among sections of a colony, which may be non-independent). The results from the pilot study at Green Island may assist in interpreting the patterns of variation observed on the other three reefs. On Centipede, Low Isles and John Brewer reefs, the effect of duration of exposure could not be satisfactorily partitioned

out by the analysis used, as the relationship of bioerosion and time was not linear. Moreover, the spatial factor 'colony' was not included in the design, since on Centipede and Low Isles reefs *Porites* colonies with more than one dead surface were rare (interestingly, they were common on both Green Island and John Brewer, where they could be the result of the multiple Crown-of-Thorns outbreaks these two reefs experienced - see COTS-CCEP Team 1986). This means that two factors that were responsible for large variations in bioerosion on Green Island (viz. duration of exposure and colony) could not be accounted for when considering inter-reef comparisons.

A comparison of the composition of boring communities across the reefs, however, showed some differences among sites and reefs. The agents of bioerosion encountered during this study displayed different temporal and spatial patterns of occurrence. The major contrast was that between the relatively uniform distribution of worms and the patchy distribution of sponges and bivalves in both time and space (Figure 5.10 to 5.13). Worms were present in all cores that had been excavated. Bioerosion by worms had a tendency to increase with time since death of the substrate at all reefs . In contrast, boring sponges did not show a clear temporal pattern, rather they occurred patchily with large excavations in both old and new substrates. However, where they were common, i.e. Green Island, bioerosion by sponges appeared to increase in older substrates (Figure 5.12). Bivalves were very patchily distributed. They occurred in a small proportion of the surfaces sampled, but this varied among reefs. Kiene and Hutchings (1992) reported patchy patterns of spatial distribution for both bivalves and sponges in experimental substrates which had been exposed for 7-9 years. Despite their patchy distribution, however, both sponges and bivalves are much more destructive than worms. This results in these two unevenly distributed groups controlling the total amount of bioerosion and overriding the temporal and spatial patterns displayed by bioerosion by worms, as it is evident from the comparison among these taxa (Figures 5.15, 5.16 and 5.18). Therefore, it is suggested that bioerosion by worms should be used to investigate changes in patterns of bioerosion, as variability in time and space of other borers is high even at the relatively large temporal and spatial scales considered in this study. However, it must be remembered that groups other than worms are

responsible for most of the internal bioerosion of reef substrates, and ultimately control the impact of macroborers on coral reefs.

Rates of bioerosion in *Porites* substrates estimated from this study and expressed as $gCaCO_3\ m^{-2}y^{-1}$ were low when compared to previous studies on the same type of substrate (Davies and Hutchings 1983; Hutchings and Bamber 1985) or different substrates (this study, Chapter 3, and Table 3.14). A possible explanation is that rates calculated over long periods of time, such as the ones from this study, are lower than rates calculated over shorter times, i.e. 1-3 years as in most experimental studies (Davies and Hutchings 1983; Hutchings and Bamber 1985; Chapter 3). This is due to two factors: firstly, rates of excavation by individual borers may be higher in the initial stages, as a result of high initial growth rates. This has been demonstrated to be the case for sponges (Rützler 1975). Secondly, the substrate may become saturated, with the borers present at any one time inhibiting the settlement or growth of other borers. Another explanation, at least for the difference in rates of bioerosion among the coral substrates considered in this study (*Porites* vs. *Acropora* spp.), may be a difference in boring community composition. The dead *Porites* surfaces sampled were mainly eroded by worms, particularly sipunculans. The composition of the boring community affects the rates considerably, as worms remove little substrate when compared to other borers (Hutchings *et al.* 1992).

The difference in composition of boring communities and relative importance of individual boring groups was a major contrast between bioerosion in dead *Acropora* (Chapter 3) and *Porites* (Chapter 5) substrates. Comparisons between the results of the two studies can only be speculative, because they were carried out on different reefs and regions of the GBR. However, such comparison is an interesting hypothesis generating exercise. The major, and striking, differences between the borers in the three species of *Acropora* and in dead *Porites* surfaces were i) the presence and bioerosive significance of sipunculans in *Porites* colonies while they were not observed in the *Acropora* colonies, where the group worms was made up almost exclusively by polychaetes; and ii) the difference in the relative importance of sponges as bioerosive agents, with this group being sporadic in *Porites* surfaces but ubiquitous

and most destructive in *Acropora* species. Hutchings (1974) at One Tree Island found the highest number of sipunculans in the habitat represented by large areas of massive dead *Porites*. On Lizard Island, Hutchings *et al.* (1992) found that probability of occurrence of sipunculans in blocks exposed for various times, increased with time of exposure. Two hypotheses may be suggested from these observations. First, sipunculans settle preferentially on dead *Porites* surfaces. This would indicate a preference for substrates exposed to grazers and with very low structural complexity. Secondly, as suggested by previous authors (Davies and Hutchings 1983 and Hutchings *et al* 1992), settle on substrates that have been exposed for at least few years. It is possible that survival of sipunculans depends on pre-existing borings excavated by previous borers, such as polychaetes. The fact that sipunculans may settle in, and enlarge, polychaete borings may explain why on the dead *Porites* surfaces sampled during this study there was no evidence of worms borings other than the ones occupied by the sipunculans.

On dead *Porites* surfaces boring sponges do not have any other mean of infestation than larval recruitment. In fact these surfaces occur on very large colonies and are usually surrounded by portion of skeleton covered with living tissue. It is interesting therefore to note that on the *Porites* surfaces sampled in this study, boring sponges, although locally very destructive, did not contribute to internal bieorosion to the same extent as in colonies of *Acropora* species. This observation supports the hypothesis presented in Chapter 3, that boring sponge distribution in newly available coral substrates, is mainly determined by the presence and growth of sponge colonies occurring in the adjacent substrates, and that dispersal via sexual reproduction may play a secondary role for this boring taxon.

5.4.2 Significance of COTS outbreaks for reef internal bioerosion

Several authors have suggested that rates of bioerosion following COTS outbreaks may be enhanced by the sudden and massive availability of dead coral substrates (Price 1975; Hutchings 1986; Glynn 1988; Hutchings and Peyrot-Clausade 1988; Scoffin 1992). The population dynamics of boring organisms may change due both to the increased availability of substrate and to the drastic reduction in living coral cover.

These changes could affect different stages in the life history of borers. For example, if more substrate is available for settlement after COTS outbreaks, the population size of borers could increase after few reproductive seasons; the reproductive output could consequently increase and so recruitment, at least for those organisms for which the reef is self-seeding and substrate availability is limiting. Processes such as pre- and post-settlement mortalities could be altered by altered predation pressures. Because boring communities are diverse, different changes in different species could also result in alteration of the community composition. Examples of changes of specific bioeroding communities due to disturbance have been previously documented (Rose and Risk 1985; Glynn 1988; Scott *et al.* 1988). Rose and Risk (1985) reported increases of up to five times in the biomass of *Cliona delitrix* in colonies of *Montrastrea annularis* due to six times increase in bacteria on reefs affected by the untreated sewage from a turtle farm. This resulted in an increase in bioerosion from 18 to 85 g of $CaCO_3$ m^{-2} (Rose and Risk 1985). Their study suggests a prompt response of boring sponges to increase of organic matter in the water. Scott *et al.* (1988) suggested that following an El Niño event, which resulted in 60 to 90% decrease in live coral cover in the East Pacific, recruitment rates of dead coral boring *Lithophaga* spp., and possibly boring sponges, increased. The present study, however, was unsuccessful in detecting any changes in the rates of excavation and patterns of distribution of internal bioeroders following severe episodes of Crown-of-Thorns outbreaks. Several factors that may account for the lack of observed changes are discussed below.

Difficulties in detecting downstream effects of COTS outbreaks have been previously documented. Williams (1986) did not detect changes in abundance of fish in reefs following outbreaks of COTS, with the exception of changes in the abundance of coral polyp feeders, such as several species of chaetodontids (Williams 1986), or in the recruitment rates of species which recruit onto living corals, such as species of chaetodontids and pomacentrids (Williams and English unpublished data, as from Williams 1986). However, it was not possible to detect the expected changes in abundance of herbivorous species following the increase in algal covered substrate after an outbreak. Sano *et al.* (1984) experimentally investigated the effect of loss of live coral tissue on coral-attached species of reef fish. They found that coral polyp

feeders disappeared from experimentally killed colonies. However, as for the study by Williams (1986), the responses of other categories of reef fish were not clear. The lack of effect on organisms such as herbivorous fish or, as in the present case, bioeroding organisms, following episodes of coral mass mortality, may be due to the complexity of the processes that affect such organisms other than live coral cover.

The potential effects that COTS may have on reef bioerosion are likely to manifest themselves over large temporal scales. This study therefore set out to investigate patterns in bioerosion in substrates that had been exposed to borers over a number of years. The analyses implemented in this study did not show any effect of previous infestations by COTS on the rates of bioerosion. However, the limitations of these analyses, as discussed above (5.4.1), should be taken into account. In particular, the impossibility to account for factors such as 'colony', which had been shown to explain a large part of the total variation at Green Island, may have lowered the power of the design to detect inter-reef differences. The results suggest that there was no major change, in either direction, in the amount of $CaCO_3$ removed per unit of surface area and time between reefs affected and non-affected by COTS outbreaks. This implies that the overall amount of *Porites* substrate reworked by borers at Green Island and John Brewer Reef will be greater as a result of the higher cover in dead *Porites* surfaces at these reefs. The increase in bioerosion by borers in *Porites* will be directly proportional to the increase in percent cover of dead *Porites* substrates. It remains to be demonstrated whether there is an effect of COTS outbreaks on the population dynamics of borers, as such an effect would result in a non-linear change in the rates of bioerosion. However, it is difficult to predict the type of change that would occur following an outbreak, as it would depend on whether borers are recruitment or resource limited and there is little or no information on the population dynamics of the major groups of borers. Furthermore as bioerosion is cumulative within the substrate, small changes at any point in time may be dampened by the events that have occurred before and after.

Results from this study show that recently dead *Porites* colonies are excavated by boring organisms at rates that may be much higher than colonies that have been dead

for few years or more. The monitoring of *Acropora hyacinthus* colonies killed *in situ* (Chapter 4) also shows that, at least for the colony size class considered in the experiment, rates of skeletal degradation are very high for this species immediately after death. The implication of high initial rates of bioerosion and external degradation (physical and/or biological) is that overall sediment production rates may temporarily increase above normal levels on reefs following a COTS outbreak. Fabricius and Fabricius (1992), following a re-analysis of data presented by Walbran *et al.* (1989), found a strong correlation between the frequency of COTS ossicles in sediment cores dating back to 7000 yrs BP, and sedimentation rates. They suggested that sedimentation may be considerably increased due to intensified erosive processes following an outbreak (Fabricius and Fabricius 1992). The study by Walbran *et al.* (1989), and consequently the re-analysis by Fabricius and Fabricius (1992), was based on a series of assumptions that have been challenged as unsubstantiated by a number of researchers (Keesing *et al.* 1992; Pandolfi 1992). The interpretation of COTS ossicles in sediment cores as evidence of past occurrence of starfish outbreaks remains speculative. However, results from the present study (Chapters 4 and 5) support a scenario of temporarily increased sediment production rates following mass coral mortality, such as described by Fabricius and Fabricius (1992). In this context, the lack of significant effect when comparing bioerosion in affected vs. unaffected reefs may indicate that measuring bioerosion as volume excavated, as in this study, may be inappropriate to investigate long-term patterns of bioerosion. This study indicates that most *Porites* substrates appear 'saturated' by excavations after few years of exposure (Figure 5.12). This means that any change in time, even a considerable one, would not be evident in data of volume excavated. The hypothesis remains, and is supported by the present study, that sediment production rates may locally and temporarily increase following an outbreak. Studies of changes in sedimentation rates on reefs affected by *Acanthaster planci* could test such hypothesis. Techniques other than the controversial analysis of COTS ossicles in sediment cores, may then be able to detect temporal changes in the reef sedimentation rates. Such techniques could include the use of sediment incorporated in coral skeletons as a recorder of past sedimentation regimes, although such technique needs to be refined in order to increase reliability of the data (Davies 1992).

Chapter 6

General Discussion

6.1 Spatial, temporal and taxonomic complexity of bioerosion

This study set out to investigate patterns of skeletal degradation, with particular emphasis on internal bioerosion, in *in situ* coral substrates at multiple spatial scales, ranging from within colonies to among reefs. The results demonstrate that degradation of *in situ* skeletons by both internal and external erosion varies considerably among coral species; between dead and live colonies; and, generally, within small spatial scales (few centimetres to tens of metres). Furthermore, this study indicates that the mechanisms of invasion of newly available coral substrates by internal bioroders differ widely across the groups of borers considered.

These results have major implications for future research in bioerosion, and these are discussed in detail in the sections below. A more general implication is that any study investigating the impact of bioerosion on reef areas must consider aspects of coral community structure and dynamics also. Moreover, the variety of patterns displayed by major groups of borers suggests that studying the process as a whole, without a deep understanding of the differences in life history strategies of boring organisms, may be misleading; an approach which may be appropriate to investigate one group of borers may overlook the patterns and importance of another. Many of the patterns identified during this study highlight the lack of, and the need for focussed research on basic life history strategies of common and important bioeroders, in order to understand the mechanisms which regulate coral reef bioerosion.

6.1.1 Coral communities and bioerosion

On the reef surface, adjacent coral colonies may be excavated to very different extents. Patchiness in internal bioerosion may be due to many factors which influence both the availability of carbonate substrates to borers and the temporal and spatial distribution of borers. As boring organisms are restricted (with few exceptions) to dead coral substrates, the extent of dead coral cover and the degree to which this changes over time and space will directly affect the distribution of the extent of bioerosion. Furthermore, patchiness in internal bioerosion results from considerable differences in extent and rates of excavation among live or dead colonies of different species (Chapters 2 and 3). This means that coral community composition and the patterns of mortality and

turnover of individual coral species will play an important role in the overall dynamics of bioerosion of the reef framework.

Inter-specific associations also have the potential to modify patterns of bioerosion at relatively small spatial scales. In this study, the occurrence of a specific association between a live-coral borer and one coral species, was responsible for large differences in skeletal excavation among coral species, both before and after death of the colonies. A large portion of the variation among species was also due to the differences in the extent of dead exposed skeleton in living colonies, which in this study was shown to be species-specific. Investigation of such live coral/borer relationships, as well as of inter-specific patterns of coral total and partial mortality and the 'skeletal durability' of corals (Chapter 4) across a range of coral communities is essential for accurate estimates of overall internal reef bioerosion.

The assemblages of coral substrates available to internal bioeroders will vary among reef habitats also (Done 1982). This has important implications for studies that investigate habitat-related pattens of bioerosion and for estimating the contribution of the particular products of different habitats to the total carbonate budget for a reef. The results of studies which use coral blocks placed in different habitats (as Davies and Hutchings 1983 and Hutchings *et al.* 1992), may not necessarily be representative of the actual bioerosion regime in that habitat, as they will not account for variation in bioerosion as resulting from the coral community composition. In such studies, sampling of *in situ* coral substrates is required to validate the representativeness of the experimental blocks. The contextual nature of reef internal bioerosion, whereas the extent of excavation may be strongly dependent on the characteristics of the coral assemblage needs to be taken into account. This is especially important when the focus of the investigation is the impact of bioerosion on reef development and calcium carbonate budget.

6.1.2 Mechanisms of dispersal of macroborers - Some hypotheses for future research

In addition to substrate-related factors, other processes are responsible for the high variation in distribution of borers at small spatial and temporal scales. As most borers

cannot survive outside their boreholes, and adults of many species will not excavate a new hole when extracted from the substrate (Rice 1969; Warme 1975), it is likely that the major controls on the distribution of most borers occur during the early stages of their life history. Very little information is presently available on the recruitment dynamics and dispersal of boring taxa. However, there are strong indications that the mode of dispersal of borers on reef substrates may vary considerably among boring taxa. The distribution patterns of borers described in Chapter 3 and 5 of this thesis independently provided grounds for the hypothesis that boring sponges may use colony growth and fragmentation as their primary mode of infestation of newly available substrates. In contrast, polychaetes and sipunculans appear to recruit to boring communities via settlement of pelagic larvae.

Previous studies by Hutchings and Murray (1982) and Hutchings *et al.* (1992) have described the temporal patterns of recruitment of polychaetes and sipunculans. In this study the strong relationship between bioerosion by worms and surface area suitable for settlement (i.e. dead surface area; Chapters 2 and 3) suggested that patterns of distribution of these categories of borers are dependent on recruitment dynamics and availability of substrate to larvae. However, no study has considered alternative modes of colonisation of a substrate by a boring taxa other than by larval recruitment. On the contrary, the general belief is that all infaunal borers recruit to coral substrates via pelagic larvae (McCloskey 1970; Hutchings 1986).

Evidence from previous studies and the results of this investigation suggest that sponges may disperse by modes other than larval dispersal. Kiene (1985) found sponge borings in dead coral blocks exposed in a lagoon environment for 3 years, but Kiene and Hutchings (1992) did not find sponges boring in blocks at the same site but exposed for 7-9 years. Samples from both studies consisted of three blocks per habitat, likely a sample size too small to infer natural variability both in time and space. In light of results from the present study, which clearly indicated that sponges were ubiquitous and extremely destructive in *in situ* corals, the fact that substrates exposed for 9 years did not show signs of activity of boring sponges appears inconsistent. In Kiene's study larval recruitment would have been the only mode of colonisation of blocks suspended on a grid. These observations reinforce the hypothesis that boring sponges may display

a dispersal strategy which relies more on colony growth and, possibly, fragmentation, than on production of sexual larvae. This hypothesis is supported by a number of observations from previous studies.

Acker and Risk (1985) observed that for the zooxanthellate *Cliona caribbea,* one of the most destructive borers on Atlantic reefs, sponge biomass does not relate to volume of boreholes, and that the sponge tissue seems to migrate towards peripheral areas of active boring. It is tempting to speculate that for sponge colonies of a certain size this may result in the fragmentation of the original colony into several colonies. This mode of dispersal has implications for patterns of abundance and distribution of boring sponges. Pang (1973b), during a thorough descriptive study of the distribution of boring sponges in *Acropora* corals in Jamaica, described a 'clumped' distribution for the three most abundant *Cliona* species. She suggested that "although initial larval settlement is on a given branch of *A.cervicornis,* the sponge will tend to invade contiguous branches" (Pang 1973b). At present, there is little known on the reproductive patterns and population dynamics of boring sponges on coral reefs. Kelly-Borges and Berquist (1988), working on fringing reefs in Papua New Guinea, found that the massive sponge *Spirastrella vagabunda,* produces larvae only every 4 to 5 years. Nevertheless, abundance of this species is high and dispersal is mainly achieved by fragmentation mediated by fish predation (Kelly-Borges and Bergquist 1988). Incidentally, *Spirastrella* is strictly related to *Cliona*, and individuals produced by larval recruitment bore into dead coral substrates (Kelly-Borges and Berquist 1988). Given the significance of boring sponges and their ubiquity on coral reefs, the question of their reproductive strategy/ies and of the relative importance of their modes of dispersal, warrant urgent further investigation. Population studies of important (highly destructive) and common boring sponges, such as, in the GBR, *Cliothosa hancocki*, are essential for understanding the dynamics of internal bioerosion of *in situ* reef substrates.

If independent of recruitment, bioerosion by sponges (and, given the importance of this group, overall internal bioerosion) may be controlled by the availability of dead substrate to a larger extent than previously thought. In this scenario, recurrent disturbance events that produce mass mortality of coral communities, such as population outbreaks of coral predators or eutrophication of coral reef waters, may be

playing a large role in the long term development of the reef, through increased bioerosion and sediment production (see also 6.2.1). Another important and practical implication of the potential greater importance of substrate infestation by sponges through growth and/or fragmentation, is that studies aimed at quantifying internal bioerosion will not account for the largest contributors to this process unless they make use of *in situ* substrates. This may explain why an experiment using coral blocks placed on grids did not detect sponge bioerosion after 18 months of exposure (Davies and Hutchings 1983) on the same reef where sponges were the major borers in experimental *in situ* colonies exposed for the same duration (Chapter 3). When the focus of the investigation is to understand factors influencing observed patterns of distribution of borers, an useful approach could be to investigate multiple scales patterns of borers in both *in situ* and experimental (grid) substrates. The comparison between rates of settlement of borers and actual extent of bioerosion in *in situ* substrates could provide useful insight in the dynamics of both borers' populations and bioerosive processes.

The organisms responsible for reef internal bioerosion belong to many and diverse taxa. They have different life histories and reproduction strategies, responses to environmental conditions, modes of excavation in the coral rock and, ultimately, impacts on the reef. The diverse responses of different macroborers to substrate features and spatial scales, as described in this thesis, highlight the need for a better understanding of both the ecology and life history strategies of individual internal bioeroders. In particular, there is a dearth of information of basic biological characteristics of boring sponges, and yet this and previous studies have demonstrated that in many situations boring sponges are responsible for most of the internal bioerosion of reef substrates (MacGeachy and Stearn 1976; Scoffin *et al.* 1980; Highsmith 1981a; Chapter 2 and 3). Future research accounting for a finer taxonomic grouping of borers (individual species or families) than the ones used in this and previous studies may lead to a better understanding of the dynamics of internal bioerosion on coral reefs.

6.2 Significance of internal bioerosion for coral reef development

6.2.1 Bioerosion and disturbance on modern coral reefs

In the present climate of concern for the global welfare of reef systems (D'Elia *et al.* 1991; Wilkinson 1992; Hughes 1994), there is an increased need for focussed and management-orientated research. In particular, it is becoming imperative that most basic reef ecological research is directed towards providing us with tools to predict, and prevent, the effects of human development on reef systems. Bioerosion is by definition a process of destruction. This type of destruction has been going on since at least the upper Lower Cambrian (James *et al.* 1977), it is a natural process which significantly contributes to the diversity and complexity of coral reef systems. Some authors have suggested that human disturbance may potentially increase this process of destruction beyond natural levels of variation (Hallock and Schalger 1986; Glynn 1988). As highlighted in the previous sections, however, our understanding of the dynamics and controls of this process, and its significance in reef development (see also 6.2.2) is poor. As a result, our ability to predict the response of bioeroding organisms to natural and human-induced disturbances is limited.

Reef bioerosion has the potential to undergo changes in the rates at which it happens following disturbance events. In particular a number of studies have suggested that reef bioerosion may be influenced by increase in the nutrients and organic matter content of reef waters (Risk and MacGeachy 1978; Highsmith 1980a; Rose and Risk 1985; Hallock 1988). In nutrient enriched waters, by both natural and anthropogenic causes, the impact of reef bioerosion is compounded by increased bioerosion rates and high coral mortality. Rose and Risk (1985) found that bioerosion by a boring sponge, *Cliona delitrix*, in the coral *Montastrea cavernosa*, was five times higher in waters adjacent to a sewage discharge, where bacteria were six times more abundant than a control reef. They suggested that the balance of reef framework formation may become tilted towards destructive processes in such situations (Rose and Risk 1985). Indirect evidence that boring sponges and bivalves may respond strongly and quickly to increased organic matter in reef waters comes also from cross-shelf studies of bioerosion recently carried out on the GBR (Sammarco and Risk 1990). Productivity on

the GBR is higher on inshore reefs (Andrews 1983), and bioerosion by both boring sponges and bivalves displays a marked decrease with increased distance from the shore (Sammarco and Risk 1990). Highsmith (1980a), after counting bivalves borings on the surface of corals deposited at a number of museums, suggested that worldwide distribution of bioerosion by bivalves may reflect global patterns of productivity. However, this hypothesis is not supported by evidence, and it seems to dismiss the existence of other factors likely to control reef internal bieorosion. Hallock (1988) suggests that increased levels of nutrients in the past may have been responsible for the demise of some coral reefs. Drowned reefs and carbonate platforms as known in the geologic record may be the result of ceased calcium deposition and increased destruction by boring communities, determined by eutrophic conditions (Hallock and Schlager 1986; Hallock 1988). In the light of this evidence, and given the current rate of human demographic growth along tropical coasts, the relationship between eutrophication and boring organisms, and the implications for reef communities, needs to be specifically addressed in future research.

As well as increased nutrients levels, other natural and human-related disturbances that potentially may affect the process of bioerosion include those that cause mass mortality of corals, such as outbreaks of coral predators and severe bleaching. The strong response of most macroborers to availability of exposed coral skeleton, as shown in this (Chapters 2 and 3) and previous studies (Highsmith 1981a; Moore and Shedd 1977), suggests that the patterns of internal bioerosion at a reef scale may be significantly influenced by recurrent episodes of coral mass mortality. This study attempted to investigate the effect of outbreaks of *Acanthaster planci* on the rates of excavation by macroborers in *Porites* substrates. Despite detecting no effect, the study has found that rates of bioerosion usually appear to be much higher in substrates that have been exposed (i.e. dead) for only few years than substrates exposed for 6-7 plus years (Chapter 5). This result, together with the finding that *in situ* coral skeletons may be destroyed at very fast rates immediately following death (Chapter 4), suggests that the production of carbonate by-products by erosive agents may increase substantially following coral mass mortality. The long-term implications of such increase for reef development remain unclear however, as the role of the process on longer temporal

scales that are relevant to reef development may at this stage be only inferred from current, short-term data.

6.2.1 Bioerosion in modern and fossil reefs

Bioerosion on modern reefs appears to be a major structuring force, as in many studies it has been found to be comparable to, if not of the same order of magnitude than, calcium carbonate depositional processes (Scoffin *et al.* 1980; Davies 1983). For a few decades now, accepted models of coral reef development have included destructive processes along with ones of production, sedimentation and cementation (Scoffin and Garrett 1974; Stearn *et al.* 1977; Scoffin *et al.* 1980; Davies 1983). More recently Hubbard *et al.* (1990) have put forward the view that our perception of coral reefs may be skewed towards 'in place' framework, while, they suggest, reefs should be regarded as mainly detrital structures. In their view, destructive processes and particularly bioerosion, together with the sedimentation regimes that they contribute to, assume a primary role in the control of reef development (Hubbard 1986; Hubbard *et al.* 1990). Most of these works have built on estimated rates of bioerosion, calcium deposition and sedimentation rates obtained on present day reefs. However, the significance of reef bioerosion for the reef morphological development can be appreciated only from information on patterns of reef bioerosion over a large (geological) temporal scale.

The information we can gather from sampling programmes and manipulative experiments on modern reefs can only provide data on the natural variability of the process over a short temporal scale. The longest running experiment using blocks of coral skeleton has run over a 9 year period (Kiene and Hutchings 1993). The present study, using datable dead coral surfaces has provided reliable data of bioerosion over a 33 years period (Chapter 5). Both studies have demonstrated that within individual types of substrates, internal bioerosion rates vary considerably in time (Hutchings *et al.* 1992; Kiene and Hutchings 1992; Musso, Chapter 5). However, such time frames are far too short to infer any role of bioerosion in geomorphological processes occurring over thousands to millions of years. Highlighting this disparity, Hutchings (1986) called for a shift of focus in bioerosion research to include comprehensive descriptions of fossil boring communities, in order to appreciate the long term dynamics of bioerosive

processes and therefore the role of bioerosion in reef development. This shift is presently occurring, as demonstrated by several presentations at the 7th International Coral Reef Symposium held in Guam in June 1992 (Vogel 1992; Edinger and Risk 1992; Bak 1992). It also parallels the recent emphasis in reef science to gain a temporally broader perspective on coral reef processes (Davies 1988; Jackson 1992).

Fossil evidence of bioeroding organisms have been recorded in samples as old as the Lower Cambrian (James *et* al 1977; Kobluk 1981). Traces of many of the present day groups of borers have been found in fossil reefs (Warme 1975). Characteristic carbonate 'chips' in all similar to the ones produced by modern boring sponges have been found in fossil reefs also (Kobluk 1981; Rutzler and Rieger 1973). Because they leave identifiable traces within carbonate substrates, reef borers are potentially ideal palaeoecological tools, and by and large, fossil traces of borers have been studied for their potential as such (Seilacher 1969, Bromley 1970; Warme 1975). However, research comparing modern and fossil reef bioerosion in an attempt to establish patterns and extent of variation of reef bioerosion over large and geologically significant periods, has been scarce. Klein *et al.* (1991) investigated internal bioerosion in modern and ancient uplifted coral reefs in the Red Sea (age ≥250,000 yrs). They concluded that the percent volume of skeleton excavated from the colony was the same for fossil and recent corals, and the relative importance of the four groups of borers considered in the study did not change. They found however that the number of borers was significantly higher in fossil reefs and suggested that this may reflect varied environmental conditions. Their evidence with regards to the abundance of bioeroders is not conclusive as their research appears flawed in several ways (failure to deal with duration of exposure and/or age in living colonies; use of percent volume of colony skeleton removed as measure of bioerosion - see 2.4, p.44). However, their study succeeded in showing that borings in reefs that are more than 250,000yrs old are similar to recent reefs and that also the relative importance of different groups seems to vary little.

As recently emphasised by Vogel (1992) and Edinger and Risk (1992), there is enormous potential for studies of bioerosion in ancient reefs. In particular, uplifted reefs

offer a brilliant opportunity, as they often consist of in place coral substrates (Mesolella 1967). Several studies have recently investigated the paleoecology of Late Quaternary uplifted reefs. A major results of these studies was to establish that patterns of abundance, diversity and dominance in many ancient coral communities compare well with some of the present day reef coral communities (Stemann and Johnson 1992; Jackson 1992). The study of fossil reefs offers a unique opportunity to acquire a 'geological' perspective of the reef bioerosive processes, and the recent enthusiasm shown for the study of fossil boring communities (Hutchings 1986; Klein *et al.* 1991; Vogel 1992; Edinger and Risk 1992; Bak 1992) indicates common acceptance that meaningful interpretation of the role of bioerosion in reef development is conditional to a broadened scale of investigation. However, it seems clear at this stage that we first need to deepen our knowledge of how bioerosion operates at different, and smaller, scales in modern day coral reefs. This requires an approach which embraces thorough sampling and experimental designs for the testing of well defined hypotheses about factors affecting the process.

6.3 Conclusions

Reef bioerosion is a complex process. The enormous variety of carbonate substrates on a reef, and the diversity of the organisms that excavate them are the cause of our limited understanding of the process. We do not know what mechanisms determine the different patterns of bioerosion among coral subtrates (as observed in this study, Chapters 2 and 3) and among reef environments, as suggested by previous studies (Davies and Hutchings 1983; Kiene 1985). This study, by using an experimental and multiple-scale approach, has contributed to our understanding of the natural levels of variability of reef internal bieorosion (see 5.4.2), has provided reliable estimates of bioerosion rates (see 3.3.10, 4.3.4 and 5.3.5) and has generated important hypotheses on the nature of the controls acting on the process. Research specifically investigating the ecology and biology of individual reef borers is required, as well as studies addressing the nature and fate of the carbonate by-products resulting from bioerosion. Without such information our attempts to establish the significance of the process of reef bioerosion in the context of issues relevant to management (ecological scale) and the geomorphological development of the reef systems (geological scale), will be futile.

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Appendix A

Tables

Data set	Raw data	$X^1 = \log(X+1)$	$X^1 = \sqrt{(X+1)}$
TOTAL	0.2423**	0.2662**	0.2753
SPONGES	0.2248**	0.2679**	0.2711*
WORMS	0.2046**	0.2692*	0.2658**
BIVALVES	0.2081**	0.2788	0.2548**
BARNACLES	0.1201**	0.1411**	0.1376**
OTHERS	0.1885**	0.2764	0.2568**

Table A1: D'Agostino's D values for departure from normality of raw data and following logarithmic and square root transformations. Data of total bioerosion and of bioerosion by the five individual taxa in living colonies of all species. Asterisks denote significant departure from normality. Critical values for $D_{0.05,90}$=0.2740 and 0.2862.

	SPONGES	WORMS	BIVALVES	BARNACLES	OTHERS
SPONGES	1	-0.02	-0.27	-0.05	0.22
	0	0.80	0.014	0.65	0.054
WORMS	-	1	0.13	0.22	0.34
		0	0.24	0.057	0.002
BIVALVES	-	-	1	-0.03	-0.01
			0	0.74	0.88
BARNACLES	-	-	-	1	0.04
				0	0.69
OTHERS	-	-	-	-	1
					0

***TableA2:** Partial correlation coefficients from the Error Variance-Covariance matrix for bioerosion by the five taxa.*

Source of variation	df	SS	MS	Fs	p
Total	89	41433			
Collection	1	648.32	648.317	13.89	0.06
Location	1	58.79	58.7928	0.58	0.52
Site	2	203.71	101.854	0.25	0.78
Species	2	426.59	213.296	0.28	0.77
SpXLoc	2	333.24	166.619	0.22	0.81
SpXColl	2	514.16	257.081	0.17	0.84
LocXColl	1	1361.7	1361.66	**29.16**	0.03
SpXSite	4	3089.4	772.349	1.87	0.12
CollXSite	2	93.38	46.6898	0.11	0.89
CollXLocXSp	2	1977.7	988.834	0.65	0.56
CollXSpXSite	4	6055.2	1513.79	**3.67**	0.009
Error	66	27256	412.963		

***Table A3:** Four-way ANOVA testing for the effect of collection (two levels: November 1990 and November 1992) on the sample volume. F values in bold and underlined are significant at α=0.05.*

Source of variation	df	SS	MS	Fs	p
Total	89	9015.6			
Collection	1	480.35	480.34	7.8	0.10
Location	1	35.33	35.33	2.84	0.23
Site	2	24.87	12.43	0.25	0.77
Species	2	3905.6	1952.81	**112.92**	0.0003
SpXLoc	2	0.45	0.22	0.01	0.98
SpXColl.	2	149.19	74.59	1.13	0.40
LocXColl.	1	0.96	0.96	0.02	0.91
SpXSite	4	69.17	17.29	0.35	0.84
Coll.XSite	2	123.11	61.55	1.25	0.29
Coll.XLocXSp	2	157.15	78.57	1.19	0.39
Coll.XSpXSite	4	264.53	66.13	1.34	0.26
Error	66	3247	49.19		

Table A4: *Four-way ANOVA testing for the effect of date of collection on total bioerosion. F values in bold and underlined are significant at α=0.05.*

Source of variation	df	SS	MS	F_S	P
Total	89	0.507			
Location	1	0.016	0.0167	14.15	0.06
Site	2	0.002	0.0012	0.47	0.62
Species	2	0.285	0.1428	**72.92**	0.0007
SpeciesXLoc	2	0.005	0.0028	1.43	0.33
SpeciesXSite	4	0.007	0.002	0.78	0.54
Error	78	0.196	0.0025		

Table A5: *ANOVA table of the ratio of dead surface area to total surface area. Data are transformed as $X^1=\sqrt{(X+3/8)}$. F values in bold and underlined are significant at α=0.05.*

Source of variation	df	SS	MS	F_S	P
Total	89	0.610			
Location	1	0.006	0.0064	1.76	0.31
Site	2	0.007	0.0036	0.77	0.46
Species	2	0.205	0.1029	**41.14**	0.002
SpeciesXLoc	2	0.004	0.0024	0.94	0.46
SpeciesXSite	4	0.010	0.0025	0.53	0.71
Error	78	0.368	0.0047		

Table A6: *ANOVA table of the colony rugosity index. Data are transformed as $X^1=\log(X+1)$. F values in bold and undelined are significant at α=0.05.*

Source of variation	df	SS	MS	F_S	P
Total	87	11.543			
Location	1	0.061	0.061	0.33	0.62
Site	2	0.375	0.1876	2.48	0.09
Species	2	4.493	2.2466	**15.78**	0.01
SpeciesXLoc	2	0.060	0.0302	0.21	0.81
SpeciesXSite	4	0.569	0.1424	1.89	0.12
Error	76	5.736	0.0755		

Table A7: *ANOVA table for total bioerosion per unit of dead surface area. F values in bold and underlined are significant at α=0.05.*

Source of variation	df	SS	MS	F_S	P
Total	87	6.080			
Location	1	0.033	0.0334	0.26	0.65
Site	2	0.254	0.127	1.9	0.15
Species	2	0.240	0.1204	1.21	0.38
SpeciesXLoc	2	0.045	0.0229	0.23	0.80
SpeciesXSite	4	0.399	0.0999	1.49	0.21
Error	76	5.077	0.0668		

Table A8: *ANOVA table for bioerosion by SPONGES per unit of dead surface area. Bonferroni corrected significance level of α=0.01 (overall significance level α=0.049).*

Source of variation	df	SS	MS	F_S	P
Total	87	0.194			
Location	1	0.0003	0.0003	0.39	0.59
Site	2	0.001	0.0008	0.38	0.68
Species	2	0.032	0.0165	14	0.01
SpeciesXLoc	2	0.001	0.0008	0.65	0.57
SpeciesXSite	4	0.004	0.0012	0.59	0.67
Error	76	0.152	0.002		

Table A9: *ANOVA table for bioerosion by WORMS per unit of dead surface area. None of the F values were significant at the Bonferroni corrected significance level of α=0.01 (overall significance level α=0.049).*

Source of variation	df	SS	MS	F_S	P
Total	87	11.288			
Location	1	0.034	0.0344	0.49	0.55
Site	2	0.139	0.0697	1.18	0.31
Species	2	6.253	3.127	**71.49**	0.0007
SpeciesXLoc	2	0.053	0.0267	0.61	0.58
SpeciesXSite	4	0.174	0.0437	0.74	0.56
Error	76	4.489	0.0591		

Table A10: *ANOVA table for bioerosion by BIVALVES per unit of dead surface area. F values in bold and underlined are significant at the Bonferroni corrected significance level of α=0.01 (overall significance level α=0.049).*

Source of variation	df	SS	MS	F_S	P
Total	87	0.011			
Location	1	0.00001	0.00001	0.05	0.83
Site	2	0.0003	0.0002	1.32	0.27
Species	2	0.00003	0.00001	0.14	0.91
SpeciesXLoc	2	0.00018	0.00009	0.76	0.52
SpeciesXSite	4	0.0004	0.0001	0.88	0.47
Error	76	0.0103	0.0001		

Table A11: *ANOVA table for bioerosion by BARNACLES per unit of dead surface area. None of the F values were significant at the Bonferroni corrected significance level of α=0.01 (overall significance level α=0.049).*

Source of variation	df	SS	MS	F_S	P
Total	87	0.530			
Location	1	0.005	0.005	1.7	0.32
Site	2	0.005	0.0029	0.5	0.60
Species	2	0.016	0.0084	1.89	0.26
SpeciesXLoc	2	0.044	0.0222	5.03	0.08
SpeciesXSite	4	0.017	0.0044	0.76	0.55
Error	76	0.444	0.0058		

Table A12: *ANOVA table for bioerosion by OTHERS per unit of dead surface area. None of the F values were significant at the Bonferroni corrected significance level of α=0.01 (overall significance level α=0.049).*

Data set	Raw data	$X^1 = \log(X+1)$	$X^1 = \sqrt{(X+1)}$
TOTAL	0.2690**	0.2833	0.2816
SPONGES	0.2619**	0.2476**	0.2811
WORMS	0.2678**	0.2763	0.2797
BIVALVES	0.2389**	0.2675**	0.2763
BARNACLES	0.0947**	0.1907**	0.1600**
OTHERS	0.1579**	0.2676**	0.2448**

Table A13: *D'Agostino's D values for departure from normality of raw data of total bioerosion, and following logarithmic and square root transformations. Data sets tested are data of total bioerosion and of bioerosion by the five individual taxa. Asterisks denote significant departure from normality. Critical values for $D_{0.05,141}$=0.2758 and 0.2856.*

Source of variation	df	SS	MS	F_S	P
Total	140	0.0187			
Location	1	0.00001	0.00001	0.03	0.86
Site	4	0.00182	0.00046	**7.59**	0.0001
Species	2	0.00909	0.00454	**62.32**	0.0001
Loc X Species	2	0.00002	9.8e-06	0.16	0.84
Species X Site	8	0.00058	0.00007	1.22	0.29
Error	123	0.00737	0.00006		

Table A14: *ANOVA table of coralline algae cover per unit of colony surface area. F values in bold and underlined are significant at α=0.01.*

Source of variation	df	SS	MS	F_S	p
Total	140	11611.27			
Location	1	27.87	27.87	0.19	0.68
Site	4	583.96	145.99	**2.51**	0.04
Species	2	3531.93	1765.96	**64.74**	0.0001
Sp X Loc	2	301.57	150.78	5.53	0.05
Sp X Site	8	218.21	27.27	0.47	0.87
Error	123	7148.49	58.11		

Table A15: *Results of ANOVA for data of total bioerosion transformed as X_1=sqrt(X+1). F values in bold and underlined are significant at α=0.05.*

Source of variation	df	SS	MS	F_S	p
Total	140	11.31			
Location	1	0.12	0.12	3.49	0.13
Site	4	0.14	0.03	1.3	0.27
Species	2	7.58	3.79	**285.7**	0.0001
Sp X Loc	2	0.29	0.14	**14.0**	<0.01
Sp X Site	8	0.10	0.01	0.48	0.86
Error	123	3.41	0.02		

Table A16: Results of ANOVA for data of total bioerosion per unit of exposed surface area. Data are transformed as X_1=sqrt(X+3/8). F values in bold and underlined are significant at α=0.05.

Source of variation	df	SS	MS	F_S	p	%
Total	42	1.61				100
Location	1	0.33	0.33	**31.06**	0.005	20.4
Site	4	0.04	0.01	0.33	0.85	2.4
Error	37	1.21	0.03			75.2

Table A17: Results of ANOVA and percent variance components of total bioerosion per unit of exposed surface area in A.cuneata colonies. Data are transformed as X_1=sqrt(X+1). F values in bold and undelined are significant at a corrected level of α=0.01 (overall significance level α=0.029).

Source of variation	df	SS	MS	F_S	p
Total	140	12.45			
Location	1	0.050	0.050	0.73	0.44
Site	4	0.274	0.068	1.19	0.32
Species	2	3.942	1.971	**27.06**	0.0003
Sp X Loc	2	1.041	0.520	**7.15**	0.016
Sp X Site	8	0.582	0.072	1.26	0.27
Error	123	7.122	0.057		

Table A18: Results of ANOVA for data of bioerosion by all groups except BIVALVES per unit of exposed surface area. Data are untransformed. F values in bold and underlined are significant at α=0.05.

Source of variation	df	SS	MS	Fs	P
Total	140	10827.2			
Location	1	3.49	3.49	0.03	0.87
Site	4	534.98	133.74	1.93	0.11
Species	2	948.48	474.24	**9.33**	0.008
Sp X Loc	2	541.88	270.94	5.33	0.05
Sp X Site	8	406.58	50.82	0.73	0.66
Error	123	8533.35	69.37		

Table A19: ANOVA table of bioerosion by SPONGES per unit of surface area. Data are transformed as X_1=sqrt(X+1). F values in bold and underlined are significant at a corrected significance level of α=0.01 (overall significance level α=0.049).

Source of variation	df	SS	MS	Fs	p
Total	703	35.99			
Species	2	0.29	0.14	4.31	0.05
Location	1	0.03	0.03	0.71	0.44
Site	4	0.17	0.04	0.85	0.50
Colony	47	2.44	0.05	1.07	0.36
Sp X Loc	2	0.26	0.13	3.98	0.06
Sp X Site	8	0.27	0.03	0.53	0.83
Sp X Col	76	4.88	0.06	1.31	0.04
Error	563	27.51	0.04		

Table A20: 4-way mixed, nested ANOVA table for bioerosion by WORMS per unit of surface area. Data are transformed as X_1=sqrt(X+1). None of the F values is significant at the corrected significance level α=0.01.

Source of variation	df	SS	MS	F_S	P
Total	140	87.34			
Location	1	7.30	7.30	**26.09**	0.006
Site	4	1.12	0.28	0.8	0.52
Species	2	31.30	15.65	**56.96**	0.0001
Loc X Species	2	1.94	0.97	3.59	0.07
Species X Site	8	2.19	0.27	0.79	0.61
Error	123	42.99	0.34		

Table A21: ANOVA table of bioerosion by BIVALVES per unit of surface area. Data are log transformed. F values in bold and underlined are significant at α=0.01.

Source	df	SS	MS	Fs	p
Total	488	46.41	3.09		
Species	1	0.58	0.58	6.05	0.06
Location	1	5.03	5.03	**85.2**	0.0008
Site	4	0.23	0.06	0.61	0.65
Colony	45	4.37	0.09	1.25	0.13
Sp X Loc	1	0.01	0.01	0.1	0.76
Sp X Site	4	0.38	0.09	0.79	0.53
Sp X Col	41	5.04	0.12	1.58	0.015
Error	391	30.44	0.07		

Table A22: ANOVA table for bioerosion by BIVALVES per unit of surface area in A.hyacinthus and A.gemmifera. F values in bold and underlined are significant at the corrected significance level of α=0.01.

Source of variation	df	SS	MS	Fs	P
Total	140	53.01			
Location	1	0.66	0.66	0.72	0.44
Site	4	3.65	0.91	2.48	0.04
Species	2	0.36	0.18	0.49	0.49
Sp X Loc	2	0.21	0.10	0.29	0.29
Sp X Site	8	2.87	0.36	0.98	0.98
Error	123	45.23	0.37		

Table A23: ANOVA table and variance components of bioerosion by BARNACLES per unit of surface area. Data are transformed as X_1=Log(X+1). NO F values are significant at a corrected significance level of α=0.01 (overall significance level α=0.049).

Source of variation	df	SS	MS	Fs	P
Total	140	82.04			
Location	1	1.32	1.32	1.39	0.30
Site	4	3.79	0.95	1.67	0.16
Species	2	4.37	2.19	6.21	0.02
Sp X Loc	2	0.22	0.11	0.19	0.83
Sp X Site	8	2.82	0.35	0.62	0.76
Error	123	69.86	0.57		

Table A24: ANOVA table and variance components of bioerosion byOTHERS per unit of surface area. Data are transformed as X_1=Log(X+1). NO F values are significant at a corrected significance level of α=0.01 (overall significance level α=0.049).

Source of variation	df	SS	MS	Fs	p
Total	184	4.580			
Status	1	0.551	0.551	**52.9**	0.018
Location	1	0.0002	0.0002	0.01	0.93
Site	2	0.055	0.027	2.57	0.07
Species	2	1.842	0.921	**64.22**	0.0009
Status X Location	1	0.040	0.040	3.85	0.18
Location X Species	2	0.009	0.004	0.32	0.74
Status X Species	2	0.085	0.042	2.98	0.16
Status X Site	2	0.020	0.010	0.96	0.38
Species X Site	4	0.057	0.014	1.32	0.26
Status X Loc X Sp	2	0.041	0.020	1.44	0.33
Status X Sp X Site	4	0.057	0.014	1.32	0.26
Error	161	1.747	0.010		

Table A25: ANOVA table of total bioerosion per unit of surface area in the living and dead ('status') coral colonies. F values in bold and underlined are significant at α=0.05. Data are log transformed.

Source of variation	df	SS	MS	Fs	p
Total	185	6.896			
Status	1	1.745	1.745	55.95	0.017
Location	1	5.60e-07	5.60e-07	0 0	0.99
Site	2	0.051	0.025	1.06	0.35
Species	2	0.936	0.468	**82.38**	0.0006
Status X Location	1	0.019	0.019	0.63	0.51
Location X Species	2	0.019	0.009	1.72	0.28
Status X Species	2	0.106	0.053	8.23	0.03
Status X Site	2	0.062	0.031	1.29	0.27
Species X Site	4	0.022	0.005	0.24	0.91
Status X Loc X Sp	2	0.019	0.009	1.54	0.31
Status X Sp X Site	4	0.025	0.006	0.27	0.89
Error	162	3.915	0.024		

TableA26: ANOVA table for bioerosion by SPONGES per unit of surface area in the living and dead ('status') coral colonies. F values in bold and underlined are significant at the corrected significance level α=0.01. Data are log transformed.

Source of variation	df	SS	MS	Fs	p
Total	185	5.820			
Status	1	3.315	3.315	**349.6**	0.002
Location	1	0.016	0.016	37.09	0.02
Site	2	0.0008	0.0004	0.04	0.95
Species	2	0.359	0.179	**31.04**	0.003
Status X Location	1	0.002	0.002	0.31	0.63
Location X Species	2	0.005	0.002	0.48	0.65
Status X Species	2	0.127	0.063	**24.71**	0.005
Status X Site	2	0.018	0.009	0.89	0.41
Species X Site	4	0.023	0.005	0.54	0.70
Status X Loc X Sp	2	0.016	0.008	3.23	0.14
Status X Sp X Site	4	0.010	0.002	0.24	0.91
Error	162	1.723	0.010		

Table A27: ANOVA table for bioerosion by WORMS per unit of surface area in the living and dead ('status') coral colonies. F values in bold and underlined are significant at the corrected significance level α=0.01. Data are log transformed.

Source of variation	df	SS	MS	Fs	p
Total	185	19.978			
Status	1	3.257	3.257	**242.46**	0.004
Location	1	0.261	0.261	52.86	0.018
Site	2	0.009	0.004	0.13	0.87
Species	2	9.090	4.545	**503.27**	0.0001
Status X Location	1	0.097	0.097	7.25	0.11
Location X Species	2	0.119	0.059	6.63	0.05
Status X Species	2	0.807	0.403	16.58	0.011
Status X Site	2	0.026	0.013	0.36	0.69
Species X Site	4	0.036	0.009	0.24	0.91
Status X Loc X Sp	2	0.151	0.075	3.12	0.15
Status X Sp X Site	4	0.097	0.024	0.66	0.62
Error	162	5.978	0.036		

Table A28: ANOVA table for bieorosion by BIVALVES per unit of surface area in the living and dead ('status') coral colonies of the three species. F values in bold and underlined are significant at the corrected significance level α=0.01. Data are log transformed.

Source of variation	df	SS	MS	Fs	p
Total	128	10.030			
Status	1	4.051	4.051	**506.46**	0.002
Location	1	0.287	0.287	**205.88**	0.004
Site	2	0.002	0.001	0.03	0.96
Species	1	0.056	0.056	6.80	0.12
Status X Location	1	0.127	0.127	15.93	0.06
Location X Species	1	0.090	0.090	10.94	0.08
Status X Species	1	0.150	0.150	3.80	0.19
Status X Site	2	0.015	0.007	0.18	0.83
Species X Site	2	0.016	0.008	0.18	0.83
Status X Loc X Sp	1	0.124	0.124	3.15	0.22
Status X Sp X Site	2	0.079	0.039	0.88	0.42
Error	113	5.081	0.044		

Table A29: Bioerosion by BIVALVES in A.hyacinthus *and* A.gemmifera *per unit of surface area in the living and dead ('status') coral colonies. F values in bold and underlined are significant at the corrected significance level α=0.01. Data are log transformed.*

Source of variation	df	SS	MS	Fs	p
Total	185	3.458			
Status	1	0.045	0.045	1.13	0.39
Location	1	0.008	0.008	0.86	0.45
Site	2	0.020	0.010	0.55	0.57
Species	2	0.003	0.001	0.07	0.93
Status X Location	1	0.013	0.013	0.34	0.62
Location X Species	2	0.018	0.009	0.37	0.71
Status X Species	2	0.011	0.005	0.91	0.47
Status X Site	2	0.080	0.040	2.09	0.12
Species X Site	4	0.101	0.025	1.33	0.26
Status X Loc X Sp	2	0.001	0.0006	0.11	0.89
Status X Sp X Site	4	0.024	0.006	0.32	0.86
Error	162	3.10	0.019		

Table A30: *ANOVA table for bieorosion by BARNACLES per unit of surface area in the living and dead ('status') coral colonies. None of the F values were significant at the corrected significance level α=0.01. Data are log transformed.*

Source of variation	df	SS	MS	Fs	p
Total	185	9.876			
Status	1	0.002	0.002	0.03	0.88
Location	1	0.012	0.012	0.29	0.64
Site	2	0.082	0.041	0.78	0.46
Species	2	0.255	0.127	4.55	0.09
Status X Location	1	0.178	0.178	1.75	0.31
Location X Species	2	0.137	0.068	2.46	0.20
Status X Species	2	0.211	0.105	10.35	0.02
Status X Site	2	0.204	0.102	1.94	0.14
Species X Site	4	0.112	0.028	0.53	0.71
Status X Loc X Sp	2	0.122	0.061	6.02	0.06
Status X Sp X Site	4	0.040	0.010	0.19	0.94
Error	162	8.572	0.052		

Table A31: *ANOVA table for bieorosion by OTHERS per unit of surface area in the living and dead ('status') coral colonies. None of the F values were significant at the corrected significance level α=0.01. Data are log transformed.*

	SPONGES	WORMS	BIVALVES	BARNACLES	OTHERS	TOTAL
SE sites:						
A.hyacinthus	0.121	0.078	0.060	0.003	0.0002	0.263
	0.042	*0.008*	*0.009*	*0.002*	*0.0025*	*0.045*
A.gemmifera	0.121	0.050	0.092	0.0005	0.0055	0.269
	0.043	*0.007*	*0.018*	*0.0009*	*0.0041*	*0.045*
A.cuneata	0.661	0.045	0.196	0.0002	-0.006	0.896
	0.115	*0.009*	*0.127*	*0.0025*	*0.0051*	*0.153*
NE sites:						
A.hyacinthus	0.190	0.053	0.006	0.002	0.013	0.264
	0.064	*0.005*	*0.005*	*0.001*	*0.003*	*0.065*
A.gemmifera	0.230	0.058	0.062	0.001	0.008	0.359
	0.069	*0.006*	*0.015*	*0.001*	*0.008*	*0.071*
A.cuneata	0.28	0.043	0.190	0.005	0.025	0.547
	0.092	*0.006*	*0.076*	*0.003*	*0.024*	*0.110*

Table A32: Untransformed mean differences of volume removed (mm^3) per unit of surface area (mm^2) between experimental and living colonies for each site and species. The experimental colonies had been dead and exposed to bioeroders for a period of 21 months. SE sites include SI and LH and NE sites include NR and WMI1 (Figure 3.1). Standard Errors of the difference between means are showed in italics.

Effect	Statistics	F	Num df	Den df	p
Time	0.388	**45.65**	1	72	0.0001
Time X Species	0.262	**12.84**	2	72	0.0001
Time X Location	0.000013	0.0009	1	72	0.97
Time X Site	0.031	0.58	4	72	0.67
Time X Sp X Loc	0.002	0.08	2	72	0.91
Time X Sp X Site	0.217	**2.49**	8	72	0.018

Table A33: Within-subject effects from Repeated Measures Multivariate ANOVA of percent decrease in size of the colonies of the three species after 34 and 90 weeks (n=5). Statistics are the values of Pillai's Trace. F values in bold and underlined are significant at α=0.05.

Effect	df	SS	MS	Fs	p
Species	2	102564.8	51282.3	**72.78**	<0.01
Loc	1	2167.5	2167.5	**7.74**	<0.05
Site	4	1119.7	279.9	0.68	0.60
SpXLoc	2	1876.6	938.3	1.39	>0.10
SpXSite	8	5636.8	704.6	1.72	0.10
Error	72	29465.1	409.2		

Table A34: Between-subject effects from Repeated Measures Multivariate ANOVA on percent decrease in size of the colonies of the three species after 34 and 90 weeks (n=5). Values in bold and underlined are significant at α=0.05.

Source of variation	df	SS	MS	Fs	p
Total	89	50058.37			
Species	2	33945.61	16972.81	**74.27**	0.0001
Location	1	1067.02	1067.02	4.71	0.09
Site	4	906.26	226.56	1.44	0.22
Species X Location	2	1021.37	510.68	2.23	0.16
Species X Site	8	1828.24	228.53	1.46	0.18
Error	72	11289.84	156.80		

Table A35: Results of the ANOVA on percent decrease in size of the colonies of the three species after 34 weeks (n=5). F values in bold and underlined are significant at α=0.05. Data are untransformed.

Source of variation	df	SS	MS	Fs	p
Total	89	109810.5			
Species	2	72260.9	36130.4	**43.54**	0.0001
Location	1	1100.6	1100.6	**8.06**	0.04
Site	4	546.2	136.5	0.35	0.84
Species X Location	2	880.7	440.3	0.53	0.60
Species X Site	8	6639.2	829.9	**2.11**	0.04
Error	72	28382.6	394.2		

Table A36: Results of the ANOVA on percent decrease in size of the colonies of the three species after 90 weeks (n=5). F values in bold and underlined are significant at α=0.05. Data are untransformed.

Effects	Value	F	Num df	Den df	p
Time					
Wilk's Lambda	0.234	**38.18**	3	35	0.0001
Pillai's Trace	0.765	**38.18**	3	35	0.0001
Hotelling-Lawley's Trace	3.272	**38.18**	3	35	0.0001
Roy's Greatest Root	3.272	**38.18**	3	35	0.0001
Time X Location					
Wilk's Lambda	0.954	0.56	3	35	0.64
Pillai's Trace	0.045	0.56	3	35	0.64
Hotelling-Lawley's Trace	0.048	0.56	3	35	0.64
Roy's Greatest Root	0.048	0.56	3	35	0.64
Time X Site					
Wilk's Lambda	0.543	**2.00**	12	92.89	0.03
Pillai's Trace	0.515	**1.92**	12	111	0.03
Hotelling-Lawley's Trace	0.732	**2.05**	12	101	0.02
Roy's Greatest Root	0.556	**5.14**	4	37	0.002

Table A37: Repeated Measures Multivariate ANOVA on untransformed differences in size of colonies of A.hyacinthus *at each census from census at t_0. Test statistics for within-subject effects. F values in bold and underlined are significant at α=0.05.*

Effects	Value	F	Num df	Den df	p
Time					
Wilk's Lambda	0.141	**70.81**	3	35	0.0001
Pillai's Trace	0.858	**70.81**	3	35	0.0001
Hotelling-Lawley's Trace	6.069	**70.81**	3	35	0.0001
Roy's Greatest Root	6.069	**70.81**	3	35	0.0001
Time X Location					
Wilk's Lambda	0.948	0.63	3	35	0.59
Pillai's Trace	0.051	0.63	3	35	0.59
Hotelling-Lawley's Trace	0.054	0.63	3	35	0.59
Roy's Greatest Root	0.054	0.63	3	35	0.59
Time X Site					
Wilk's Lambda	0.561	**1.88**	12	92.89	0.04
Pillai's Trace	0.507	**1.88**	12	111	0.04
Hotelling-Lawley's Trace	0.662	**1.85**	12	101	0.04
Roy's Greatest Root	0.421	**3.89**	4	37	0.009

Table A38: Repeated Measures Multivariate ANOVA on untransformed percent decrease in size of colonies of A.hyacinthus *at each census from census at t_0. Test statistics for within-subject effects. F values in bold and underlined are significant at α=0.05.*

Effect	df	SS	MS	Fs	p
Location	1	1115918965	1115918965	0.81	0.40
Site	4	5474325545	1368581386	2.19	0.08
Error	37	2.3106e+10	624493090		

Table A39: Multivariate Repeated Measures ANOVA on untransformed differences in size of colonies of A.hyacinthus *at each census from census at t_0. Test statistics for between-subjects effects.*

Effect	df	SS	MS	Fs	p
Location	1	7114.01	7114.01	6.35	0.05
Site	4	4480.86	1120.21	1.98	0.11
Error	37	20983.98	567.13		

Table A40: Multivariate Repeated Measures ANOVA on untransformed percent decrease in size of colonies of A.hyacinthus *at each census from census at t_0. Test statistics for between-subjects effects.*

Effects	df	SS	MS	F	p	G-G p	H-F p
Time	3	6491513819	$2.164e^{+09}$	**73.37**	0.0001	0.0001	0.0001
TimeXLoc	3	89911101.4	29970367	1.02	0.38	0.37	0.38
TimeXSite	12	484858977	40404915	1.37	0.19	0.21	0.20
Error	111	3273437846	29490431				

Table A41: Univariate Repeated Measures ANOVA on untransformed differences in size of colonies of A.hyacinthus *at each census from census at t_0 Univariate statistics for within subject effects. G-G p and H-F p are the Greenhouse-Geisser and Huynl-Feldt adjusted probabilities.*

Effects	df	SS	MS	F	p	G-G p	H-F p
Time	3	31225.08	10408.36	**97.2**	0.0001	0.0001	0.0001
TimeXLoc	3	253.83	84.61	0.79	0.50	0.49	0.50
TimeXSite	12	2278.53	189.87	1.77	0.06	0.06	0.06
Error	111	11885.54	107.07				

Table A42: Univariate Repeated Measures ANOVA on untransformed percent decrease in size of colonies of A.hyacinthus *at each census from census at t_0 Univariate statistics for within subject effects. G-G p and H-F p are the Greenhouse-Geisser and Huynl-Feldt adjusted probabilities.*

Source of variation	df	SS	MS	Fs	p
t_1-t_0 (11 weeks)					
Total	42	8289.88			
Location	1	2311.3	2311.3	**8.45**	0.04
Site	4	1093.78	273.44	2.14	0.09
Error	37	4718.61	127.53		
t_3-t_0 (34 weeks)					
Total	42	12046.8			
Location	1	2697.77	2697.8	6.54	0.05
Site	4	1649.84	412.46	1.89	0.13
Error	37	8057.48	217.77		
t_4-t_0 (52 weeks)					
Total	42	13978.7			
Location	1	1136.63	1136.6	1.56	0.13
Site	4	2912.85	728.21	2.61	0.05
Error	37	10343.1	279.54		
t_6-t_0 (90 weeks)					
Total	42	11876.2			
Location	1	1222.15	1222.1	4.43	0.10
Site	4	1102.93	275.73	1.05	0.39
Error	37	9750.37	263.52		

Table A43: Results from ANOVA on each of the differences in size between each census and the size at t_0, in colonies of A.hyacinthus. *F values in bold and underlined are significant at α=0.05.*

Source	df	SS	MS	Fs	p
Total	183	3.574			
Status	1	0.739	0.739	**30.28**	0.03
Loc	1	0.007	0.007	**29.51**	0.03
Site	2	0.0005	0.0002	0.03	0.97
Species	2	0.770	0.385	**37.67**	0.003
StXLoc	1	0.004	0.004	0.18	0.71
SpXLoc	2	0.005	0.002	0.25	0.79
SpXSt	2	0.234	0.117	**22.2**	0.007
StXSi	2	0.048	0.024	2.57	0.07
SpXSi	4	0.040	0.010	1.08	0.36
StXLocXSp	2	0.025	0.012	2.44	0.20
StXSiXSp	4	0.021	0.005	0.56	0.69
Error	160	1.517	0.009		

Table A44: ANOVA table for the colony rugosity index (colony surface area to colony volume ratio) in living colonies and colonies which had been dead and exposed for 21 months. F values in bold and underlined are significant at α=0.05. Data were transformed as X^1=arcsine(sqrt(X)) to obtain homoscedasticity.

	F dev. lin.	num. df	den. df	F regr.	num. df	den. df
Colony 1	0.49	2	16	**36.89**	1	18
Colony 2	2.32	1	12	**42.08**	1	13
Colony 3	0.01	1	12	**28.86**	1	13
Colony 4	0.37	2	16	**12.52**	1	18
Colony 5	0.04	2	16	**17.37**	1	18
Colony 6	**7.26**	2	16	**17.67**	1	18
Colony 7	0.19	1	12	**63.27**	1	13
Colony 8	2.24	1	12	**68.79**	1	13

Table A45: F values for testing deviation from linearity and significance of the regression of total bioerosion on 'time' for the eight colonies at Green Island. F values in bold and underlined are significant at α=0.5.

	Untransf.	log(x+1)	1/x+1	1/sqrt(x+1)	$1/(x^2+1)$	$1/(x^4+1)$
C1	**10.00**	**7.89**	1.20	1.80	1.06	1.12
C2	**11.16**	**13.67**	1.46	**3.33**	1.00	0.98
LI1	0.99	**3.39**	**3.27**	**4.51**	**2.89**	2.70
LI2	**3.64**	**4.90**	**7.91**	**8.72**	**3.53**	1.08
GI1	1.28	1.00	1.05	1.32	0.81	0.82
GI2	0.47	1.48	1.13	1.43	0.84	0.90
JB1	**5.87**	**6.77**	1.48	**3.27**	0.48	0.48
JB2	**5.21**	**4.38**	1.90	2.52	1.33	1.30

Table A46: F ratios to test for deviation from linearity of the regressions of the extent of total bioerosion at each site on duration of exposure. Numerator and denominator degrees of freedom for C1, LI1, LI2, JB1 and JB2 are 6 and 40; for C2 are4 and 28; for GI1 6 and 32 and for GI2 are 4 and 24. F ratios in bold and underlined are significant at α =0.05.

Source of variation	df	SS	MS	Fs	p
Total	137	3393.08			
Time	1	582.18	582.18	**38.50**	0.00001
Status	1	1.42	1.42	0.02	0.92
Reef	2	270.95	135.47	1.25	0.38
Site	4	373.53	93.38	**6.07**	0.0002
TimexStatus	1	32.02	32.02	0.38	0.62
TimexReef	2	265.64	132.82	2.13	0.24
TimexSite	4	229.25	57.31	**3.79**	0.006
Error	122	1844.67	15.12		

Table A47: ANCOVA table for total bioerosion. Data are transformed as Sqrt(x+1). F values in bold and underlined were significant at α=0.01.

Source of variation	df	SS	MS	Fs	p
Total	91	3450.30			
COT	1	93.46	93.46	0.47	>0.5
Stage	1	440.31	440.31	2.37	>0.5
Reef	2	399.93	199.96	5.07	0.15
Site	4	157.79	39.45	2.07	0.19
StageXCOT	1	52.84	52.84	0.28	>0.5
StageXReef	2	371.10	185.55	1.49	>0.5
StageXSite	4	496.41	124.10	**6.52**	<0.001
Error	76	1445.18	19.02		

Table A48: ANOVA table for extent of bioerosion by all taxa. Data are transformed as Sqrt(x+1). Values of F in bold and underlined are significant at α=0.01.

Source of variation	df	SS	MS	Fs	p
Total	91	1821.79			
COT	1	1.05	1.05	0.06	>0.5
Stage	1	772.53	772.53	20.46	0.08
Reef	2	33.74	16.87	0.56	>0.5
Site	4	120.01	30.00	**5.46**	<0.001
StageXCOT	1	88.02	88.02	2.33	>0.5
StageXReef	2	75.51	37.76	0.51	>0.5
StageXSite	4	295.79	73.76	**13.44**	0.001
Error	76	417.21	5.49		

Table A49: ANOVA table for extent of bioerosion by WORMS. Data are transformed as Sqrt(x+1). Values of F in bold and underlined are significant at α=0.01.

Appendix B

Publications from the thesis

(as at October 1994)

Effects of *Acanthaster* predation on bioerosion: design and preliminary results.

Barbara M Musso
Department of Marine Biology,
James Cook University of North Queensland,
Townsville QLD 4811

Citation:
Musso, Barbara M. (1993) Effects of Acanthaster predation on bioerosion: design and preliminary results. In: Workshop series no 18 : the possible causes and consequences of outbreaks of the crown-of-thorns starfish (18), pp. 133-144. From: The Possible Causes and Consequences of Outbreaks of the Crown-of-Thorns Starfish, 10 June 1992, Townsville, QLD, Australia.

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Rates of Skeletal Degradation Following Death in Three Species of *Acropora*

B. M. Musso

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Citation:
Musso, B.M. (1993) Rates of skeletal degredation following death in three species of Acropora. In: Proceedings of the 7th International Coral Reef Symposium, pp. 414-419. From: 7th International Coral Reef Symposium (ICRS), 22-27 June 1992, The University of Guam, Mangilao, GU.

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