

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

Abstract

The downstream effects of COTS outbreaks on non-coral organisms have rarely been investigated. The present work is concerned with the effects of outbreaks on the process of biological degradation of the reef framework. On reefs that have experienced severe outbreaks, the overall reworking of calcium carbonate by biological agents is expected to be greater than on reefs with high live coral cover. To establish whether the rates of bioerosion per unit area of substrate are enhanced on a reef following an outbreak, and what are the causes and effects of degradation of the standing coral skeletons left behind by COTS predation, two research programs have been undertaken. An experimental program consists of simulating COTS predation by killing coral colonies *in situ* in restricted areas on the reef crest. Three species of *Acropora*, usually highly preyed upon by *Acanthaster*, have been used. To date, results show that *Acropora hyacinthus* undergoes rapid skeletal degradation by external destructive agents, while skeletons of *A. gemmifera* and *A. cuneata* remain for longer periods exposed to the action of excavating organisms. The second research program consists of sampling dead substrates occurring on large *Porites* bommies, on both COT-affected and unaffected reefs. The year of death of these substrates can be estimated, and rates of bioerosion relative to periods of over 30 years could be calculated. Preliminary results show that the method is a powerful tool for establishing both large scale and disturbance-induced variations in the process of internal bioerosion.

Introduction

Since the "Acanthaster phenomenon" (Moran 1986) started in the early 1960's, a massive bulk of literature has accumulated on the starfish and on various aspects of the outbreak events. However, studies on the consequences of heavy outbreaks on the

reef components other than corals are scarce. In an annotated bibliography of the publications up to 1988 (Moran 1988) relative to the crown-of-thorns starfish (COTS), only 16 out of approximately 470 titles, were in some way concerned with the effects of outbreaks on non-coral organisms. Most of the research induced by the *Acanthaster* debate has focussed on the biology of COTS, in the attempt to shed some light on the origins and causes of the outbreaks. In contrast to the small number of specific studies, many authors have pointed out the importance of investigating the responses of the reef system to the massive coral mortality resulting from a large outbreak (Potts 1981, Bradbury *et al.* 1985, Bradbury and Mundy 1990, Moran 1986). Some downstream effects of outbreaks have been investigated, notably those on algae (Price 1972, 1975, Belk and Belk 1975, Bradbury and Mundy 1990), soft corals (Pearson 1981, Bradbury and Mundy 1990) and fish communities (Sano *et al.* 1984, 1987, Williams 1986).

The consequences of large outbreaks on bioeroding organisms have never been investigated. A number of authors have recognised the potential of the process 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 these substrates predominate on the reef surface following COTS outbreaks. Fabricius and Fabricius (1992) report a high correlation between sedimentation rates and abundance of COTS skeletal elements in subsurface sediment cores from two reefs on the Great Barrier Reef. Although they are unable to relate the relative abundances of skeletal elements in the sediment to absolute population sizes (ie. outbreak population sizes), they discuss the increased susceptibility to erosion (and consequently to sedimentation rates) of a reef surface that has experienced high rates of predation by *Acanthaster*. The present study specifically addresses the effects of extensive coral mortality due to COTS feeding activity on bioerosion. The potential mechanism by which large outbreaks may potentially affect bioerosive processes on a reef is twofold. Firstly, a rapid, dramatic increase in dead coral cover which 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. Information of this nature is not available at present. Previous studies which pioneered research on bioerosion on the Great Barrier Reef, have used artificial or transplanted substrates. Their purpose was to quantify the contribution of factors such as surface area, seasonality in recruitment of borers and duration of exposure to the observed rate of erosion (Hutchings and Bamber 1985, Davies and Hutchings 1983, Kiene 1985). Although much information has been gathered on the pattern of succession of boring organisms, nothing is known on how different dead coral skeletons are degraded on the reef surface. The second mechanism through which an outbreak could affect the overall process of bioerosion consists of possible changes in the population dynamics of the organisms responsible for the erosion of the reef framework (ie. boring infauna and vertebrate and invertebrate grazers), which may result in a non-linear increase of the rates of destruction.

The two mechanisms mentioned above are investigated here in two different studies. The first experiment simulates an *Acanthaster* feeding episode on reef crest habitats. It is aimed at estimating rates and nature of degradation in the skeleton of corals that are usually heavily preyed upon by COTS. The relative importance of external and internal bioeroders, and the temporal and spatial variability at a reef scale is estimated in the different coral species. This experimental approach has the advantage of controlling for factors such as time of death and type of substrate, which are responsible for most of the noise usually confounding studies on bioerosion.

The second study is one of the long term rates of bioerosion (over 4 to 33 years) on affected and unaffected reefs. It is designed to estimate possible changes in both rates of bioerosion and community composition of bioeroding invertebrates following A.

planci outbreaks. A new method of estimating rates of bioerosion using datable dead coral substrates has been employed to obtain long-term rates.

Methods

Simulation of Acanthaster predation

This experiment commenced at Lizard Island in February 1991 and will run up to February 1993. Coral colonies belonging to 3 species of *Acropora* (*A. hyacinthus*, *A. gemmifera* and *A. cuneata*) have been killed *in situ* on the reef crest. A total of 180 coral colonies have been killed and tagged. Their skeletons will be collected at the end of the experiment and analysed for the extent of internal bioerosion. A total of 90 living colonies (30 of each species) have been tagged and are monitored along with the killed ones.

The colonies are monitored every 3 months with photographic techniques in order to detect and quantify the changes in size due to external degradation. The method is similar to the one used by numerous researchers to study community dynamics of corals by estimating their changes in size and interactions through time. Colonies are photographed from above and the resulting images are digitised which provides an estimate of the planimetric, or projected, surface area of the colony. An estimate of the precision of the technique for parallax error was made by taking replicated photos of the same colonies from angles judged as perpendicular by the photographer. This gave an estimate of the technique bias of about 5% of the area. Presently 5 censuses have been completed (February, May, July and November 1991, February and August 1992) and the data from the first 4 censuses processed and analysed (Musso, *in review*).

The experiment follows a three-way, mixed model, nested ANOVA. In 2 locations (SE winds exposed reef crest / NW winds exposed reef crest), 3 sites per location have been set up. In each site colonies belonging to 3 species have been killed and mapped. The replication for each species is 10 colonies. At the same sites the same number of living colonies have been mapped and are monitored as controls. Due to a lack of independence among observations, data relative to external degradation were analysed with a Repeated Measures Multivariate ANOVA.

In order to convert the changes in surface area observed in *A. hyacinthus* into changes in calcium carbonate weight, 20 recently dead colonies were photographed underwater before and after removing the margins of the plate. The fragments removed were dried and weighed. The planimetric surface areas and dry weight of the margins of recently dead plates of *A. hyacinthus* were significantly correlated. A conversion factor of surface area to weight was estimated as the regression coefficient of a Model II Regression ($b = 0.01365$, C.L. 0.0123 and 0.015; Bartlett's three groups method for Model II Regression, see Fig. 1).

Living colonies belonging to the same species as the experimental ones have been collected and processed to obtain an estimate of the extent of internal bioerosion prior death (Musso, *in review*). The colonies are sectioned in 5 mm thick slices with a rock saw. Each slice is photocopied and the boreholes on the sectioned surfaces are digitised using an image analyser. This provides an accurate estimate of the volume of skeleton removed from the colony. For each slice and colony the relative contribution to bioerosion of different boring taxa has been recorded. Data on extent and species composition of internal bioeroders communities in the three species have been collected and analysed (Musso, (a) *in preparation*).

COTS outbreaks and long-term rates of bioerosion

The sampling of dead substrates on reefs with known history of past outbreaks has been carried out on Green Island (Musso, (b) *in preparation*) and John Brewer Reef (both experienced outbreaks in the 60's and 80's), and Centipede Reef (no evidence of outbreak since 1973; a large population of COTS was reported in 1971 but coral cover remained high). The second unaffected reef included in the design is the reef surrounding Low Isles. Sampling at this reef is scheduled for late January 1993. The reefs were chosen after consultation of the data collected by the A.I.M.S. survey teams.

The sampling is carried out on the dead surfaces occurring on big *Porites* bommies and resulting from partial mortality events (Anonymous 1985). These surfaces are sampled by drilling shallow cores (5 cm diameter by about 8 cm depth) with a pneumatic-drill, driven by a compressor running on the support vessel. One long core (2.5 cm diameter by 25 cm height) is also taken from each sampled surface for determining the year of death. The shallow cores are sectioned and the sections digitised to estimate the total volume removed by the major taxa of borers. The long cores are sectioned longitudinally and placed under UV light to analyse the fluorescent bands in the skeleton. These bands result from skeletal incorporation of run-off humic acids during particularly wet seasons and they allow the dating of the dead surface (Isdale 1984). A year of death is therefore estimated for each substrate sampled. A rate of bioerosion is calculated for each substrate as the volume of calcium carbonate removed divided the number of years since death.

The design includes 4 reefs (2 affected and 2 non-affected) and 2 sites per reef. Although the effect of COTS status on internal bioerosion in each reef could be confounded with other factors, especially shelf position, the levels of such factor are interspersed within the levels of the main treatment. At each site 4 *Porites* bommies with 2 or 3 different aged dead substrates each, have been sampled. For each substrate, 6 replicate cores are taken. The data obtained are analysed by regression analysis and ANCOVA following angular transformation.

Results

Simulation of Acanthaster predation

This paper summarises the major results in order to discuss them in relation to the effects of COTS outbreaks on the degradation of the reef surface. The detailed, preliminary results of this ongoing study may be found in Musso (*in review*).

The 3 species of *Acropora* used in the experiment differ greatly in the rates of erosion. High rates of external degradation occurred only in dead colonies of *Acropora hyacinthus* (Table 1). The other 2 species showed no changes or changes too small to be detected with the technique employed. There was a significant effect of time, with early, rapid degradation levelling off after three and six months since death in *Acropora hyacinthus* (Fig. 2). No significant interactions between time and location, or time and sites were found for *Acropora hyacinthus*. Univariate analyses performed on the data collected after 11 and 34 weeks and relative to *Acropora hyacinthus* showed a significant location effect, with the area removed being higher in the most exposed, S.E. sites (Fig. 2).

Table 1: Percent surface area removed from the experimental colonies after 9 months since death. Mean values are shown with standard errors and sample size in parenthesis (from Musso, *in review*).

	S.E. SITES			N.E. SITES		
	1	2	3	1	2	3
<i>Acropora hyacinthus</i>	49.34 ± 6.92	54.72 ± 8.08	57.24 ± 2.47	37.69 ± 4.02	48.51 ± 5.95	27.12 ± 8.43
sample size	(8)	(6)	(10)	(8)	(7)	(4)
<i>Acropora gemmifera</i>	17.28 ± 7.91	6.93 ± 3.08	4.38 ± 2.14	-0.21 ± 3.63	5.96 ± 3.21	3.64 ± 2.96
sample size	(8)	(8)	(10)	(8)	(9)	(10)
<i>Acropora cuneata</i>	-0.25 ± 1.75	-3.40 ± 2.48	2.13 ± 2.04	-2.25 ± 4.00	-1.17 ± 1.59	4.38 ± 1.47
sample size	(5)	(4)	(4)	(8)	(8)	(8)

Table 2: Percent of volume removed by internal bioeroders in living coral colonies. Data were pooled within location. Means are shown with SE.

	S.E. Sites	N.E. Sites
<i>Acropora cuneata</i>	5.99 ± 1.01	7.01 ± 1.71
<i>Acropora hyacinthus</i>	1.10 ± 0.31	1.22 ± 0.38
<i>Acropora gemmifera</i>	3.47 ± 0.92	1.25 ± 0.25

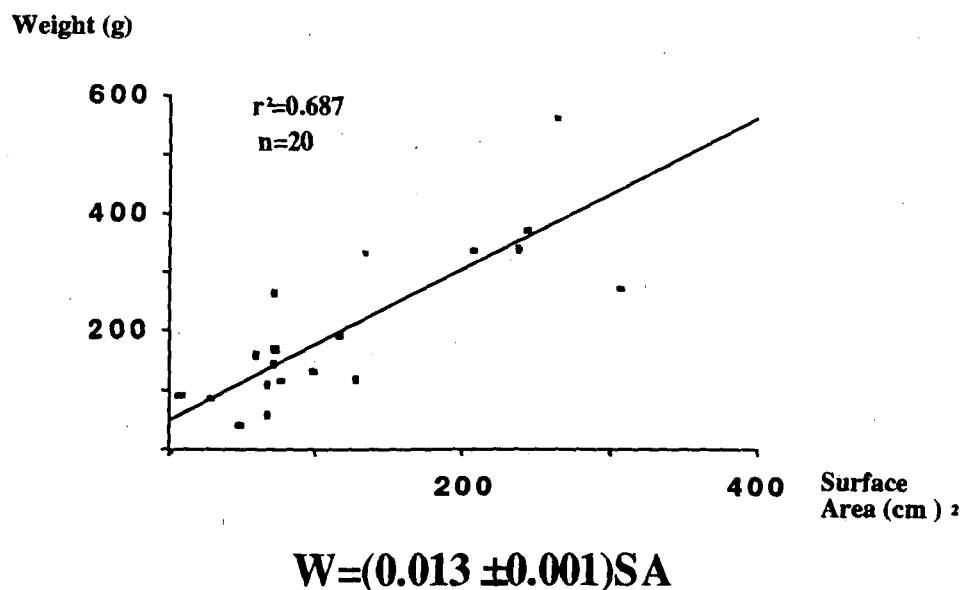


Figure 1: Conversion factor used for transforming surface areas in dry weight estimates for *A. hyacinthus* plates (from Musso, *in review*).

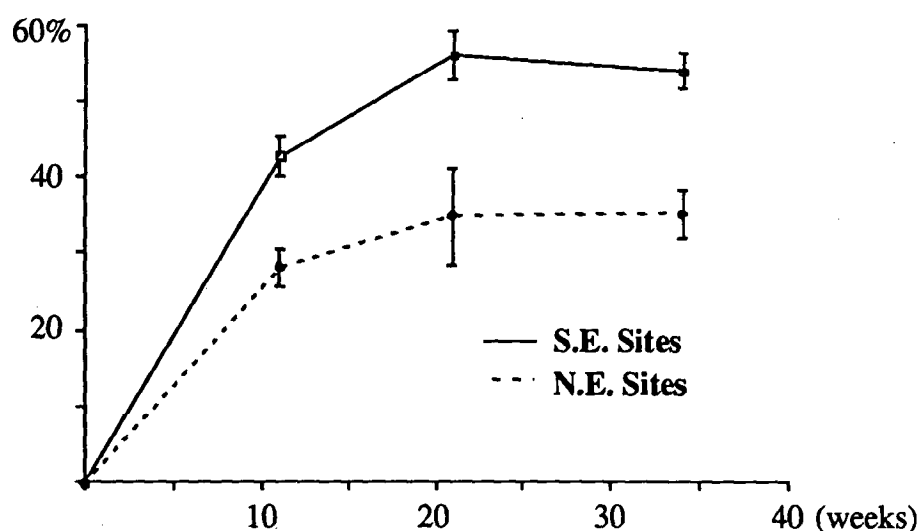


Figure 2: Percent of the initial planimetric area of *A. hyacinthus* plates removed plotted against time, for the two locations. Points are means and error bars are SE (from Musso, *in review*).

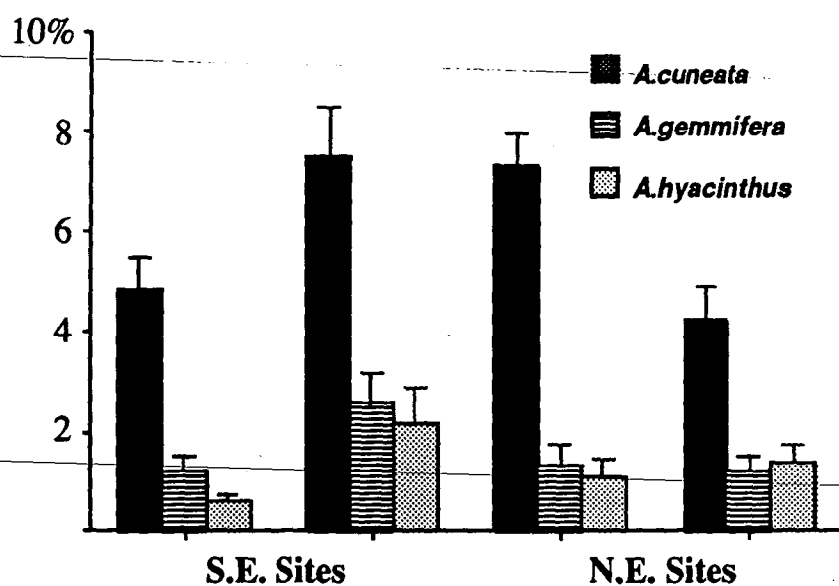


Figure 3: Estimate of the percent volume of skeleton removed by internal bioeroders in the three coral species prior to death (from Musso, *in review*).

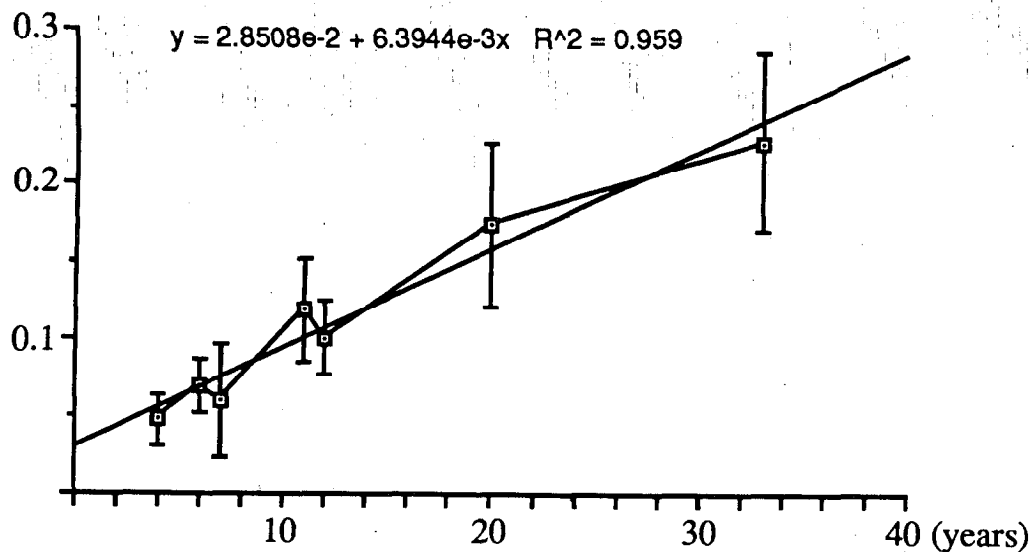


Figure 4: Common regression line of proportion of volume removed (data expressed as *arcsin* of square root of the raw data) from dead *Porites* substrates. Substrates and sites pooled after analysis.

The loss of calcium carbonate from each plate colony after 9 months since death was estimated to be 327.3 g (confidence limits: 296.6 g and 361.6 g) and 226.7 g (confidence limits: 205.5g and 250.5 g) respectively at the more exposed and less exposed locations.

The estimate of the percent volume removed by borers in the three species before death was significantly greater in *A. cuneata* than both *A. hyacinthus* and *A. gemmifera* (Fig. 3, Table 2). Preliminary analysis of the taxonomic composition indicates that bioeroding communities in *A. cuneata* differ from the other two species (Musso, (a) in preparation).

COTS outbreaks and long-term rates of bioerosion

Data were obtained and analysed from the sampling at Green Island (Musso, (b) in preparation). The method of dating dead *Porites* by using skeletal fluorescent bands proved feasible for substrates which died less than 33 years ago. In the case of older substrates, the fluorescent bands were less identifiable. Only data from reliably dated substrates were included in the analysis.

At Green Island a rate of internal bioerosion was obtained for each of eight *Porites* bommies. Each bommie was sampled at two differently aged dead layers (corresponding generally to the time of the two major COTS outbreaks). For each bommie a rate was obtained using regression analysis. A test for homogeneity of slopes showed that the rates of bioerosion were not significantly different among bommies within each site. Finally, an Analysis of Covariance showed no significant difference among the two sites. Power of the test to detect differences among sites was very high ($1-b = >0.94$). Such results allowed for the estimation of a common regression coefficient, ie. rate of internal bioerosion.

Discussion

The results of the experimental study (simulation of COTS feeding episode) are discussed firstly in relation to previous analogous work on the Great Barrier Reef and secondly to their implications in the context of outbreak events. Also, the results from the pilot study at Green Island on the long term rates of bioerosion are discussed, and possible paths of propagation of the outbreak effects to the bioeroding component of the reef system are presented.

After nine months of monitoring of the colonies killed by simulating *Acanthaster* predation, the results suggest that in plate coral colonies of *A. hyacinthus* very rapid skeletal degradation occurs soon after death. The agents responsible for skeletal degradation act differentially on the skeletons of different coral species. There does not appear to be any relation between the estimated extent of internal bioerosion at the time of death and the rates of the subsequent external degradation. It is likely that both physical degradation and biological erosion by grazing activity (mainly parrotfishes) are responsible for the high size reduction in the skeletons of *A. hyacinthus*. Sammarco *et al.* (1986) conducted a similar experiment with transplanted colonies of a foliaceous coral (*Pachyseris speciosa*). They implemented treatments with and without cages, which allowed them to conclude that the large skeletal degradation observed was mainly due to grazing activity by parrotfish. In the present study the spatial pattern observed in relation to site exposure suggests that physical erosion by wave action is also important. A pilot study for an experiment implementing wide-mesh cages for exclusion of excavator parrotfish is currently underway. The relative importance of these two agents (grazers vs. wave action) is relevant to the carbonate budget of the reef crest, as the two have different by-products, thereby recycling calcium carbonate in different compartments of the reef (Davies 1983).

The preliminary results of this study suggest that after an outbreak of *Acanthaster planci* occurs on the reef crest, the plate colonies that have been preyed upon are likely to disappear quickly. These corals represent the most preferred prey for *A. planci*. (De'ath and Moran, *in press* Faure 1988) and even under non severe outbreak conditions are likely to undergo extensive mortality, especially medium size colonies like the ones considered in this experiment. Larger colonies might be affected only by partial mortality during non severe outbreaks, thus escaping death. A study by Musso and Nelson is currently under way to investigate the effects of simulated scars on plates of *Acropora hyacinthus*.

Following an outbreak, the high rates of degradation in plate corals will result in the reworking of a large amount of calcium carbonate and in a reduction in the rugosity of the reef surface. In contrast, no immediate skeletal degradation appears to occur in the other two species under investigation. This suggests that the process of degradation of the reef surface, and the quantity of calcium carbonate reworked following an outbreak, will depend on the relative abundance of different coral species and on the species composition of the community affected by COTS predation. Thus, it might be possible to make minimum estimates of the effect of an outbreak on the erosion of a coral community, given data on the relative abundance and mortality of different species.

The topographical changes of the reef surface resulting from the quick disappearance of tabulate corals may affect the coral community structure and, in post-outbreak situations, the patterns of coral settlement on the recovering reef. The role of the plate corals in structuring the composition and in increasing diversity of the understorey community has been investigated by some authors with sometimes different results (Sheppard 1981, Stimson 1985). According to Stimson (*op. cit.*) the understorey community has lower density and lower diversity than open substrate. Recently Fisk and Harriott (1992) have reported much lower rates of recruitment under tabulate corals compared to more exposed substrates. However, especially in those habitats that are dominated by *Acropora* plates, ie. the upper slope, structural complexity and tri-dimensionality of the reef surface must rapidly decrease with massive coral mortality. Some effects on the recovering community have to be expected and should be further investigated.

So far I have discussed what I regard as the "immediate" effects of an outbreak on bioerosion: that is to say the linear increase in bioerosion resulting from the increase in

"bioerodable" substrate. Another possible effect that is likely to manifest itself over a larger temporal scale is the one resulting from changes in the population dynamics of dead coral indwelling organisms, after living coral cover gets drastically reduced. These changes could affect different stages of the life history of these organisms. For example, if more substrate is available for settlement after COT outbreaks, the population sizes 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. Processes like 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 organisms to disturbance have been documented (Rose and Risk 1985, Scott 1990).

The study I started at Green Island is aimed at detecting changes that may occur, after large COTS outbreaks, in the long term rates of bioerosion and in the composition of boring communities. Studies investigating bioerosion have generally pointed out the high levels of variability which characterises the process. Sammarco and Risk (1991) reported that up to the 56% of the variance in the extent of bioerosion in *Porites* heads was due to variability among heads and a further 20% to variability within heads. Factors such as duration of exposure (Davies and Hutching 1983, Kiene 1985) as well as type of substrate (Highsmith 1981) are responsible for most of the noise usually confounding studies on bioerosion. Therefore, a fundamental difficulty in determining extent and rates of bioerosion is that an accurate estimate of the time of death of the substrates to be sampled is necessary. This difficulty has usually been circumvented by implementing experimental substrates, for which the time of exposure to bioeroders is known. This implies that the temporal scale over which the rates of bioerosion are calculated is limited by the duration and resources of the study.

This study uses naturally occurring *Porites* substrates for which the time of death can be accurately estimated. The pilot study shows that substrates as old as 33 years can be reliably dated. This length of time spans a period which includes the two major outbreaks reported for the Great Barrier Reef. The analysis of the data from the pilot study at Green Island indicates that when only one type of substrate is analysed for internal bioerosion, and the variability due to the duration of exposure of the substrate to borers can be accounted for, then the variation of the rates of bioerosion within that substrate is low, and consequently power of the tests for detecting treatment effects is likely to be high. The method represents a powerful tool for isolating large spatial scale variability in the process of bioerosion, and variability due to disturbance events like *A. planci* outbreaks. This is the first study of long term rates of bioerosion with the potential of investigating such questions.

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