TOURIST IMPACT ON REEF CORALS

1984 Report to
Great Barrier Reef Marine Park Authority

A.M. Kay: Research Fellow.
M.J. Liddle: Principal Investigator.

SCHOOL OF AUSTRALIAN
ENVIRONMENTAL STUDIES
GRIFFITH UNIVERSITY

TOURIST IMPACT ON REEF CORALS

By

A.M. Kay: Research Fellow.
M.J. Liddle: Principal Investigator.

School of Australian Enviromental Studies
Griffith University
Nathan, Qld. 4111.

Report to G.B.R.M.P.A.
March 1984

Financed by the Great Barrier Reef Marine Park Authority and undertaken with the co-operation of the Qld. National Parks and Wildlife Service.

CONTENTS

The work in this report is the joint production of A.M. Kay and M.J. Liddle but primary responsibility for each chapter is indicated on this page.

EXECUTIVE SUMMARY

AIMS

The major objective of this project was to provide a scientific basis for the management of reef walking in the Great Barrier Reef. We used an experimental approach involving controlled manipulations of coral communities and coral species on Heron Island Reef to fulfil this general aim. These experiments were designed to answer the following broad questions.

1. Are the coral communities in the reef crest and outer reef flat zone equally susceptible to trampling damage?

2. If not, what factors might be responsible for any difference found and what are the long term effects of trampling at different intensities on the coral communities in each zone?

3. What is the vulnerability of selected common reef flat corals to immediate physical damage (resistance) and once damaged, what is the probability of their survival (tolerance) and how quickly do they regrow (resilience)?

4. Are the guided reef walks from the Heron Island resort altering the reef flat community over which they pass?

RESULTS

Our experiments demonstrated that the coral community in the reef crest zone was at least 16 times less vulnerable to trampling damage than that in the outer reef flat zone. This was due to differences in the morphologies of the corals and the structure of the dead coral substrata between the two zones.

The low compact forms of coral on the reef crest were relatively resistant to mechanical disturbances and long term trampling had no effect on the hard level substrata of this site. The fragments of coral which were broken off were mostly washed away in the relatively turbulent conditions of the reef crest zone and no rubble accumu-

lated. The visible effects of trampling were confined to breaks in live coral visible immediately after trampling and as many as 480 traverses along a pathway over 18 months did not change the composition of the coral community.

In contrast trampling broke up many of the upright branching corals and most of the unconsolidated uneven substrata found at the outer reef flat site. Rubble accumulated in the ditches formed by repeated trampling along pathways and after only 30 traverses over 18 months the composition of the coral communities had drastically changed. In addition, trampling broke off eight times as much coral on the outer reef flat as on the reef crest.

These results and some simple arguments about the structural strength of different shaped coral colonies were used to formulate a scheme (the morphology/substrate type scheme) which can be used to rank different sites on a scale of vulnerability to trampling damage.

The resistance (vulnerability to physical damage), tolerance (probability of survival after damage) and resilience (rate of growth after damage) characteristics displayed by the four common corals which we examined indicated that their response to physical disturbances, and trampling in particular, were different. These responses fell into three distinct categories which may represent more general survival strategies. They were:

Resistant: high resistance, low tolerance and resilience;
Resilient: low resistance, high tolerance and resilience;
Recruitment: intermediate resistance, tolerance and resilience with a high colonization rate.

The morphology/substrate type scheme suggests that resistant corals are the most likely to survive in heavily trampled areas despite their low tolerance and resilience. However the resilient and recruitment corals will recover move rapidly during a period of closure.

At the time of writing the experiment which was designed to determine the impact of the guided reef walks from the Heron Island resort is still in progress. So far there is no evidence that the tours are causing any damage however the experiment needs to be conducted for at least four years (continued for two more) before any conclusions can be made.

MANAGEMENT IMPLICATIONS

The primary aim of managing reef walking is to provide the best possible experience for present and future generations of reef walkers and, in some cases, an environment which is as natural as possible for scientific research. To satisfy this aim a high quality environment must be maintained. This can be achieved by keeping the intensity of use below the level where there is long term degradation of the habitat or alternatively at a level where recovery from damage occurs within a reasonable time during a closed season.

Our results indicate that different reef flat communities are not equally susceptible to trampling damage and this fact must be taken into account when setting maximum levels of use for various reefs and sites within reefs. As a general recommendation sites made up of low compact corals and hard substrata will withstand quite high levels of use, equivalent to five or six people walking along exactly the same route each week. However a site made up of upright branching corals and honeycombed unstable substrata will not withstand even low levels of use, such as one person walking along exactly the same route every two weeks.

There are a variety of management techniques which can be used to limit the level of use at a vulnerable site without imposing excessive restrictions on the visitor. These are discussed in this project report.

In conclusion it is our view that management decisions about reef walking near popular tourist or educational facilities must take the nature of the site into account. For instance, unrestricted widespread reef walking is unlikely to degrade reef crest sites, however, without appropriate management vulnerable outer reef flat sites on the same reef would be severely damaged by this activity.

CHAPTER 1 INTRODUCTION

CHAPTER 1 INTRODUCTION

1.1 THE CONTEXT OF THIS STUDY

Most wilderness areas which are also tourist resources have been utilised by man for many thousands of years. The advent of European man to the Australian environment has brought many changes. At first these were associated with the introduction of his large-scale techniques for agricultural production and harvesting of natural resources. But with the increasing affluence of western societies, there has been a concomitant increasing surplus of wealth and of leisure time. This has provided the means for day trips and holidays away from home for large numbers of people and the consequent rise of the tourist industry.

From 1950 to 1970 there was a steady rise of about 11% per annum in the money spent by tourists in foreign countries. In 1972 it is estimated that over 200 million tourists world-wide spent 24 billion U.S. dollars in foreign countries and by 1978 this had risen to 264 million tourists who spent 63 billion U.S. dollars (Pigram 1983). This rapid expansion may now be levelling out as the economies of western societies enter a non-expansionist phase, but the idea of travelling to a place away from home for an annual holiday is an entrenched expectation for a high proportion of people in western society.

The general flow of tourists is from the more developed, industrialised areas to warmer, generally less densely populated areas closer to the equator (Pigram 1983). The numbers of visitors to tropical and sub-tropical Queensland has also risen with the general trend and in 1981/82 there were 285,702 international visitors bringing an estimated 311 million dollars to the Queensland economy (Queensland Tourist and Travel Cooperation). Quite a number of these tourists, visited the Great Barrier Reef at some point, in spite of the extra cost involved in flying, taking a helicopter or boat from the mainland to the Reef itself. As tourist operators have realised the size of the market, there have been increasing numbers of ways to reach the reef and more facilities continue to be provided. It is, therefore, likely that the number of tourists visiting the reef will continue to rise in spite of the general recession and 'the uncertainty of future trends' (Mercer 1981).

There are over 20 oceanic reefs which are advertised to receive visitors on a regular basis and many more which are occasionally visited by charter and other vessels. It is, then, pertinent to ask 1) why the reefs are so attractive, 2) what kinds of people do they attract, 3) are they changing as a result of this use, and 4) what are the likely consequences of this change if it is occurring?

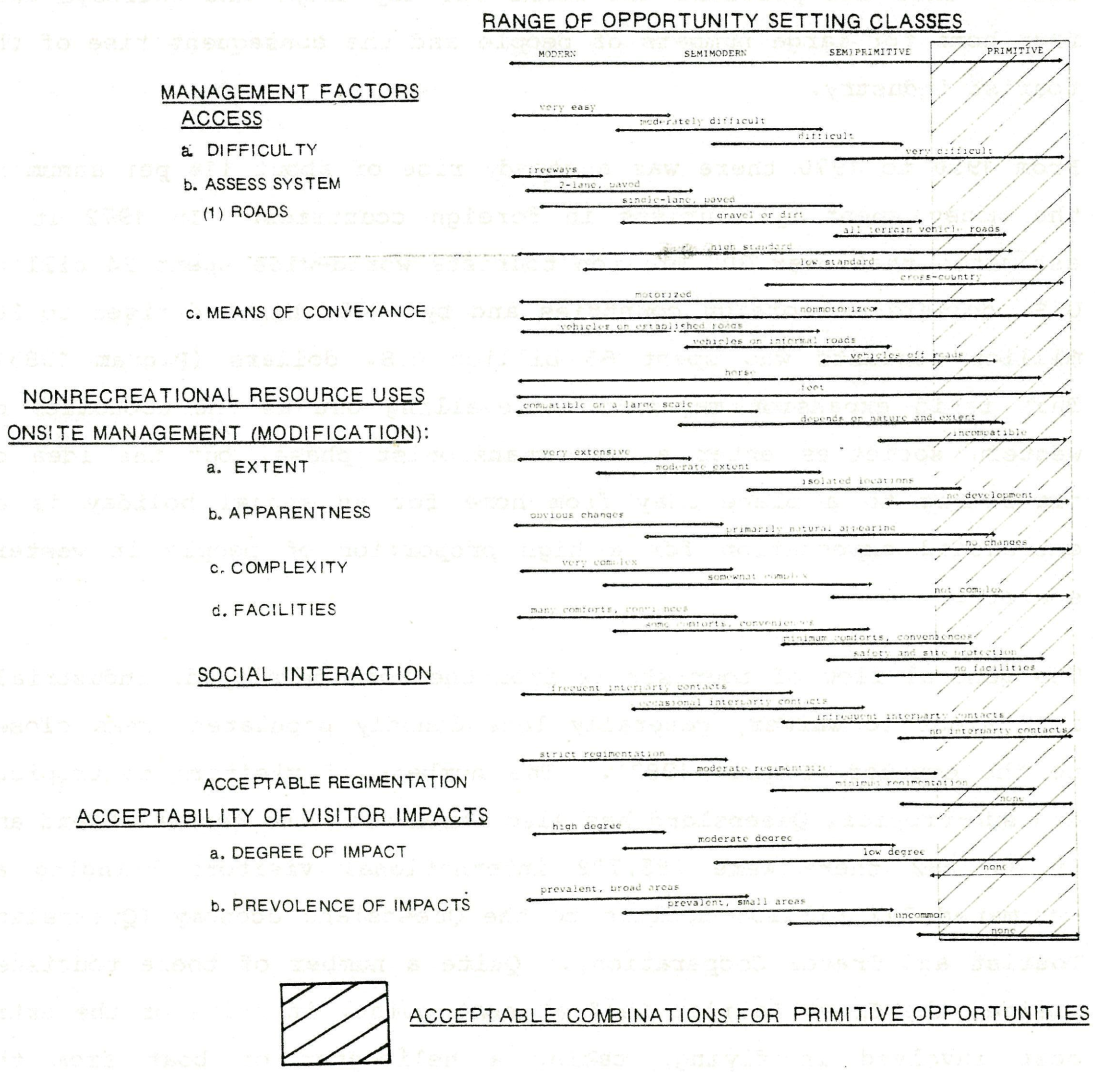


Figure 1.1 Factors defining outdoor opportunity settings or The Recreation Opportunity Spectrum. (After Clark and Stanky, 1979).

1) The first question can be approached by consideration of the range of recreation opportunities as presented in the Recreation Opportunity Spectrum, Fig. 1.1 (Clark & Stanky 1979). In general, the qualities of the reef come under the heading of primitive, with access being very difficult and ultimately on foot, there are no non-recreational resources which are compatible with use for recreation use and virtually no on-site management modifications. Social interaction with other groups is at a low level and only minimum regimentation is acceptable to visitors. It follows from this description and the Clark and Stanky (1979) concepts that, if the reefs are to remain attractive to these visitors, then visible visitor impact is not acceptable or only at a low level, and that the impacts must not be very widespread (see Fig. 1.1).

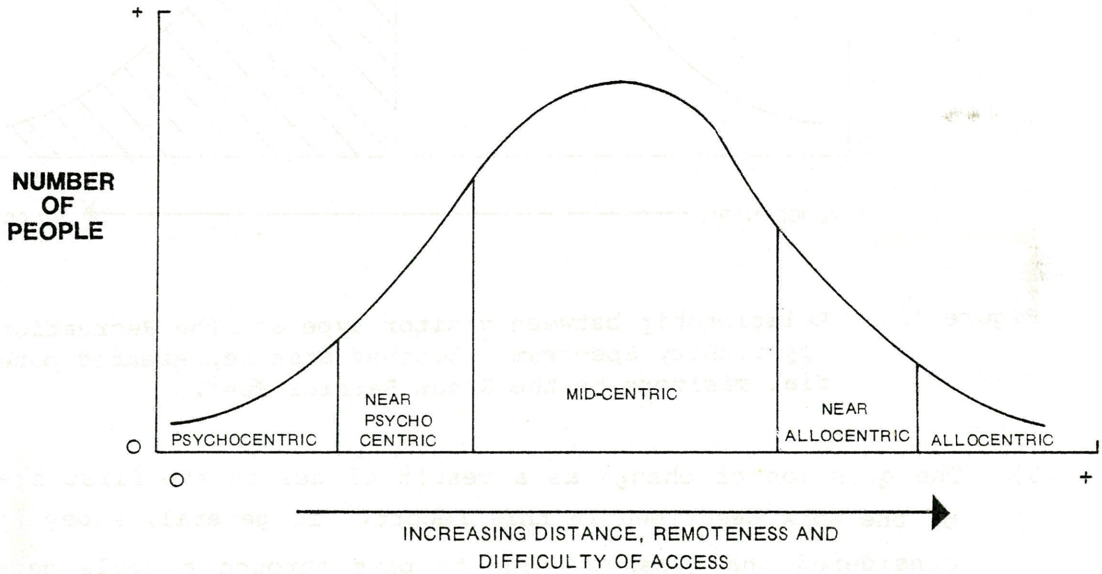


Figure 1.2 Type of tourist in relation to type of place visited. (Source Kaiser and Helber, 1978; after Pleg, 1972).

2) The kind of person that has been attracted to the reef would be classed as near allocentric and allocentric by Ploeg (1972) Fig. 1.2. Allocentric persons are defined as being self-confident, successful, high earners and frequent travellers who prefer uncrowded destinations (see Pigram 1983). Psychocentric persons are, in contrast, unsure of themselves, low earners and infre-

quent travellers who seek the security of tours and familiar destinations. The relationship between the type of users and the type of preferred environment is shown in Fig. 1.3. A semi-primitive example might be Masthead Island (Plate 1.1) and a primitive one, Polmaise Reef (Plate 1.2).

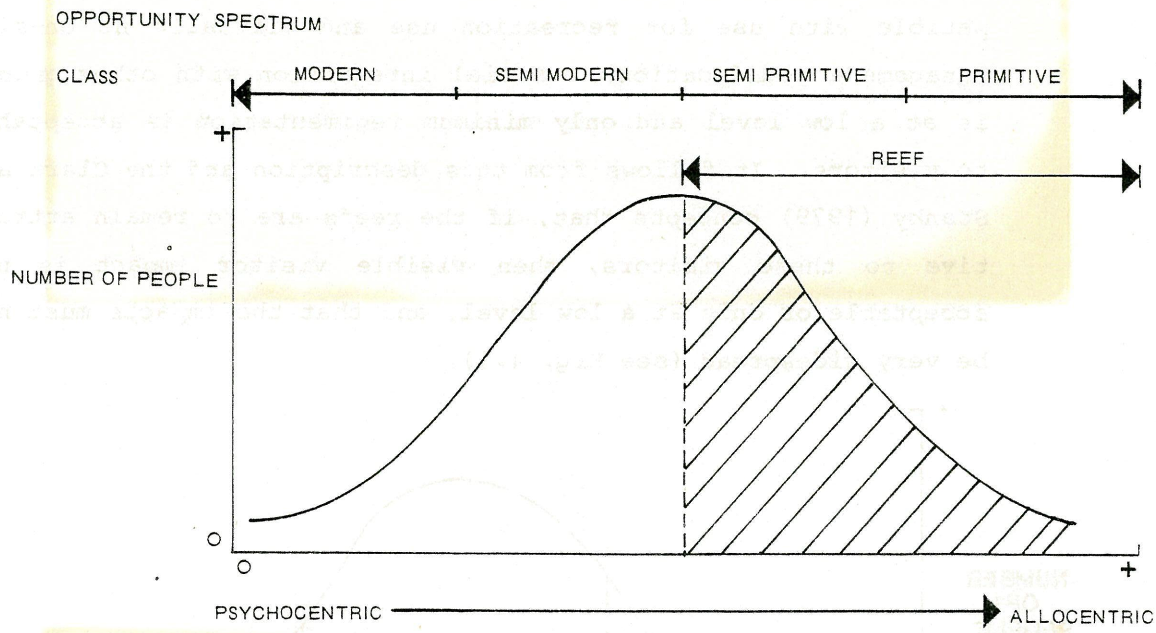


Figure 1.3 Relationship between visitor type and The Recreation Opportunity Spectrum. Hatched area represented potential visitors to the Great Barrier Reef.

3) The question of change as a result of use is the first element of the work described in this report. In general, Ploeg (1972) considered that resorts tend to pass through a cycle development, which would start as 'Primitive' in Clark & Stanky's (1979) terms and end as a declining 'Modern' environment, appealing first to allocentric and finally to psychocentric visitors. The increasing numbers of visitors to the reef and the increasing provisions for tourist support this hypothesis, although it would be a serious error to consider that the whole of the Great Barrier Reef provides only one type of visitor experience.

Plate 1.1 Masthead Island from 4,000 feet

Plate 1.2 Polmaise Reef from 4,000 feet

In general, therefore, numbers of visitors are going to rise at [illegible] percentage rates [illegible] that [illegible] may be met with [illegible] more [illegible] at all in the [illegible]. However, [illegible] a resource of this site [illegible]. [illegible] in order to [illegible] possible to [illegible] the whole range of experience [illegible] potentially [illegible] that there [illegible] of the impact caused by people [illegible] and [illegible] wildlife [illegible] management that [illegible]. Finally [illegible] local people [illegible] for visitors, [illegible] and [illegible] needs.

In theory, then, management of the land at a Nature Reserve for various types of visitor can only succeed [illegible] there is an understanding of what the different kinds of visitors need for a satisfying, and perhaps [illegible] experience, and once the [illegible] between visitors and the environment [illegible]. In [illegible] management must be based on [illegible] at present [illegible] available information, [illegible] however incomplete, and the information should be interpreted and [illegible] becomes available.

Our objectives in carrying out this project have been to provide information that could be used as a general basis for both [illegible] management [illegible] and to form a [illegible] and other [illegible] the [illegible]. Our study [illegible] limited to [illegible] it would be reasonable to [illegible] them to other [illegible] and [illegible] with the [illegible].

1.4 EXISTING RESEARCH

The various studies on [illegible] aspect of [illegible] recreation [illegible] number of [illegible] previously introduced [illegible] that [illegible]

4) In general, increasing numbers of visitors are going to have an increasing impact on the reef and create problems that can only be met with on-site modifications in the heavily used areas. However, with a resource of this size it is clear that it is going to be possible to provide the whole range of experience within the Recreation Opportunity Spectrum, providing that there is an adequate knowledge of the impact created by any particular level of use and that techniques are adopted to manage the environment and control the demands that are made upon it. As Pigram (1983) comments, 'good planning ... attempts to attract, guide and ultimately satisfy the consumer's needs'.

In theory, then, management of the reef as a tourist resource for various types of visitor can only proceed at a detailed level once there is an understanding of what the different kinds of visitors need for a satisfying, and perhaps in view of the cost, extraordinary experience, and once the interaction between visitors and the environment is reasonably understood in a quantitative way. In practice, management must be carried out at present and all available information will therefore be utilized, however incomplete, and new information should be interpreted and disseminated as soon as it becomes available.

Our objectives in carrying out this project have been to provide information that can be used as a general basis for both immediate management decisions which have to be made in the near future and to form a foundation for more detailed and wider ranging studies in the next phase of the work. Our study is limited to the effects of trampling on coral reefs, although it would be reasonable to relate them to other mechanical influences, such as the use of vehicles or accidental damage by boats colliding with the reef.

1.2 EXISTING KNOWLEDGE

Previous studies of the impact of trampling on reef corals appear to be limited to that of Woodland and Hooper (1977). They carried out a number of traverses on a previously untrodden reef flat and found that 41% cover of live coral was reduced to 8% cover after 18 passa-

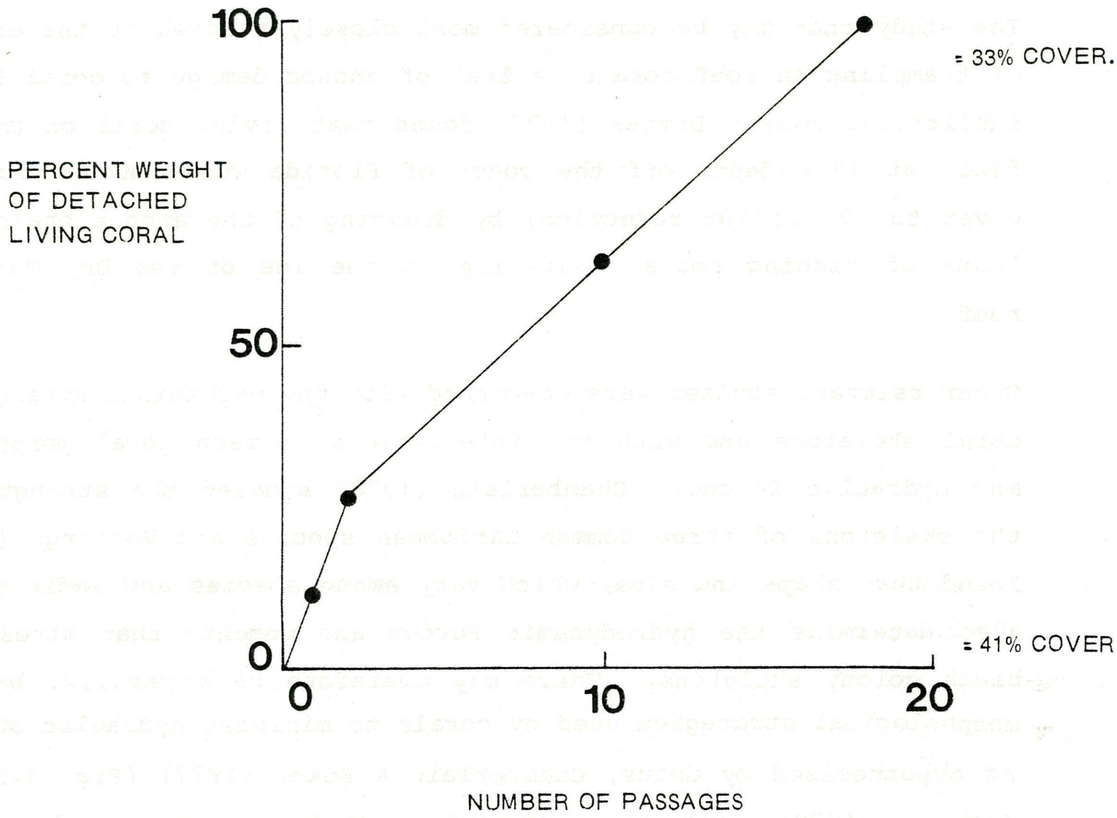


Figure 1.4 The weight of live coral detached from 50m^2 of reef flat by up to 18 passages. The total weight of detached coral was 607kg (12 kgm^{-2}). Forty-one per cent of the area was initially covered by live coral which was reduced to 31% cover. From data of Woodland and Hooper (1977).

ges, and that a mean of 12kg. m^{-2} of live coral was detached; the relationship between the number of passages and detached coral is shown in Fig. 1.4. This study was particularly useful in showing that trampling on corals, at least on the reef flat, could cause considerable damage and should be taken seriously as a part of the management of coral reefs as a tourist resource.

While the Woodland and Hooper (1977) study was valuable in drawing attention to the problem of tourist impact on reef corals, it was inevitably very limited. Since there have not been any other published studies of human trampling on reef corals until the work reported on here was commenced, it is pertinent to review other work on corals that might throw some light on the problems.

The study that may be considered most closely related to the effects of trampling on reef corals is that of anchor damage to coral in the sublittoral zone. Davies (1977) found that living coral on the sea floor at 12m. depth off the coast of Florida was reduced from 40% cover to 32% (a 20% reduction) by dragging of the anchor chains and lines of fishing boats sheltering in the lee of the Dry Tortugas reef.

Other relevant studies were concerned with the mechanical strength of coral skeletons and with the interactions between coral morphology and hydraulic forces. Chamberlain (1978) studied the strengths of the skeletons of three common Caribbean species and Vosburgh (1982) found that shape and size, which vary among species and individuals, also determine the hydrodynamic forces and moments that stress and break colony skeletons. There may therefore be a parallel between morphological strategies used by corals to minimise hydraulic stress, as hypothesized by Graus, Chamberlain & Boker (1977) (Fig. 1.5) and Jackson (1979), and the strategies which are more tolerant to trampling.

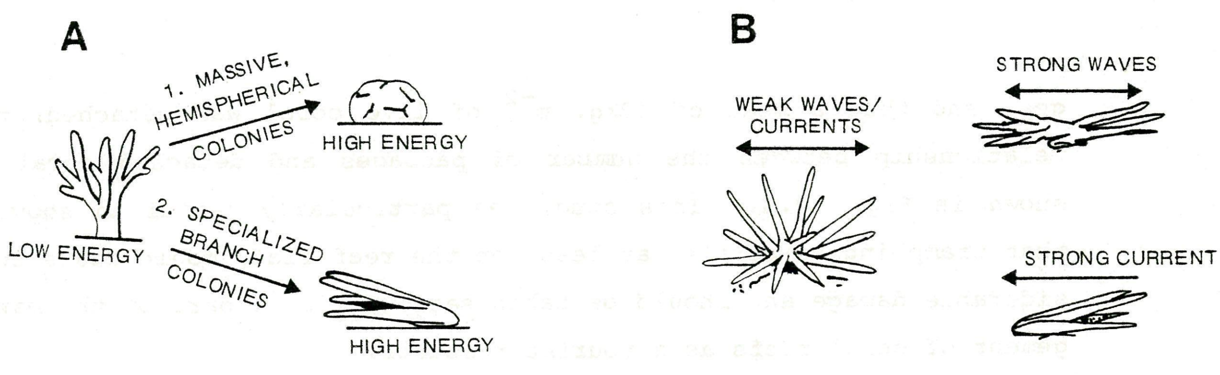


Figure 1.5 Adaptive growth strategies used by corals to minimise hydraulic stress. A. General adaptive trends. B. Branching phenotypes developed in different flow regimes. Redrawn from Graus , Chamberlin and Baker (1977).

1.3 MANAGEMENT PROBLEMS

The objectives of the work described in this report have been to provide data that would be of direct use in solving management problems, or, to quote Edington and Edington (1977) 'to organise our information in terms of the enterprises that are common currency of planning'. Where possible, we have also attempted to advance the theory relating to human impacts on natural ecosystems. In order to provide cogent information, we defined the likely management objectives that may be applied to tourism in the reef environment. Our first general assumption was that tourism is unlikely to be a threat to the conservation of the whole reef and, therefore, the management problems would be local and the objective would be to provide a high quality environment for the reef-walking tourist, or in some cases for scientific research.

The first and most general question is, does reef-walking have any effect on the reef corals or the reef environment? Secondly, which reefs or parts of reefs would be best used for reef walking? This second question has two parts relating to the intrinsic quality of the reef; the first is, what kind of reef is best able to sustain continued use by reef-walkers, and the second, what kind of reef gives the reef-walker most satisfaction?

In terrestrial habitats used for recreation it is immediately evident that walkers are changing the biota and other aspects of the environment as use tends to be concentrated on paths and there are adjacent, relatively undisturbed areas. The general effects of walking can, therefore, be studied in relation to these undisturbed areas which may be used as controls in an observational approach (Bayfield 1979; Liddle & Greig-Smith 1975a, 1975b; Crawford & Liddle 1977; Bowles 1981). However, walkers on the reef flat tend to spread out over large areas where there are no well-defined paths and the consequences of trampling on the biota are not so obvious.

1.3.1 Management philosophy

In the discussion above it became clear that tourists who visit the reef do so because they are seeking a 'primitive' or 'semi-primitive' experience. This emphasizes the importance of the resource as the centre of the experience. It is, therefore, the maintenance of the resource that has to be at the centre of any management plan, if only because it is the attraction which ultimately draws the tourists to spend money with any particular tourist enterprise. With respect to use for tourism, the degree of naturalness that is set for the management aim will depend on the position of any particular area in relation to the Recreation Opportunity Spectrum. This may refer to the present condition of the resource or the condition that is seen to be desirable in the future. The recreation resource can be defined on a similar spectrum from Artificial to Undisturbed, as is used for the recreation opportunity spectrum. This means that for informed management the resource must be evaluated, a policy determined in relation to its degree of naturalness and the management standards set for each site and appropriate portions of that site.

These management processes can be subdivided into four logical stages.

A. The first requirement is, then, a knowledge of the present condition of the resource and how far, if at all, it departs from its range of natural or undisturbed condition.

B. The quality of the resource having been defined, it can then be located in its particular place on the recreation resource spectrum.

C. The third requirement is to understand what effect the various management techniques will have on the quality of that resource and its location in the spectrum.

D. Finally, decisions can then be taken which match appropriate techniques (C) to the requirements set out in B.

1.3.2 Management techniques

A recreation manager has the option of controlling either the visitor or the resource and usually some blend of the two is used (Goldsmith

1974). Figure 1.6 lists some techniques which could be used for the management of reef walking according to this classification. In the following sections we have used this basic dichotomy as a framework in which the particular management techniques considered in our work can be discussed.

Figure 1.6 Techniques for managing human trampling on coral reefs.

Control of People	
General principle	Technique
Markers in the environment	Signposted pathway
Guidance by people	Tours
Provide information	Educational leaflets
Restrict access	Limited transport

Control of Resource
Transplantation of coral and other animals
Stabilizing coral rubble
Creating passages between pools

1.3.2a Visitor control

There are two general aspects to the control of visitor activity. Firstly the manager needs to decide what areas and locations should be used (area of use) and secondly what is the optimum pattern of use in these areas in terms of the numbers of people which visit them and when they do it (intensity and frequency of use).

(i) Area of use

In a coral reef system the area of use can be considered on several spatial scales and the area selected will depend on its attractiveness to reef walkers and its vulnerability to trampling damage.

1) The first decisions are, which reefs should be used by tourists and what is their quality or place on the Recreation Resource Spectrum? This is done in the zoning plans prepared by GBRMPA.

2) The next decision to be made is which area of the reef is to be used for reef-walking? This selection is likely to be based on a local quality of the reef and its ability to retain that quality under the effects of reef-walking. Visitors may be controlled by the location of the landing point, tourist camp grounds or accommodation.

3) The next scale will be at the size of areas of different types of habitat. For example, the sandy in-shore area, the outer reef flat, the boulder field and reef crest. Local survival of these types under the effect of trampling becomes very important. Control at this level is an unresearched subject but will include general information made available to visitors and routes chosen by reef walk guides.

4) The micro scale relates to the size of pools, live coral patches and rubble areas. At this level, a knowledge of the ability of different morphologies and species to resist trampling damage and survive and regrow when they are damaged is essential. Control of the distribution of visitors may be by guides, local markers or paths and detailed information made available to the tourists before venturing on the the reef flat.

(ii) Intensity and frequency of use

Decisions about the intensity (number of people per unit area per unit time) and frequency (number of times a site is used) of use will depend very largely on a knowledge of the vulnerability of a given area to trampling damage and the ability of corals in that area to recover. A manager may opt to permanently limit use at an intensity where no damage occurs in the long term or to temporarily limit use at a higher intensity where damage will occur prior to a rest period of no or very limited use where the damage can be repaired (closed seasons and rotational use). In either case control may be exercised by encouraging people to keep to marked paths, less vulnerable reef areas, limiting transport to isolated reefs or reef areas and providing guided tours.

The length and timing of closed seasons will vary according to the size and nature of the reef area, the damage it has suffered and the seasonal cycles of the biotic community it contains.

The management of people at the periodicity of the seasons is a frequent phenomena where publicity is either directed at the season with the most favourable climatic conditions for outdoor recreation or at filling spaces in the low season. However, the nature and particularly the growing seasons of the resource should also be considered. For example, it was found that use of a grassland in winter followed by a rest period in the productive spring and summer season maintained a greater cover than summer use and winter recovery period (Liddle 1973).

Various other factors will also influence management decisions about levels of use. For example, the lunar monthly cycle of tides is bound to be important from the point of view of visitor convenience as very early or late evening reef walking is not a majority activity! This leads to a consideration to the time of day in relation to low tide and the emergence and activity of the coral polyps. Tourist capital could be realised by limited night reef-walking and perhaps from the coral spawning time, as this process becomes more fully understood.

1.3.2b Resource control

There has been relatively little direct management of the reef resources, except indirectly through the management of people. There is, however, a considerable potential for innovative management approaches in the future and some of these are mentioned below.

Management of the non-living parts of the biota may involve the creation of paths by moving or stabilizing coral rubble, cutting through dead or living corals to link 'wadeable' pools into a pathway or cutting steps where appropriate. These techniques also involve controlling visitors. The location of these pathways would primarily be determined by the occurrence of living coral, its susceptibility to trampling damage and ability to recover from that damage and its appeal to the visitor.

Techniques applied to living organisms may involve the transplanting of coral or seahares, shellfish or other organisms that make for a satisfying visual experience for the visitor. Transfer of crown of thorns starfish away from the recreation site has been locally successful. The transplanting of small portions of coral which grow fast may be a possible technique of stabilizing rubble pathways or embankments as well as creating a visual experience.

It may also be possible to alter the environment of selected small areas of coral by applying special treatments which encourage growth in a similar way to which 'Lund tubes' are used in lakes.

1.3.2c Conclusion

The primary need is to understand the interactions that occur between the people and the reef organisms they come to see. This involves a particular knowledge of the susceptibility of corals to trampling damage, the probability of their survival once damaged and their recovery rate after known intensities and frequencies of trampling or of recovery rate from a particular point on the Recreation Resource Spectrum.

1.4 THE NATURE AND PURPOSE OF THE EXPERIMENTS

1.4.1 Research approach

As a general principle, we designed the experiments to give information relevant to as wide a range of management problems as possible.

As a general guide to the philosophy of our research approaches, we took the work on the effects of trampling in terrestrial environments (see Liddle 1975, Wall and Wright 1979, Speight 1973 for reviews) and the methodology commonly used in the investigation of sessile communities in marine environments (see Paine 1977). These approaches fall into two broad categories, analytical and experimental.

1. Analytical

This approach is basically observational and involves surveys of trampled areas or paths and adajacent untrampled areas. It involves no controlled manipulations and assumes that the whole area was homogenous prior to trampling, that the trampling is confined with measurable boundaries and that no significant environmental changes have occurred since the trampling commenced.

2. Experimental

This approach involves controlled manipulations by a researcher and can be subdivided into three groups.

a) experimental trampling in the field on a long or short term basis in areas which have not been previously trampled.

b) the exclusion of human walkers from plots within an area which is regularly trampled so that the impact, if any, of this activity can be assessed.

c) experiments with individual species in the field or laboratory designed to quantify those properties which determine how trampling effects their abundance.

The relevant literature is reviewed in each chapter and will not be further discussed here. It is, however, pertinent to point out that the analytical approach was not immediately applicable to Heron Island reef (see Section 4.1), although we do not dismiss it as a possibility. In order to clarify our thinking we developed a general model of the events which occur when the reef flat is trampled, based on the one in Liddle (1975) for terrestrial situations (Fig. 1.7). This considers the major effects of trampling on the five substrate types that are common on the Heron Island reef flat. The model can be used to place the information gained from our experiments into its dynamic context.

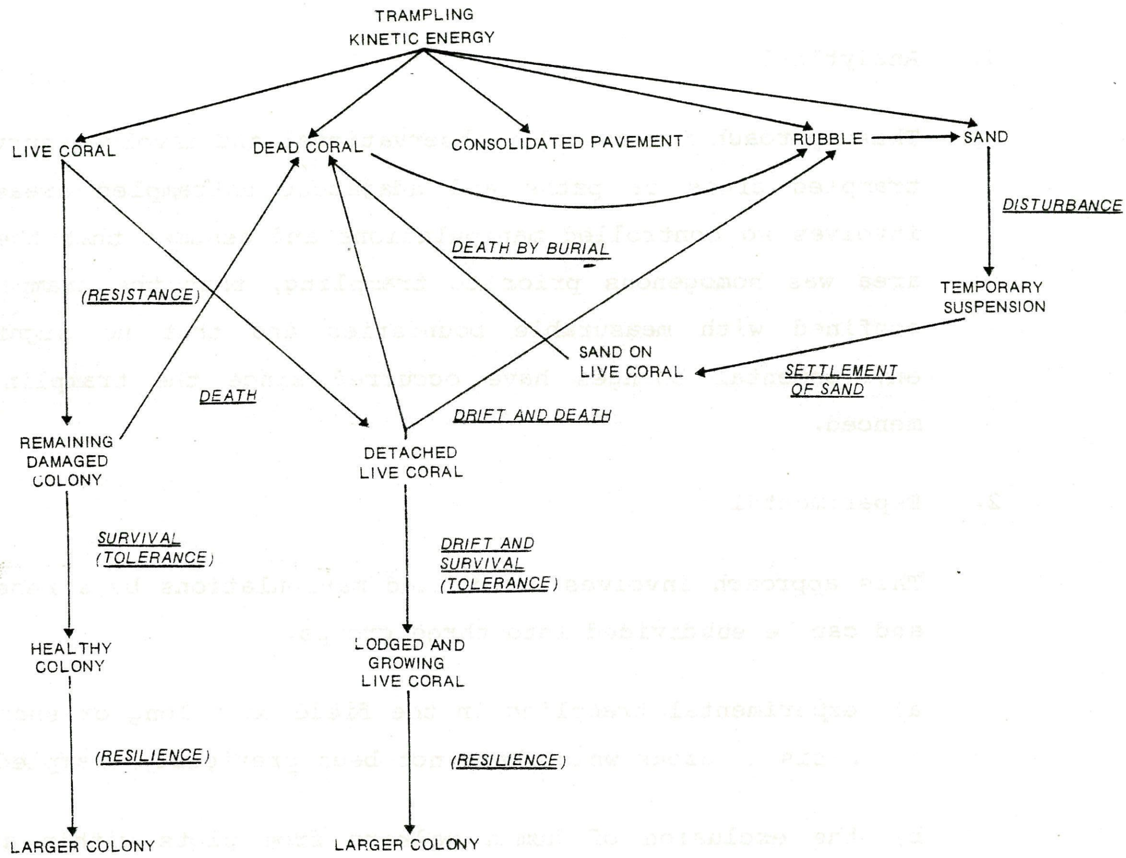


Figure 1.7 Logical model of some of the processes and consequences of human trampling on reef corals. Processes are indicated in italics.

As a general rule we have placed greatest emphasis on the ecological problems that can be solved by the management of people, as this is more easily done, often cheaper to carry out and presently the favoured way of managing the reef as a tourist resource.

All of the work was carried out on Heron Island (Fig. 1.8) or in the laboratory at Griffith University. The location of the experiments on Heron Island reef is shown in Fig. 1.9.

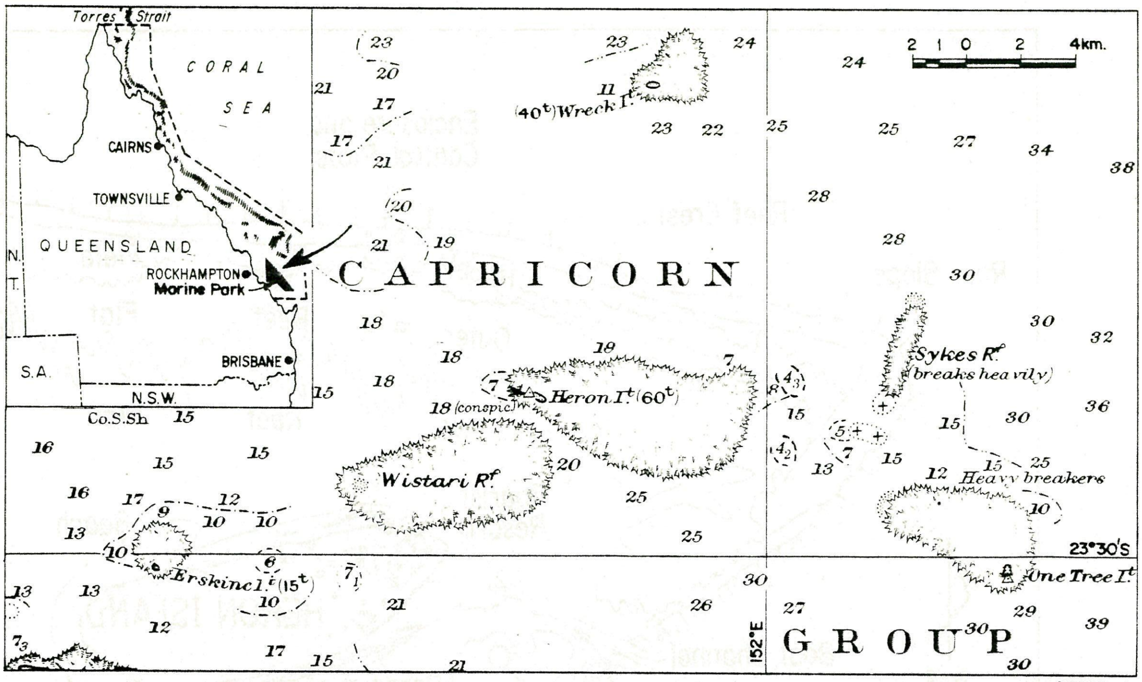


Figure 1.8 Geographical location of the Great Barrier Reef and of Heron Island in the Capricorn Bunker Group of reefs.

1.4.2 Chapter 2 - The long-term trampling experiment

This experiment is at the centre of our project and required the largest single investment of labour. Trampling at different intensities was carried out quarterly on the reef crest and reef flat. Records of the percentage cover of macroscopic algae, each coral species and substrate type, and the number of broken ends of coral were recorded at six-monthly intervals. The experiment was continued for 18 months.

This work was designed to give a direct answer to the central management question of what changes will take place on the reef crest and on the reef flat when they are subject to certain intensities of trampling? In addition the results were used to develop a classification scheme based on the morphologies of coral colonies and dif-

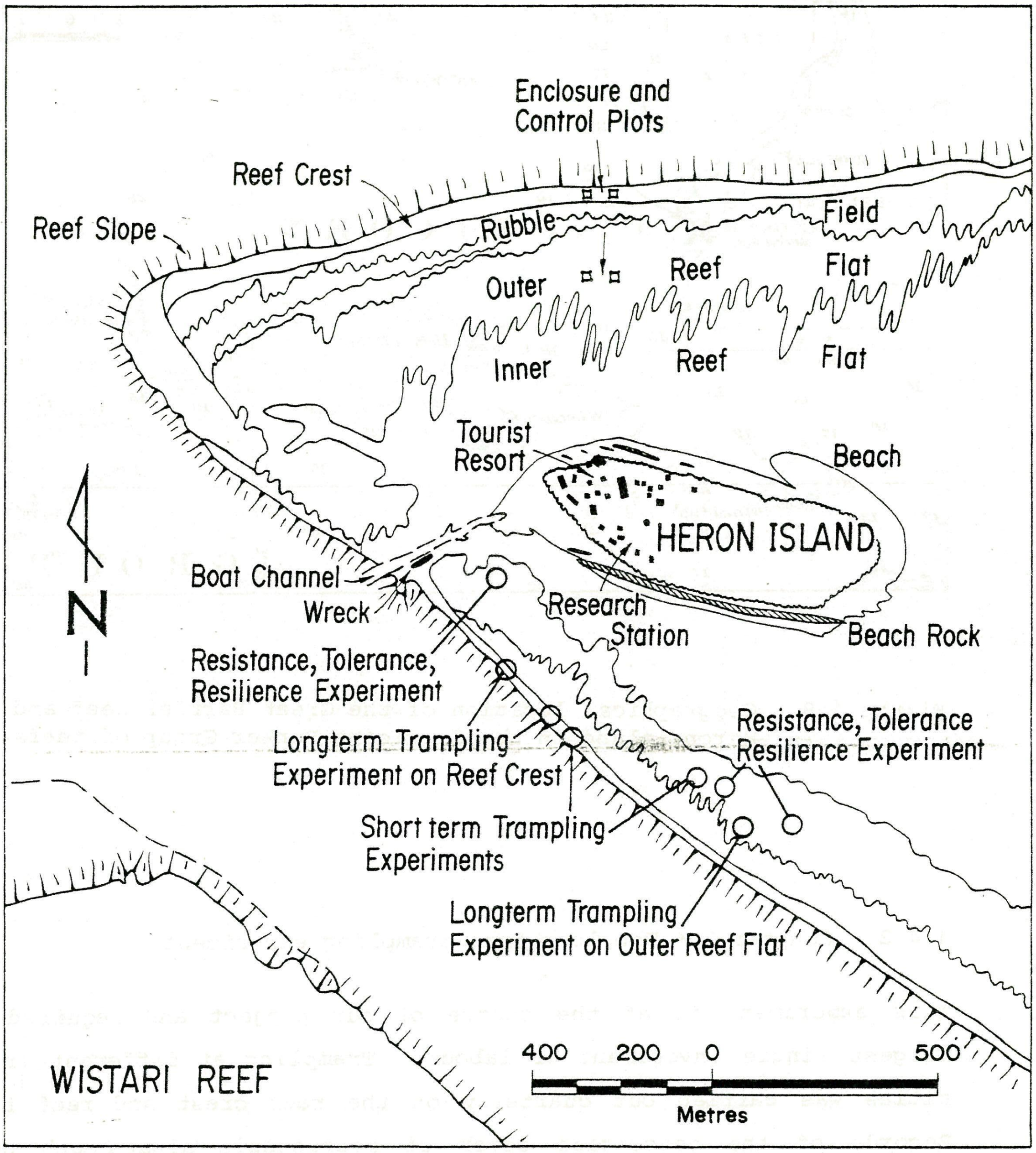


Figure 1.9 Location of various experimental sites at the west end of the Heron Island reef.

ferent substrate types which can be used to arrange sites on a scale of vulnerability to trampling.

1.4.3 Chapter 3 - Short-term trampling and drift experiments

There were two kinds of information sought in this set of experiments.

1) What is the size and weight range of broken portions of branching corals that are detached at different trampling intensities on the reef flat and reef crest?

2) Is there any difference between the drift distances of various sized portions of three branching corals both on the reef flat and on the reef crest?

These experiments were each carried out within one week, and involved selection of particular areas or species on which they were carried out. They also involved changing the environment in a way that would have invalidated the longer-term trampling experiment had they been incorporated therein.

The knowledge gained is pertinent to the production of detached portions of corals after certain levels of trampling and can be used as a management guide to one aspect of the likely recovery of trampled areas.

These experiments also provide a link between the longer term trampling experiments and the survival and recovery experiment with coral fragments and suggest a relationship between the long-term trampling and rubble production and movement (see Fig. 1.7).

1.4.4 Chapter 4 - The recovery experiment

This is a straight-forward exclosure experiment in which four areas of the reef used by tourists from the Heron Island resort were enclosed within a low wire fence. The cover of coral genera and forms have been recorded, together with the major types of non-living substrate. The data from within the plots is compared with data from adjacent trampled (unenclosed) plots.

The recordings have been made annually and it is anticipated that this should continue for at least four years.

This experiment was designed to determine whether the long continued use of the island and, more recently, the guided reef walks from the resort, had damaged the area of reef flat to the north of the cay which is used for the walks. If they have, our results will also give an indication of the time period required for the recovery of such an area and the feasibility of closed seasons and rotational resting. The growth rates of the different genera and morphologies may also be estimated from the longer-term results of this experiment.

The process of post-trampling recovery comes at the end of our proposed scheme of trampling processes. Fig. 1.7.

1.4.5 Chapter 5 - Damage and recovery at the species level

The experiments described in this chapter were all designed to clarify the concepts involved in the mathematical model described by Kay & Liddle (1983) and ultimately to given quantitative information that could be incorporated into it. Resistance was measured by determining the bending moment required to break branches of the three digitate species, tolerance by determining the numbers of colonies which survived various levels of damage, and resilience by recording the rate of growth after the colonies had been damaged. The definitions of these qualities are given in chapter 5. Tolerance and resilience were also determined for detached portions of the species chosen for our experiments.

The model is being developed as a predictive tool so that more precise quantitative estimates of likely changes due to trampling in the reef environment can be made. Eventually it should be applicable at all scales of management problem from whole reefs to the location of a particular pathway.

1.4.6 Chapter 6 - Summary of results

Our experimental findings are presented in summary form.

1.4.7 Chapter 7 - Management implications

This chapter summarises the implications of the various experiments and applies them to management problems. It is intended as a ready working reference to our work, although we do not recommend that the conclusions be used in isolation from the rest of this report.

1.4.8 Chapter 8 - The future

Here we discuss the experiments presently in progress that we feel should be continued and outline additional research work and surveys which need to be done for the management of reef walking.

CHAPTER 2 THE LONG-TERM TRAMPLING EXPERIMENT

CHAPTER 2 THE LONG-TERM TRAMPLING EXPERIMENT

2.1 INTRODUCTION

The last three decades have seen an increasing interest in the environment and in the ecological effect of man on natural habitats. One of the consequences has been many experimental studies of the impact of various vehicles and walkers on habitats used for recreation. In spite of the fact that nearly all the work has been published in the last decade, a concensus of approaches to experiments on the effects of human trampling is emerging. This is shown here by an analysis of the methodologies in 19 recent papers which describe experiments involving human trampling on natural ecosystems (Table 2.1).

In any consideration of a body of work on a particular topic, it is important to examine the purpose for which it was carried out as this will, consciously or otherwise, impose constraints and directions on the methodology and interpretations adopted by the authors. Of the 19 papers on experimental trampling reviewed here over half the authors imply or state overtly that their aim is to provide information that can be used by managers of the habitat or type of habitat in which they were working. There is a parallel view, expressed by nine of the authors, that the ecological processes of human trampling on natural environments need to be understood as a part of the natural system. However, only one refers directly to the visitors perception of the area and therefore considers the "consumer's" point of view (Falinski 1976). This is not to say that conventional scientific measures of vegetation such as cover, height, biomass and even species number do not reflect the visitors perception of the environment though I doubt if diversity statistics (eg. Liddle and Greig-Smith 1975b) are perceived visually even by most ecologists! So we have a body of work on the impact of outdoor recreation which is useful for managers, scientists and may incidently be relevant to visitors' experience in the countryside.

By definition, all the papers reviewed report on work in natural ecosystems and without exception visually homogeneous areas have been

Table 2.1 The Nature of Previous Trampling Experiments

1. Experimental treatment

Path	2,3b,7,8,9,10,11,13,14,15,16,17
General area of plot	1,3a,4,5,6,12,18

2. Path or plot length

1/3m	4,6
1m	3a,15
3m	10,14
4m	3b
4.6m	1
5m	8
6m	5,15
10m	12
12.5m	18
16m	4
20m	7,9,11,16
30m	17

3. Maximum number of passages

18	18
300	3a,3b
480	10
512	2,8
768	13
1000	17
1050	14
1200	2
1300	12
1400	6
2400	5
2560	7,11
3500	13
4200	15

4. Treatment time span

<1 week	1,3a,6,7,15,18
1 month	2,5,13,14,15
2 months	8,9,17
3 months	4,12,16
4 months	3a,4,7,9,10
6 months	9,11
12 months	3b,6

5. Nature of control

Measurement before wear	1,2,8,9,10,11,12,13,14,15,16,17,18
Untrampled path	1,3b,4,9,10,12,13,14,15,16
Adjacent to path (for relative measure)	3a,5,6,7,11

6. Replication

One path/plot	4,5,6,11,12,13,15,16,17,18
2 replicates	2,3b
3 replicates	1,2,9,10,14
4 replicates	3a,7
8 replicates	8

7. Minimum dimension of quadrat

10cm	2
25cm	3b,7,9,11,16
30cm	8
50cm	3a,5,6,10,15,17
100cm	4,12
120cm	1
200cm	13,14
400cm	18
Line transect	2,3b,11
Point quadrat	3b,5,7,10,11

8. Placing of quadrat/pins

Subjective	14,15,17
Regular	3b,4
Random	12,16
Whole path/plot	1,2,3a,5,6,7,8,9,10,11,18

9. Measurement

Cover (species)	1,2,3b,6,8,9,10,12,13,14,15,16,17,18
Frequency	7
Biomass	2,4,8,18
Sociology	4
Number of plants	3a,6,9,12,16
Height	3a,12,13,15
Morphology	6
Phenology	12
Microscopic	15

10. Length of time between treatment and recording

<1 week	1,2,4,7,8,9,11,14,15,16,17,18
2 months	5,13
3 months	3b
6 months	5,10,11,13
8 months	12
9 months	3b,13
12 months	1,2,3a,3b,4,5,6
24 months	1,4,6,10

11. Type of statistical analysis

Standard errors	1,3a,4,7,8,17
ANOVA	1,3a,10,11

Regression	7,8
T test	3a,14
Covariance	9
Duncan's multiple range test	10
Principal components	3a
Mean only	2,5,18
Complex polynomial	7
Unknown	12,13
Simple sign test	17

Code numbers for the various references: 1. Bayfield (1971); 2. Bell & Bliss (1973); 3a.Dune; 3b.heath grasland, Bowles & Raven (1982); 4. Falinski (1975); 5. Harrison (1980); 6. Holms & Dobson (1976); 7. Hylgaard and Liddle (1980); 8. Kellomaki (1973); 9. Kendall (1982); 10. Leney (1974); 11. Liddle (1973); 12. Little (1974); 13. Ploeg and Wingerden (1974); 14. Rogova (1976); 15. Studler (1980); 16. Thyer & Liddle (in press); 17. Weaver and Dale (1977); 18. Woodland & Hooper (1977)

selected for the experimental sites. The treatments have been applied either in the form of general trampling within the designated plots or more often in the form of a pathway up to 30m long (Table 2.1). They were subjected to a varying number of walkers (passages or traverses) up to 4200 (Studlar 1980) and frequently over 1000. (Table 2.1). These treatments were often applied on one day but over varying time spans up to one year, are not uncommon (Table 2.1). The paths were all placed in previously untrampled areas and in about half the experiments, measurements were made before treatment. Most of the experiments also incorporated an untrampled path or plot adjacent to the paths as a control against which the effects of trampling could be compared (Table 2.1). One feature of the design of many experiments is that because of the extremely labour intensive nature of the treatments, a particular treatment is only given to one path and the measurements are taken from within that path (Table 2.1). This approach requires an initial demonstration that all the paths used for the various treatments are from this same statistical population ie. the area is truly homogeneous. This can be tested if measurements are made from all the plots before work commences. It also assumes that the whole experimental area has a similar environment and is reacting to subsequent changes in a similar way. Given the initial confirmation of homogeneity, the assumptions appear to have held sufficiently well for reasonable conclusions to be drawn from most of these experiments. This design is considerably strengthened when the results are expressed in relation to closely adjacent controls to each path which remove the effect of local variation (Table 2.1). In other more traditional blocked experiments the general number of replicates is three or four. Measurements has usually been with rectangular quadrats with up to 50cm minimum width although most single file human paths are not much over 25cm wide. Line transects have been used in two cases (Table 2.1). The quadrats have generally measured the whole of the treated path (or plot) although various other subsampling systems have been used (Table 2.1).

The measurements have most commonly been of cover sometimes expressed as relative cover, but sociological (Raunkier net) records, of biomass, plant numbers, height, morphology, phenology and even microscopic examination of damaged to mosses have been used (Table 2.1). The measurements have often been made immediately after treatment but varying times up to two years have been used to record the capacity of the vegetation to recover (Table 2.1). Finally the type of statistical analysis used to evaluate the results has been very varied with standard errors on the figures and analysis of variance being the most common.

The study of the impact of human walkers on reef corals (Woodland & Hooper 1977) included in Table 2.1, involved one short term experiment at one locality on an outer reef flat zone at Wistari Reef adjacent to Heron Island (Figure 1.9). Their results summarized in section 1.2 clearly showed that intensive trampling can cause extensive breakage of living coral but they did not attempt to investigate the more complex and long term phenomena of human trampling on coral reefs.

The long term trampling experiment described in this chapter has been designed to provide answers for broader questions. These involve the relative vulnerability of different reef zones and the long term effects of trampling at various intensities. This type of information is of primary importance as a basis for the choice and formulation of management techniques described in section 1.3.2. Specifically, we investigated the changes that occur in coral communities which are trampled for a period of 18 months and how these changes are related to trampling intensity and the nature of the communities themselves. The results from the short term trampling experiments designed in conjunction with this longer term experiment which are reported in chapter 3 are also considered in the discussion at the end of this chapter as they enable a fuller interpretation of the results.

2.2 METHODS

2.2.1 Field Locations

The intertidal portion of the reef surrounding Heron Island can be divided into four general zones, namely the inner reef flat, outer reef flat, rubble field and reef crest (Figure 1.9). The general physical characteristics of each zone for this reef are listed in Table 2.2. However the inner and outer reef flats usually grade into each other and considerable variations in the composition of the biotic communities exist within zones.

Table 2.2 General physical characteristics of the intertidal zones of the reef surrounding Heron Island.

Zone	Physical Structure
Inner reef flat	Broad expanses of sand surrounding clumps of algae and dead or live coral
Outer reef flat	Sand patches in pools or channels surrounded by more or less continuous live and dead coral colonies
Rubble field	Boulders and heaps of coral rubble
Reef Crest	Dead coral skeletons cemented together by coralline red algae to form a solid pavement, live corals grow on this

Our observations indicated that reef walkers did not trample living organisms or significantly disturb the non-living substrate by walking in the inner reef flat or rubble field. They kept to the sand on the inner reef flat and walked around the coral and algae clumps. In the rubble field the sessile organisms are attached to the undersides of boulders and thus cannot be trodden on. Conversely, humans frequently trod on coral colonies on the outer reef flat and on the reef crest.

Visually the typical sessile community on the crest appeared nearly "two-dimensional" with low, compact and encrusting colonies common while that on the outer reef flat had a much greater vertical component as upright bushy, arborescent, platelike and moundlike colonies predominated (Plate 2.1, 2.2). Areas with communities displaying a visual intermediate aspect also occurred on the reef slope-reef crest interface and in the outer reef flat zone but these were less common.

Two sites each containing a sessile community which represented one of the two extremes in the above morphological spectrum were chosen for the experiment in areas usually visited by few reef walkers but within a reasonable distance of the research station (Figure 1.9). The outer reef flat site (Plate 2.1) contained large numbers of arborescent colonies while the reef crest site (Plate 2.2) contained large numbers of very low digitate and encrusting colonies.

2.2.2 Experimental Design

Sixteen 20 metre transects (paths) were located within each of the two study sites and marked at each end by a 40 cm long zinc galvanized tent peg which was hammered into the reef platform.

On the reef crest the transects were positioned parallel to the reef edge in four separate groups of four as shown in Figure 2.1. On the reef flat the transects were positioned so that the amount of bare sand they traversed was minimized resulting in the more haphazard arrangement shown in Figure 2.2.

Four trampling treatments with four replicates were used in the experiment. At both sites one treatment was a control where no

Plate 2.1 The outer reef flat

Key to tracing

solid : consolidated dead coral

diagonal lines : unconsolidated dead coral

dots : sand

Coral Morphologies

MA : massive

EN : encrusting

WE : wedge, blade line or thick knotty branches

DI : digitate to low corymbose or caespitose

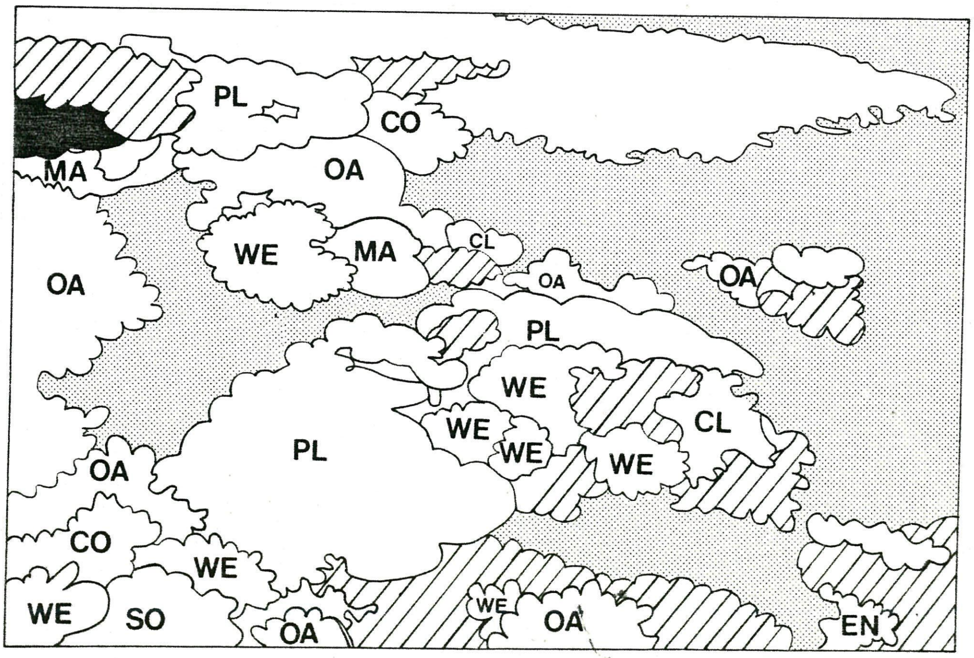
CL : clustered branchlets

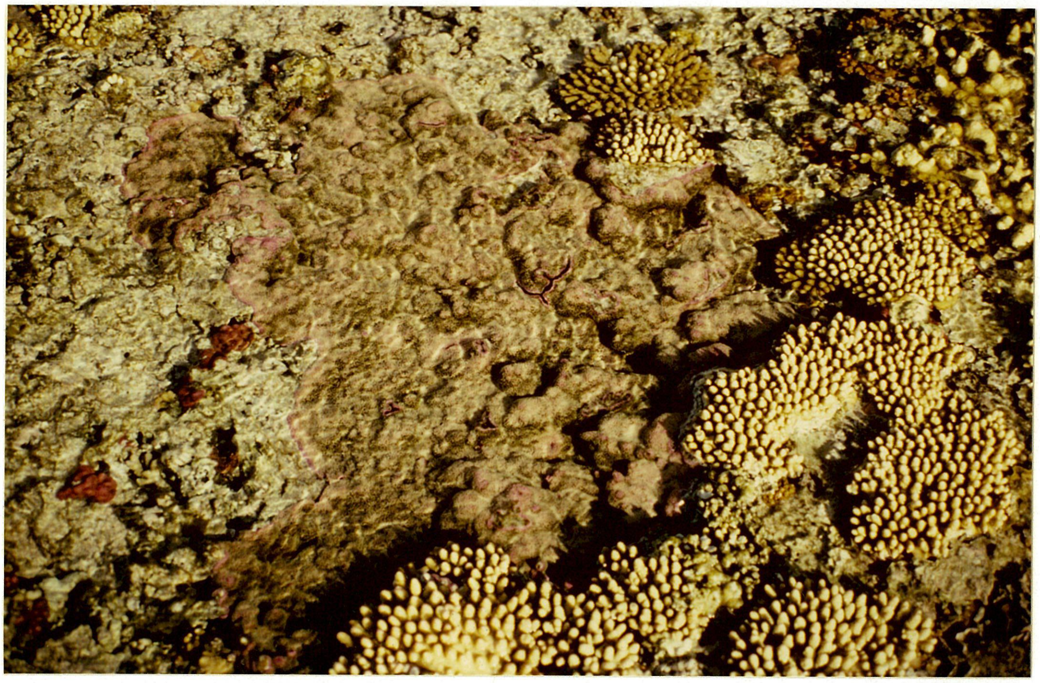
CO : high corymbose or caespitose

OA : open arborescent

PL : plate

SO : zoanthid


PL
CO
MA
OA
WE
MA
CL
OA
OA
OA
PL
WE
CL
WE
WE
PL
WE
OA
CO
WE
WE
SO
OA
WE
OA
EN



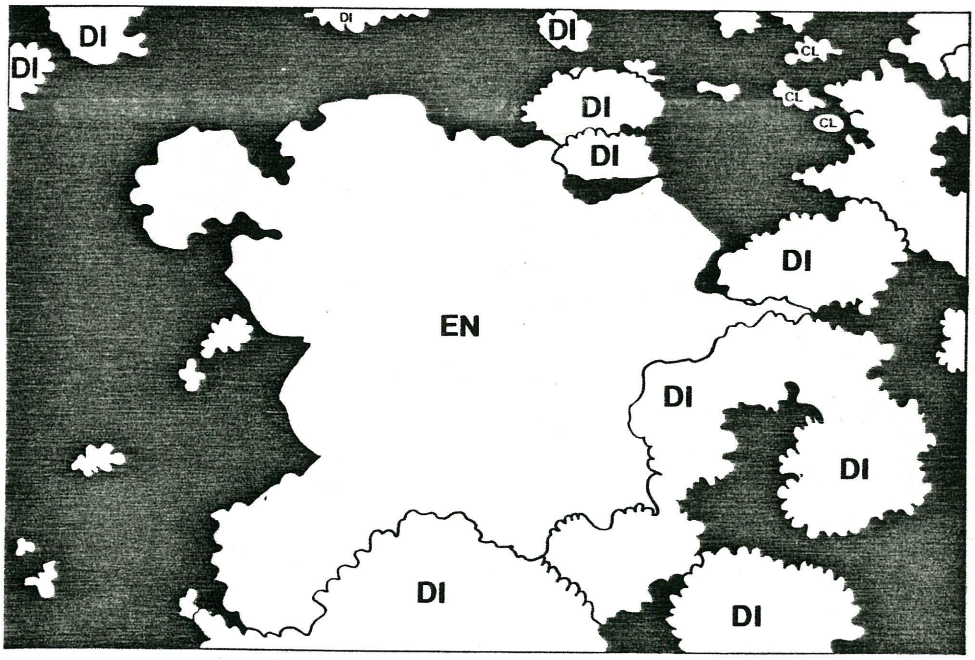


Plate 2.2 The reef crest

For key see caption to plate 2.1.

experimental trampling was done along the transect while the other three treatments represented different intensities of trampling as summarized in Table 2.2. They were chosen with the aim of recording the broadest range of damage, from slight to severe, caused by increasing numbers of walkers in both types of intertidal reef community. The choice was based on subjective assessment of the damage caused by preliminary trampling trials in the field and on the work of Woodland and Hooper (1977).

Table 2.2 Treatments for long term trampling experiment. One passage is equivalent to walking along a transect once. Treatments repeated at 12 weekly intervals.

Treatment	Code	Number of Passages	
		Reef Crest	Outer Reef Flat
Control	C	0	0
Level 1	L1	20	5
Level 2	L2	40	10
Level 3	L3	80	20

On the reef crest treatments were allocated to transects using a 4x4 latin square arrangement (Figure 2.1). On the outer reef flat the sixteen transects were divided into four blocks running along an axis parallel to the reef edge and treatments were allocated to transects using a randomized complete blocks design (Figure 2.2). The preceding field layouts were used so that treatments could be statistically handled in blocks (see Winer 1971 chapter 3) because of the heterogeneity of the reef habitat. Both sites exhibited changes in structure along an axis parallel to the reef edge and in the case of the reef crest there was also an obvious change perpendicular to the reef edge.

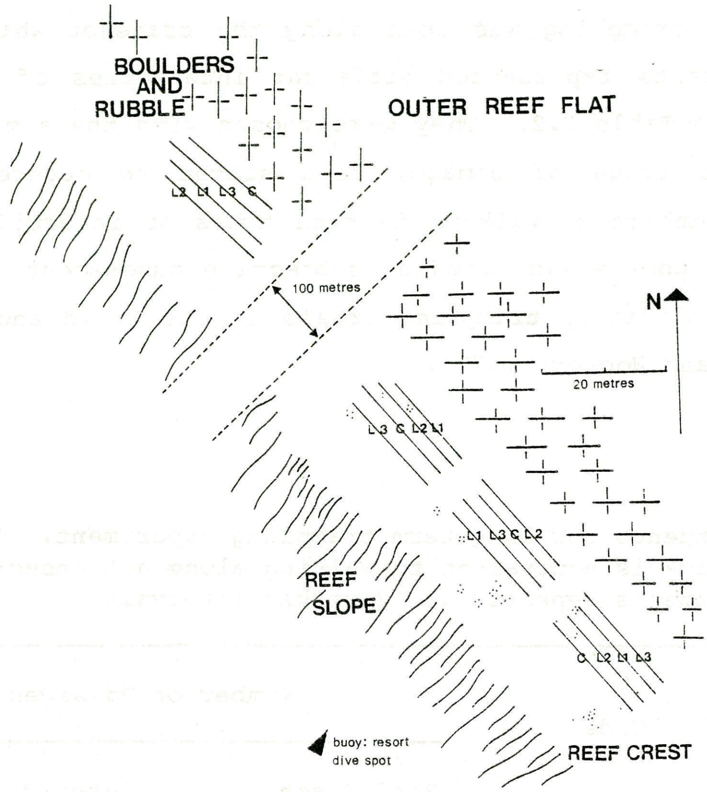


Figure 2.1 Location of transects on the reef crest for the long-term trampling experiment.

The data produced by this experiment was not, with the exception of that for species number, normally distributed and nonparametric tests have been used for analysis. Friedman's two way ANOVA (Siegel 1956) was used to analyze the reef crest data and transects at approximately the same distance from the reef edge were treated as a block as shown in Figure 2.1. Field observations indicated that the structures of the transects at a given distance from the reef edge were more similar than those at the same position with respect to the reef edge but at different distances from it.

The transects were set up during April 1982 and the first trampling treatments were performed during May 1982 and were repeated at intervals of 12 weeks for 18 months.

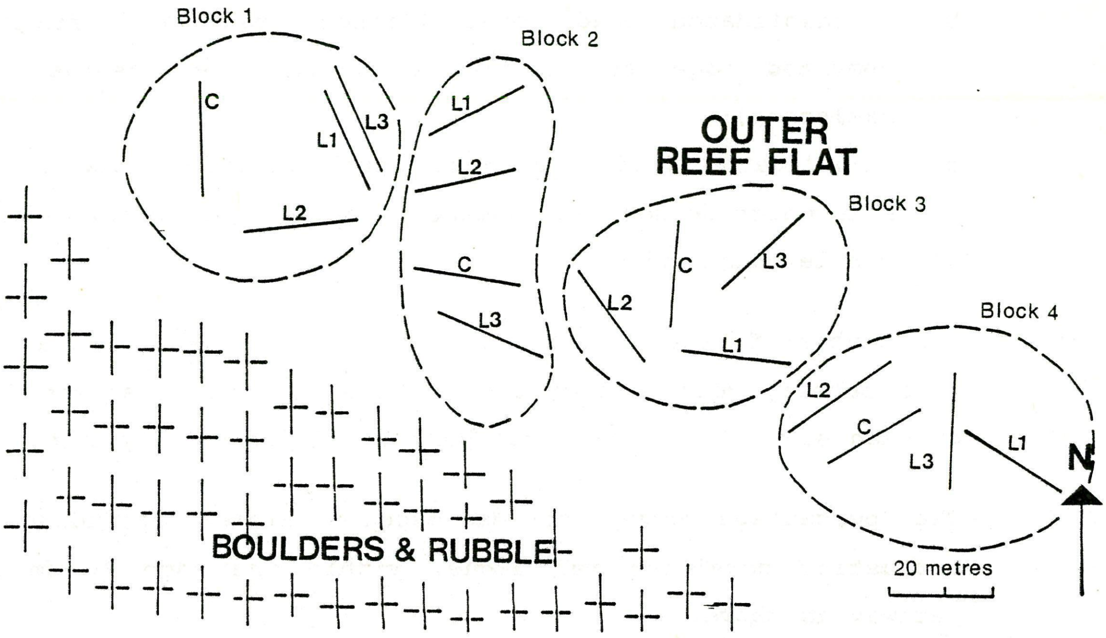


Figure 2.2 Location of transects on the outer reef flat for the long-term trampling experiment.

2.2.3 Sampling procedure

The following data were recorded in April 1982 when the experiment was begun and at six monthly intervals for 18 months after that. The measurements were made before the trampling treatments were carried out except for the number of breaks in live coral which were also counted after trampling. The data are:

1. The number of sessile animal species along each transect. As detailed in Section 2.3.1 some species could not always be reliably distinguished in the field and were grouped together. The word species underlined includes individual species and these species groups.

2. The percentage cover of sessile animal species and unoccupied substrata along each transect. The latter is divided into four categories.

   a) sand;

b) consolidated dead coral (either dead coral fragments cemented together to form a pavement or massive coral skeletons);

c) unsolidated dead coral (all coral skeletons remaining in situ which do not have a massive or encrusting morphology);

d) mobile coral rubble.

3. The number of breaks in the live coral colonies within a 25 cm wide pathway centred over each of the 20 metre transect (12.5 cm each side of the transect) before and after trampling.

4. The percentage cover of macroscopic algae, excluding the encrusting coralline red algae, within the same 25 cm wide pathway as above.

The percentage cover data was measured using the line intercept method (Stoddart 1969). The number of breaks and the percentage cover of algae are recorded in each of the eighty 25 cm x 25 cm squares making up the 25 cm pathway along the transect. A 25 cm x 25 cm bisected quadrat fitted into the bottom of a perspex viewing box with a grid, lines 5 cm apart, scratched on its base was used to delineate each 25 cm x 25 cm area.

Table 2.4 Code for recording algae along transects in the trampling experiment.

Data Code	Percentage cover of algae in 25 cm x 25 cm quadrat
0	0
1	0.1 - 10
2	10.1 - 20
3	20.1 - 30
4	30.1 - 40
5	40.1 - 50
6	50.1 - 60
7	60.1 - 70
8	70.1 - 80
9	80.1 - 90
10	90.1 - 100

The number of breaks per 25 cm pathway is the sum of these eighty counts. The percentage cover of algae in each square is estimated by eye and recorded using the code in Table 2.4. The total percentage cover for a transect is given by the formula -

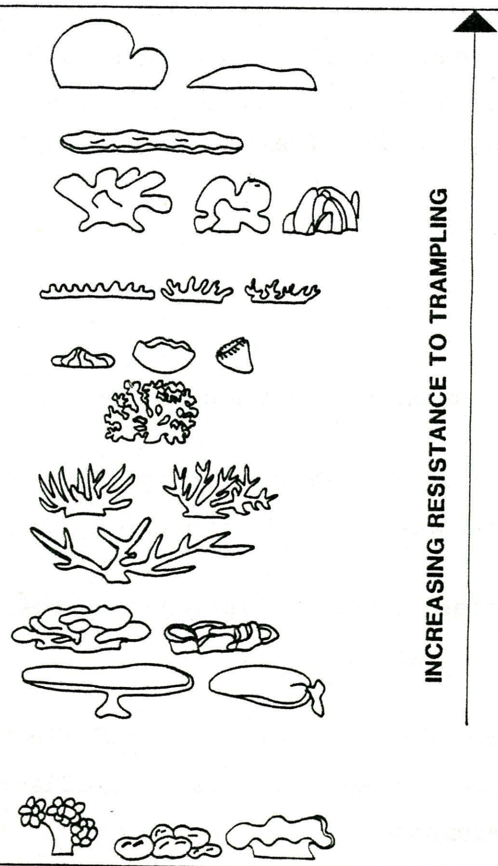
DATA/8

2.2.4 Data Processing: Coral Morphology

In addition to the preceding data the percentage cover of the various morphological categories displayed by the sessile animal species was calculated for each transect. These categories are listed and illustrated in Table 2.5. They are derived from the descriptive terminology used in coral taxonomy (Wallace 1978, Veron 1980) and the analysis of sessile animal form done by Jackson (1980).

Table 2.5 The different morphologies of the scleractinian corals and other sessile invertebrates on an intertidal reef flat.

Morphological Categories	Typical colonies	Taxa typically displaying morphology
massive		many Faviidae, some Porites spp.
encrusting		Montipora spp
wedge, blade like or thick knotty branches		Acropora spp. stout Pavona spp
digitate to low corymbose or caespitose		Acropora spp
solitary		many Fungiidae Tridacna spp *
clustered branchlets		Pocillopora spp
high corymbose or caespitose		Acropora spp
open arborescent		Acropora spp
foliaceous		Montipora spp Pachyseris spp
plate		Acropora spp Leptoseris spp
sessile animals without hard solid skeletons		Alcyonacea* Zoanthidea*



Each of these morphological types will be more or less resistant to physical damage depending on the mechanical properties of the skeleton material and the geometry of the colonies. The compressive strength of coral skeletons varies between species (Chamberlain 1978) however studies of the adaptations of corals to mechanical stresses (Chamberlain 1978, Vosburgh 1977, Botjer 1980) indicates that differences in geometry are responsible for most of the differences in overall colony strength. On the basis of the ideas expressed in these papers we have ordered the morphological categories, with the exception of the soft coral group, into a hierarchy (Table 2.5) which indicates the resistance a type may have, relative to the others, to mechanical damage produced by human trampling. Consideration of skeleton geometry indicates, for example, that massive forms will break less easily than branched forms, short thick branches less easily than long slender ones and dense clusters of branches less easily than isolated branches.

The aim of this classification, together with that used for the unoccupied substrata, is to permit interpretation of trampling effects in terms of the physical structure of the two study sites. The potential of both systems for the development of a predictive scheme whereby the live and dead sessile components of the intertidal communities on coral reef flats can be assessed on a scale of vulnerability to trampling damage is considered in section 2.4.2.

2.3 RESULTS

2.3.1 Species recorded on the transects

Not all species could be reliably distinguished from each other in the field and thus have been lumped into the species groups below.

1. *Acropora* species group a (spp.a) includes *Acropora nasuta*, *A. diversa* and *A. valida*.

2. *Acropora* species group b (spp.b) includes *Acropora formosa*, possibly a complex of species itself (Wallace 1978), *A. intermedia* and *A. robusta*.

3. *Acropora* species group c (spp.c) represents a small group of irregular bottlebrush to caespitose colonies which have no specific identification as yet.

4. *Acropora palifera* is mostly *Acropora palifera* with some *Acropora cuneata*. These species were occasionally confused in the field and have thus been recorded under the same heading.

5. *Montipora* spp.a is made up of exclusively encrusting colonies including *Montipora foveolata, M. solandri* and *M. erythracea* and other unidentified species.

Additionally *Acropora* sp.a is a densely branched arborescent to sturdy caespitose species which was consistently and easily distinguished from the more open arborescent colonies of *Acropora* spp.b.

A total of 56 <u>species</u> were recorded along the 32 transects with 49 recorded on the crest transects and 41 on the outer reef flat transects (Table 2.6). Over seventy-five per cent of these were scleractinian corals at both sites with zoanthids and alcyonaceans ("soft" corals) making up most of the remainder. Third-four <u>species</u> were common to both sites.

Table 2.6 Species or species groups recorded on the transects of the long term trampling experiment. "X" indicates a species was recorded at that site.

	Reef Crest	Outer Reef Flat
Cinidaria		
Anthozoa		
Hexacorallia		
Scleractinia		
Acroporidae		
Acropora aculeus	X	X
A. aspera	X	X
A. digitifera	X	X
A. humilis	X	X
A. hyacinthus	X	X
A. millepora	X	X
A. palifera	X	X
A. pulchra	X	
A. sarmentosa	X	X

Table 2.6 cont'd.

	Reef Crest	Outer Reef Flat
A. squarrosa		X
Acropora sp.a		X
Acropora spp.a	X	X
Acropora spp.b	X	X
Acropora spp.c	X	X
Montipora sp.a	X	X
Montipora spp.a	X	X
Agariciidae		
Pavona decussata	X	X
P. varians	X	X
Faviidae		
Faviid sp.a	X	
Cyphastrea chalcidicum	X	X
Favia pallida	X	X
Favites abdita	X	X
F. pentagona	X	
Favites sp.a	X	
Goniastrea cf. *favulus*	X	X
G. pectinata	X	X
G. retiformis	X	X
Hydnophora exesa	X	X
Leptoria phrygia	X	X
Platygyra daedalea	X	X
Platygyra sp.a	X	
Plesiastria versipora	X	
Fungiidae		
Fungia fungites		X
Mussidae		
Lobophyllia hemprichii	X	X
Oculinidae		
Archelia horrescens	X	
Galaxea fascicularis	X	
Pocilloporidae		
Pocillopora damicornis	X	X
Seriatopora hystrix		X
Stylophora pistillata		X
Poritidae		
Goniopora sp.a	X	X
Porites annae	X	X
Porites lutea	X	X
Zoanthidea		
Zoanthid sp.a	X	
Zoanthid sp.b	X	
Palythoa caesia	X	X
Palythoa sp.a	X	
Palythoa sp.b	X	
Octocorallia		
Stolonifera		
Tubiporidae		
Tubipora musica	X	X
Alcyonacea		
Alcyoniidae		
Lobophyton sp.a	X	X
Sarcophyton trocheliophorum		X
Sarcophyton sp.a	X	
Sinularia sp.a	X	X

Table 2.6 cont'd.	Reef Crest	Reef Flat
Nephtheidae		
Nephthya sp.a		X
Hydrozoa		
Milleporina		
Milleporidae		
Millepora cf. *platyphyllia*	X	
Mollusca		
Bivalvia		
Tridacnidae		
Tridacna maxima	X	X
Porifera		
Sponge sp.a	X	

2.3.2 Species number

Due to the difficulty of distinguishing some species in the field and the possibility that some other species may, in fact, represent several species, especially in the case of the genus *Acropora*, the number used in our calculations will be an underestimate of the real number of species found on the transect. Nevertheless we think it is a meaningful parameter which indicates the biological complexity of the sessile fauna occurring on the transects and we will retain it as such.

In all treatments on the outer reef flat and in the control treatment on the reef crest there were no marked changes in species number during the experiment. However, species number did appear to fall during the experiment along the trampled transects on the reef crest (Figure 2.3).

This trend is not greatly pronounced however, and at the beginning and end of the experiment there are no significant differences in species number between the four treatments (Friedman's 2-way ANOVA df=3, 0 months $\chi_r^2 = 1.4$ $.8>p>.754$, 18 months $\chi_r^2 = 1.9$ $.677>p>.649$). We have therefore concluded that trampling does not appear to have significantly altered the number of species at either site.

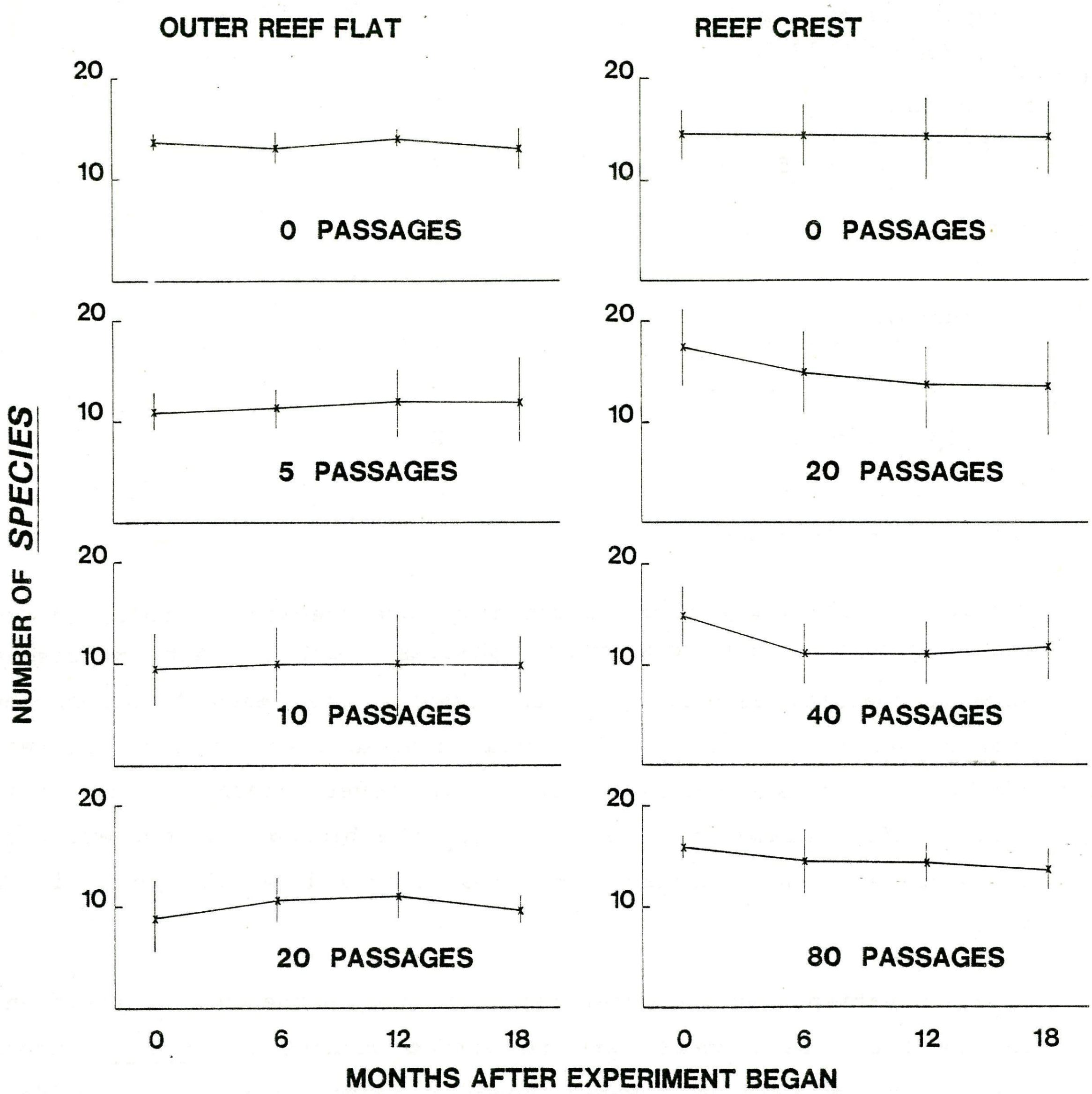


Figure 2.3 Mean and standard deviation of the number of species recorded along the transects at both sites in the long term trampling experiment in each treatment on all sample dates.

2.3.3 Structure and abundance of unoccupied substrata

At both sites the percentage cover of unoccupied substrata was over fifty per cent along the pathways in all treatments when the experiment began (Figure 2.4). It gradually increased to over seventy-five

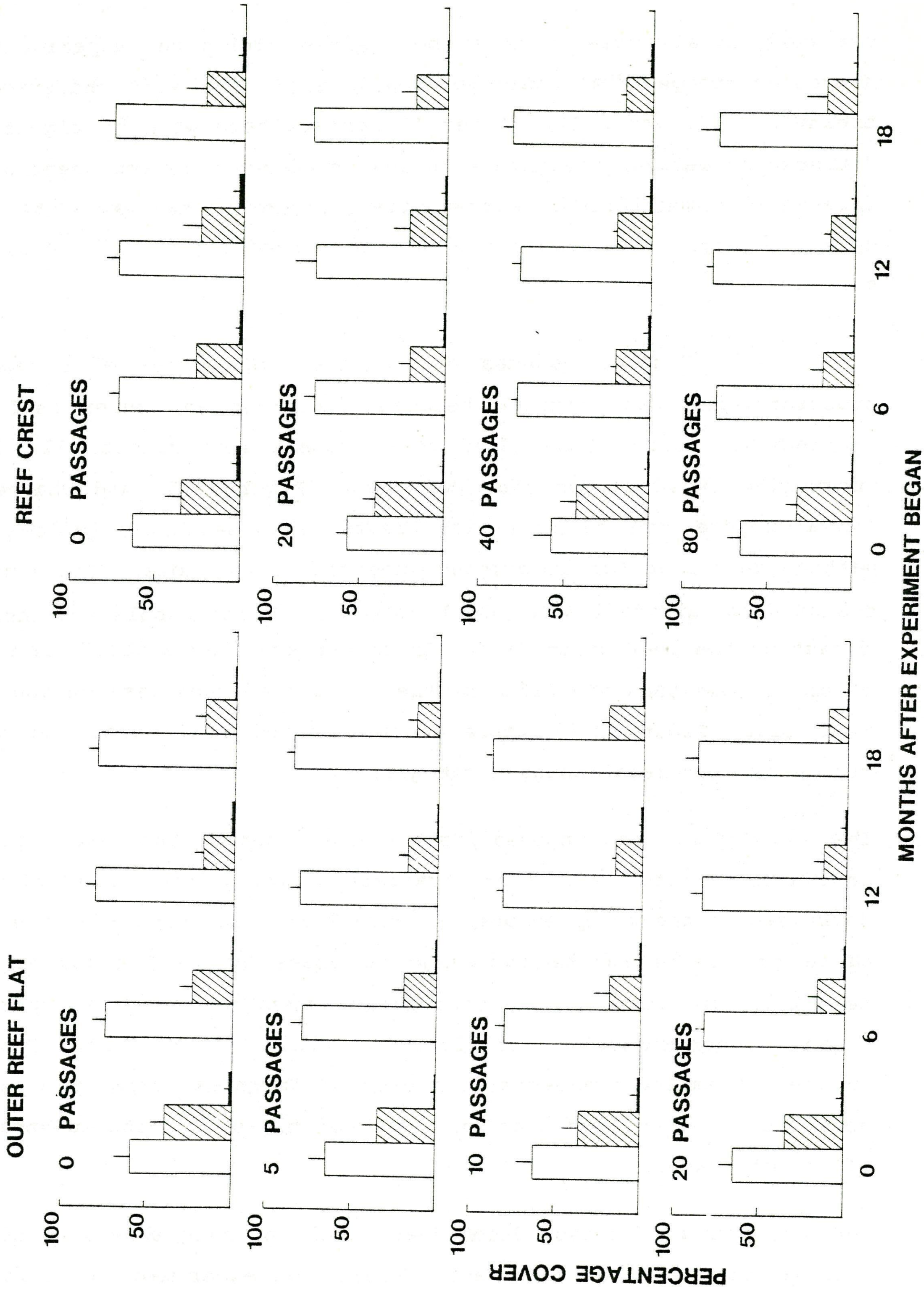


Figure 2.4 Mean (bar) and standard deviation (line) of the percentage cover of
(a) inert substrata (open bar)
(b) scleractinian corals (diagonally lined bar)
(c) other sessile invertebrates (solid bar)
along the transects at both sites of the long-term trampling experiment in each treatment on all sample dates.

per cent in all treatments at both sites during the experiment and showed no changes that could be clearly associated with the trampling treatments (Figure 2.4). After 18 months there were no significant differences between treatments in the abundance this component of the intertidal communities at either site (Friedman's two-way ANOVA df = 3, crest: ^{2}r = 1.5 p = .754, outer reef flat: r^{2} = 4.5, p = .242).

The abundances of the four categories of unoccupied substrata differed markedly between the crest and outer reef flat transects. Consolidated dead coral constituted almost all of the unoccupied substrata on the reef crest (Figure 2.5) and changes in its abundance over time in each treatment consequently followed the pattern described for unoccupied substrata as a whole. The abundances of sand, unconsolidated dead coral and mobile rubble are insignificant at the reef crest site. In comparison consolidated dead coral makes up less than one fifth of the unoccupied substrata on the outer reef flat (Figure 2.5) where unconsolidated dead coral and mobile rubble are the most abundant categories.

The abundance of unconsolidated dead coral increased on the untrampled outer reef flat transects during the experiment but decreased on the trampled ones (Figure 2.5). In comparison the abundance of mobile rubble increased on these trampled transects from less than one sixth of the unoccupied substrata when the experiment began to approximately half after 18 months (Figure 2.5). However, on the untrampled transects it showed no increase during the experiment and makes up less than one tenth of the unoccupied substrata at all sample dates.

The abundances of consolidated dead coral and sand showed no changes related to trampling treatments during the experiment at this site and each made up, respectively, less than one fifth and one tenth of the unoccupied substrata (Figure 2.5).

Table 2.7a shows that the abundances of the above substrata categories did not differ significantly between treatments on the first and last sample dates at each site. However, the probability of the

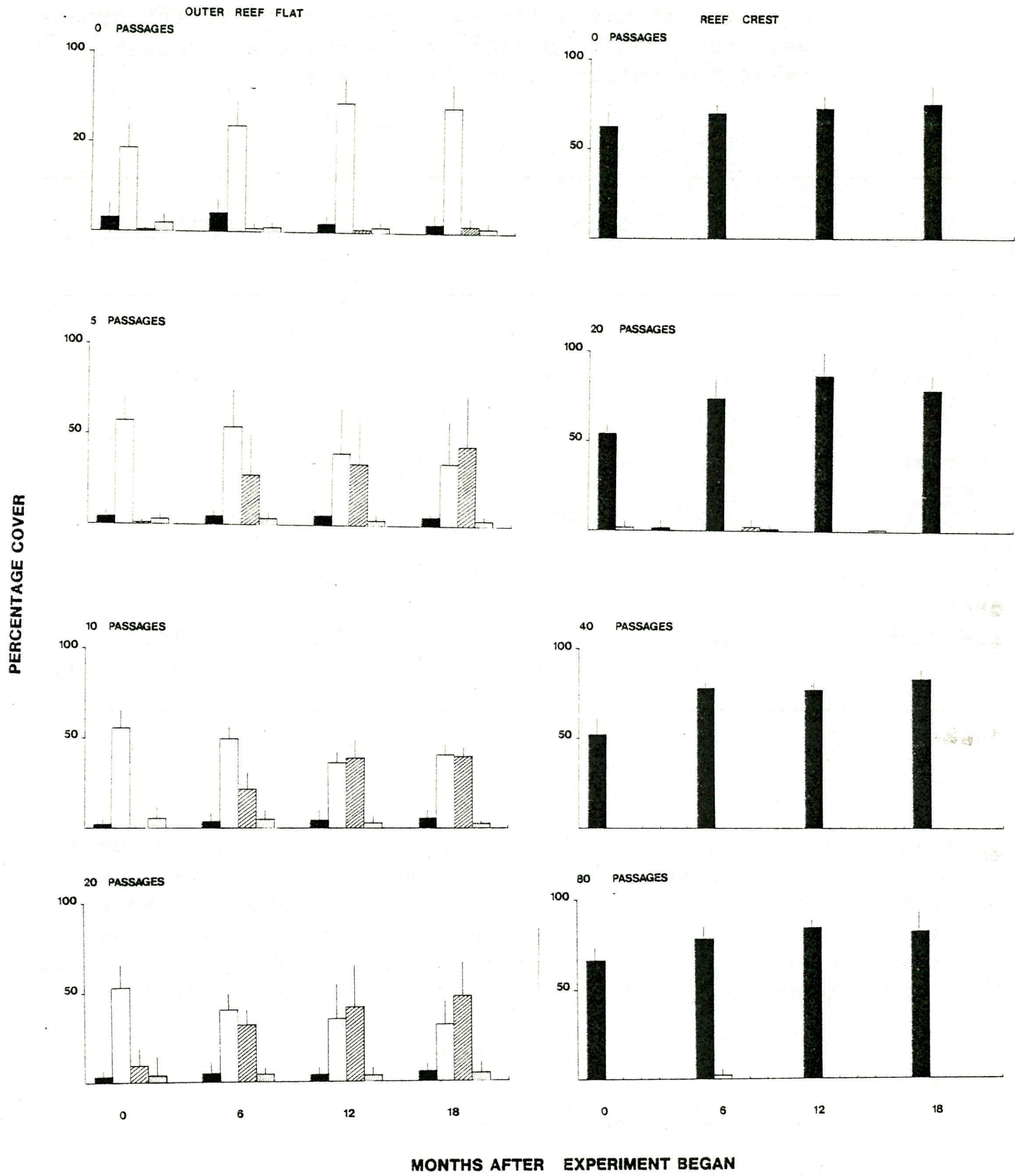


Figure 2.5 Mean (bar) and standard deviation (line) of the percentage cover of
(a) consolidated dead coral (solid bar)
(b) unconsolidated dead coral (open bar)
(c) rubble (diagonally lined bar)
(d) sand (dotted bar)
along the transects at both sites of the long term trampling experiment in each treatment on all sample dates.

Table 2.7 (a) Results of Friedman's 2-way ANOVA used to compare the percentage cover of substrates between treatments in the long term trampling experiment. p is the probability that the differences between treatment groups were observed by chance χ_r^2 is the test statistic k=N=4 * significant at the 5% level.

Site and data	0 months χ_r^2	0 months p	18 months χ_r^2	18 months p
Crest:				
consolidated coral	5.7	.141	1.5	.754
Outer reef flat:				
consolidated coral	1.3	.8>p>.754	1.5	.754
unconsolidated coral	1.5	.754	5.1	.19
mobile rubble	4.6	.242>p>.2	7.5	.052
sand	1.3	.8>p>.754	0.5	.992>p>.928

(b) Results of Mann-Whitney U-tests used to compare the percentage cover of mobile rubble between treatments on the outer reef flat transects at the end of the long term trampling experiment. n1=n2=4. The probabilities that differences between treatment groups were observed by chance are shown in the table * significant at the 5% level. The test is 2-tailed.

number of passages		number of passages 0	5	10
	20	.028*	1.0	.342
	10	.028*	1.0	
	5	.028*		

observed differences between treatments is very low, close to the 5% significance, level for mobile rubble on the outer reef flat transects on the last sample date (Table 2.7a). Further pairwise comparison between treatments (Table 2.7b) indicates that there is significantly more mobile rubble on the trampled pathways than the untrampled pathways at this site at the end of the experiment but the amount of rubble does not differ significantly between trampling treatments.

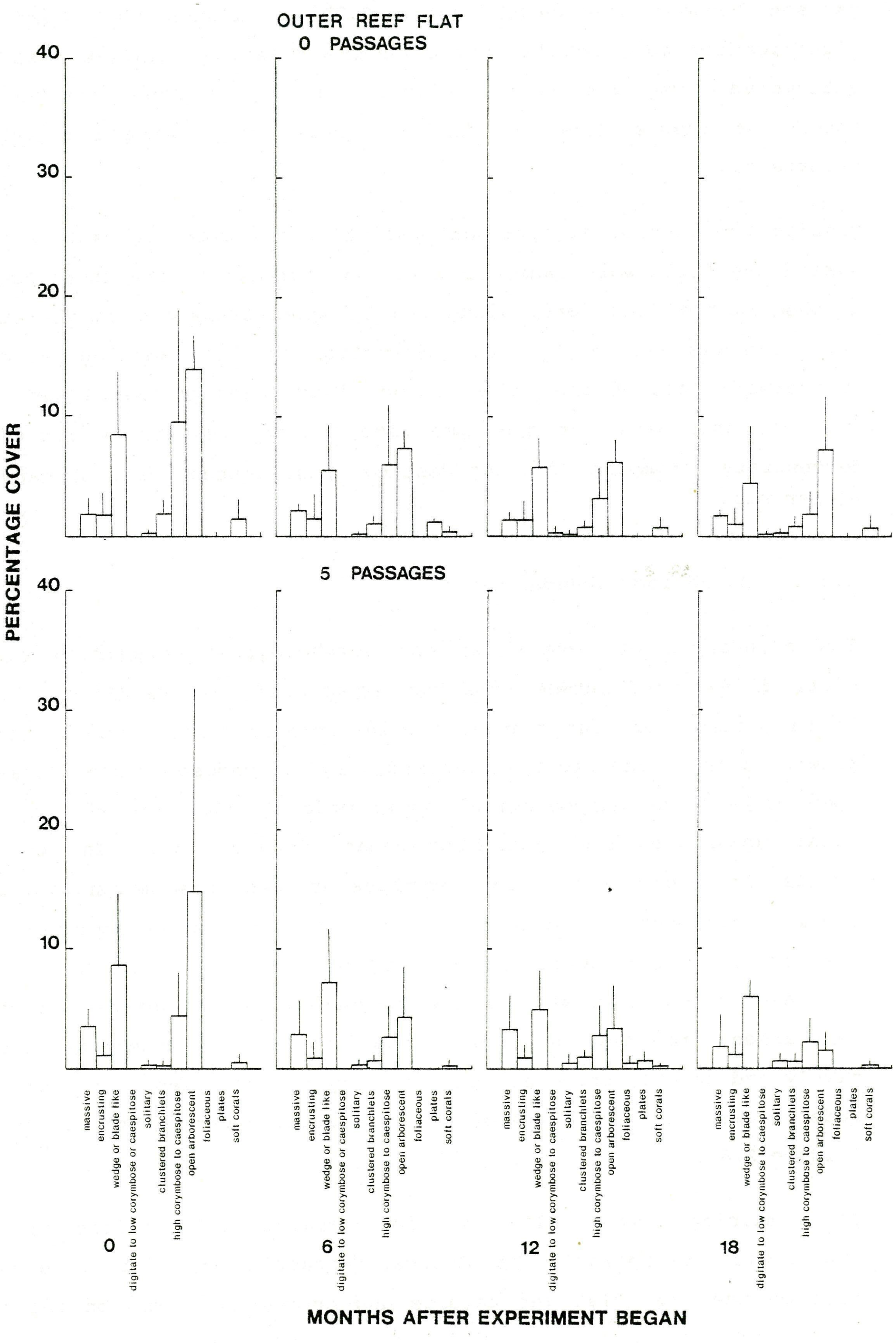
Despite the lack of significant statistics observations made on site during the field work indicate that the decrease in the abundance of unconsolidated dead coral along the trampled transects on the outer reef flat was due to physical destruction by the trampling process. Furthermore part of the rubble found along these transects was produced in this way. At the same time, as the results here clearly demonstrate, trampling did not destroy consolidated coral or sand at either site.

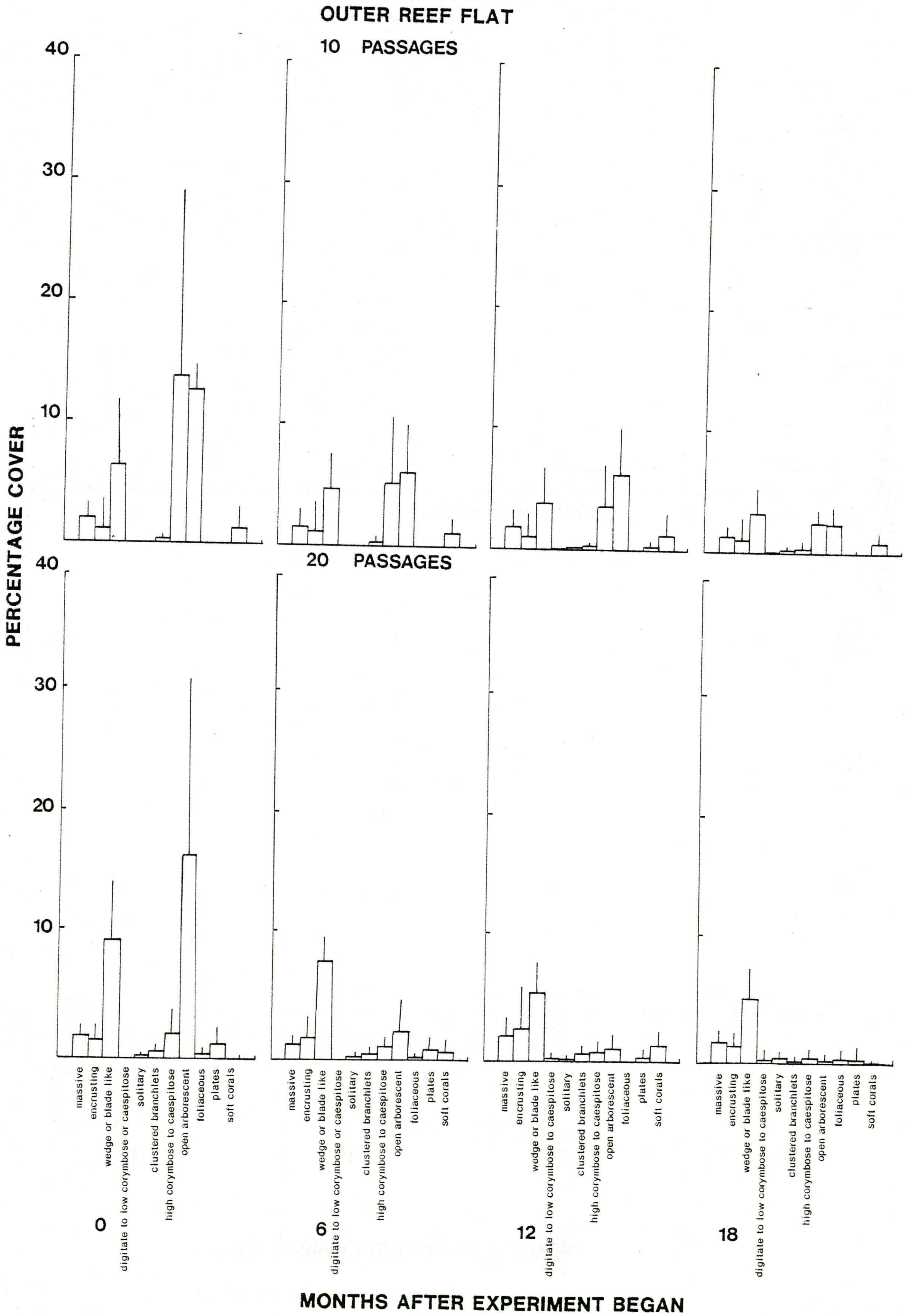
2.3.4 Morphology abundances

The abundances of several of the morphological categories showed clear differences between the two experimental sites (Figure 2.6). On the outer reef flat transects scleractinian corals with branching growth forms of the stoutly branched, high corymbose or caespitose or open arborescent morphological types made up over 80% of the live coral cover when the experiment began (Figure 2.6). In contrast corals with a digitate to low corymbose or caespitose morphology were the most abundant on the reef crest transects making up approximately 70% of the live coral cover (Figure 2.6). Corals with open arborescent and digitate to low corymbose and caespitose colonies were absent from the reef crest and outer reef flat transects respectively and stoutly branched and high corymbose or caespitose colonies made up less than one sixth of the live coral cover on the reef crest (Figure 2.6).

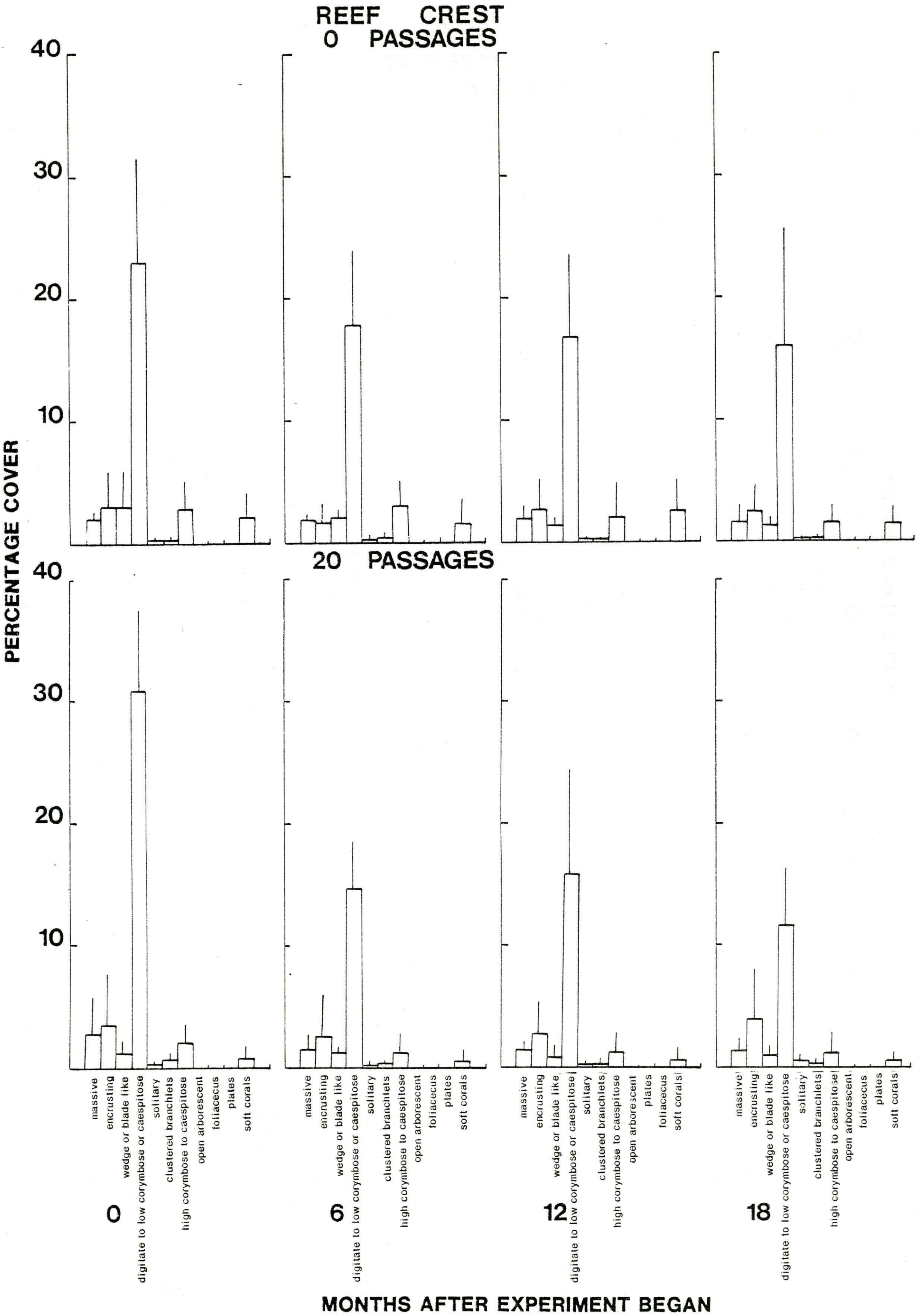
The remaining live coral cover, approximately 20% or less at both sites, was made up mainly by massive, encrusting and plate like colonies on the reef flat and massive and encrusting forms on the reef

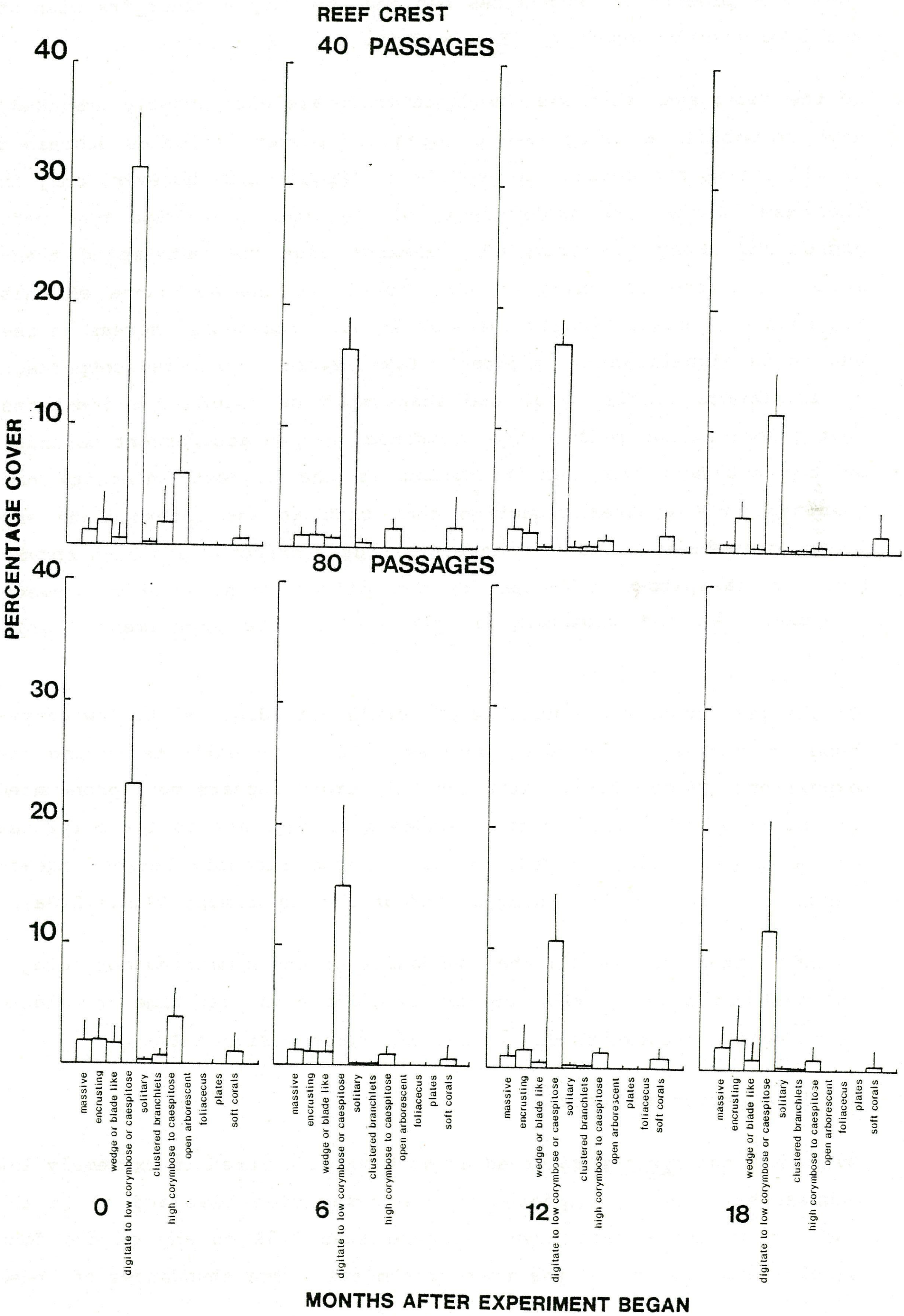
Figure 2.6 Mean (bar) and standard deviation (line) of the percentage cover of the different morphological types found along the transects at both sites of the long-term trampling experiment in each treatment on all sample dates.





OUTER REEF FLAT
10 PASSAGES
20 PASSAGES
PERCENTAGE COVER
40
30
20
10
massive
encrusting
wedge or blade like
digitate to low corymbose or caespitose
solitary
clustered branchlets
high corymbose to caespitose
open arborescent
foliaceous
plates
soft corals
0
6
12
18
MONTHS AFTER EXPERIMENT BEGAN


REEF CREST
0 PASSAGES
20 PASSAGES
PERCENTAGE COVER
40
30
20
10
massive
encrusting
wedge or blade like
digitate to low corymbose or caespitose
solitary
clustered branchlets
high corymbose to caespitose
open arborescent
foliacecus
plates
soft corals
0
6
12
18
MONTHS AFTER EXPERIMENT BEGAN


REEF CREST
40 PASSAGES
80 PASSAGES
PERCENTAGE COVER
40
30
20
10
massive
encrusting
wedge or blade like
digitate to low corymbose or caespitose
solitary
clustered branchlets
high corymbose to caespitose
open arborescent
foliaceous
plates
soft corals
0
6
12
18
MONTHS AFTER EXPERIMENT BEGAN

crest (Figure 2.6). Sessile invertebrates without solid hard skeletons were present at both sites but made up only a minor fraction of the live sessile community (Figure 2.6).

On the outer reef flat the abundance of corals with stoutly branched, high corymbose or caespitose or open arborescent colonies decreased in all treatments during the experiment (Figure 2.6) however, only in the case of the open arborescent colonies was this trend much more pronounced along the trampled transects than the untrampled transects. At the beginning of the experiment the abundance of this morphology is statistically the same in all treatments whereas at the end it is significantly different (Table 2.8a). Pairwise comparison of treatments (Table 2.8b) and inspection of Figure 2.6 indicates that trampling has reduced the abundance of open arborescent colonies on the pathways and that trampling at the highest intensity has resulted in a greater reduction than that at the intermediate and lower intensities. The abundance of stoutly branched and high corymbose or caespitose colonies do not differ significantly between treatments at the beginning or the end of the experiment (Table 2.8a).

On the reef crest the abundance of corals with digitate to low corymbose or caespitose colonies decreased in all treatments during the experiment (Figure 2.6). Although this trend appears more pronounced on the trampled transects the abundance of digitate to low corymbose or caespitose colonies did not differ significantly between treatments at either the beginning or end of the experiment (Table 2.8a).

At both sites, changes in the abundances of the remaining morphological categories do not show any consistent trends over time or related to trampling treatments during the experiment (Figure 2.6).

2.3.5 Species abundances

Over half the species recorded at each site occurred in extremely low abundances. Only 20 species on the outer reef flat and 19 on the reef crest had a mean cover of more than 0.5% on any of the four sample dates in any of the four treatments. The abundances of these

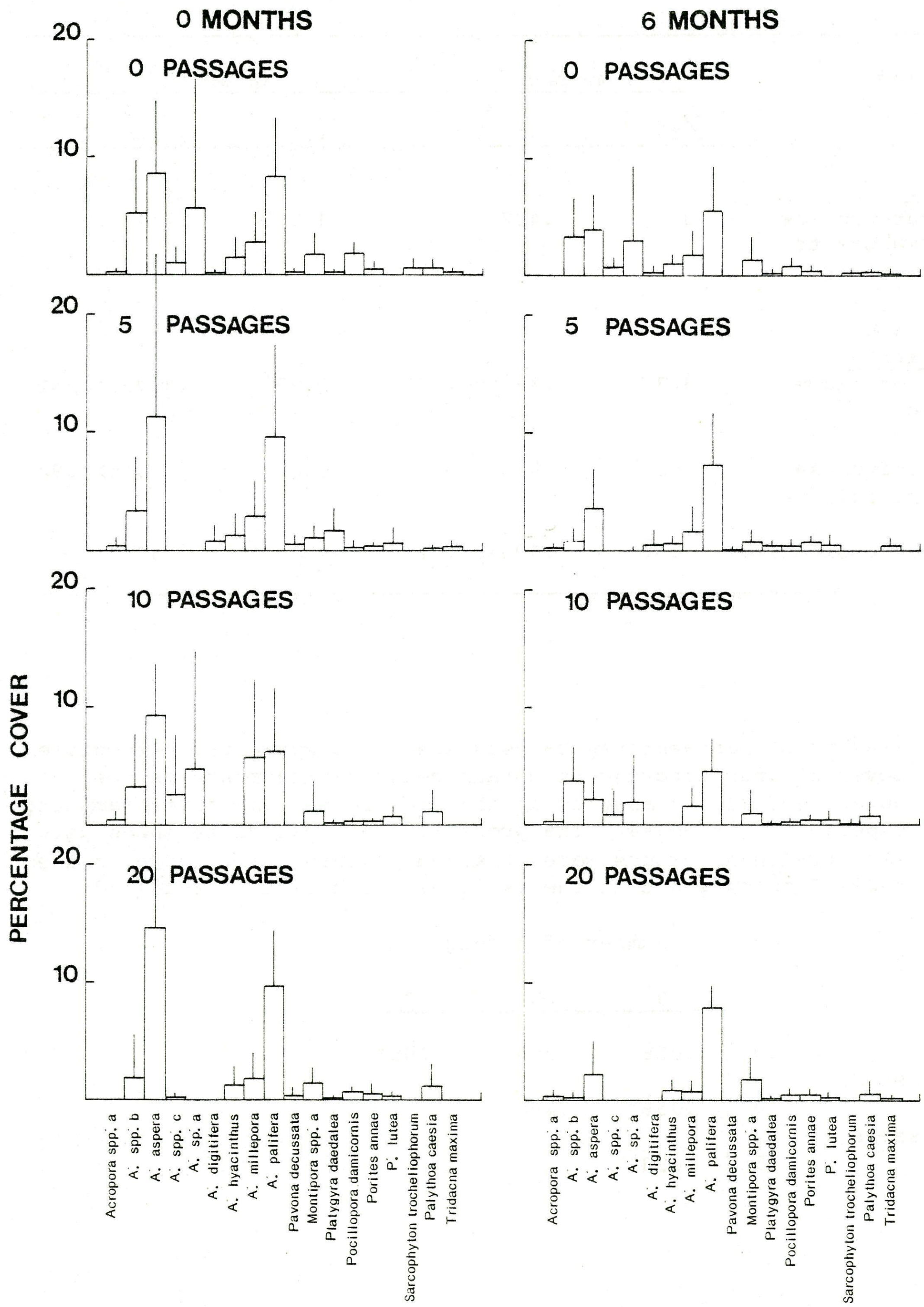
Table 2.8 (a) Results of Friedman's 2-way ANOVAs used to compare the percentage cover of morphological categories between treatments in the long term trampling experiment. p is the probability that the differences between treatment groups were observed by chance χ_r^2 is the test statistic R=N=4 * significant at the 5% level.

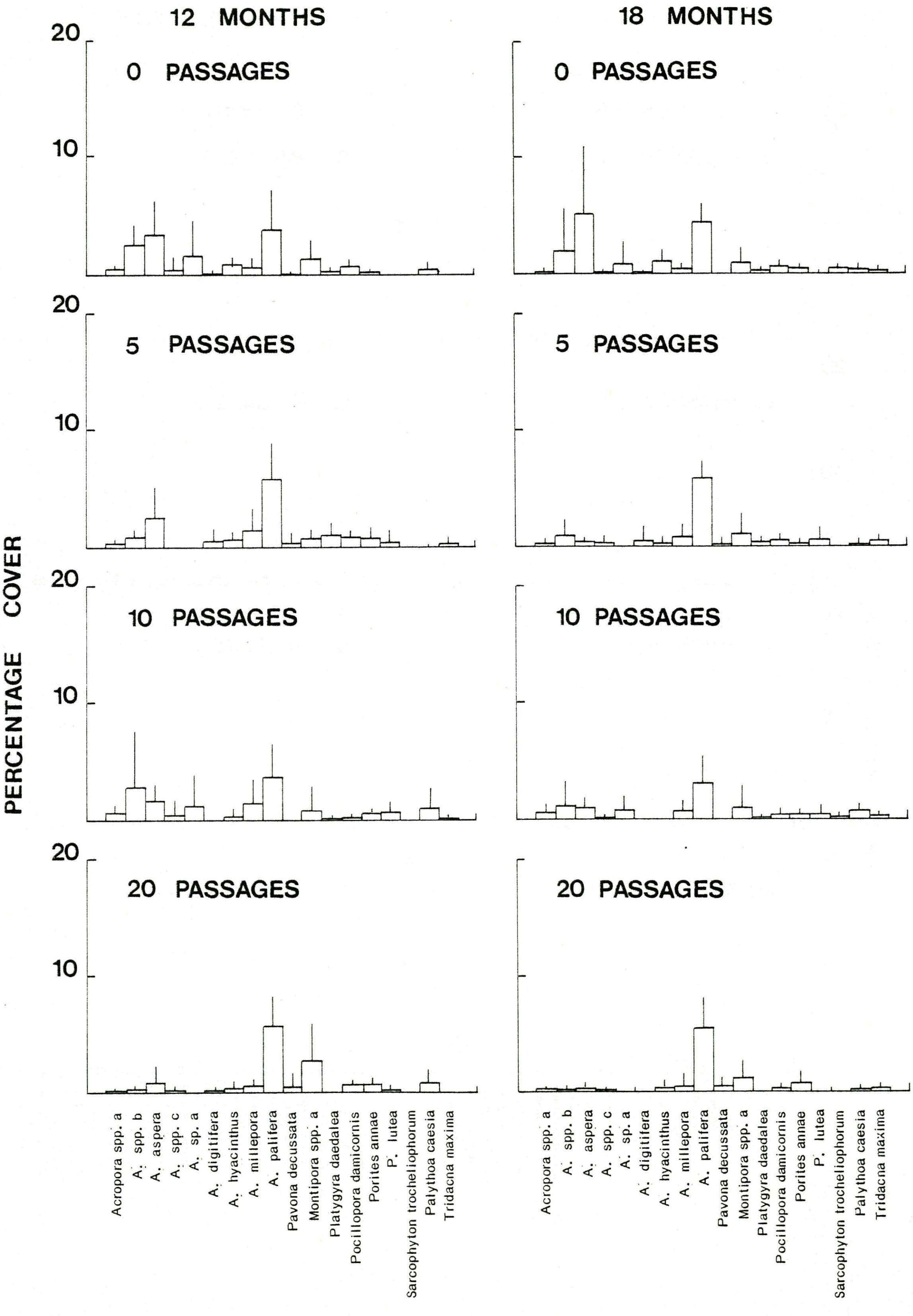
Site and data	0 months		18 months	
	χ_r^2	p	χ_r^2	p
Crest:				
digitate to low corymbose to caespitose	3	.432	1.5	.754
Outer reef flat:				
wedge or blade like	3.37	.389>p>.355	3.97	.324>p>.242
high corymbose to caespitose	1.2	.8	6.07	.105>p>.094
open arborescent	.525	.992>p>.928	10.8	.0016*

(b) Results of Mann-Whitney U-tests used to compare the percentage cover of open arborescent corals between treatments on the outer reef flat transects at the end of the long term trampling experiment. n1=n2=4. The probabilities that differences between treatment groups were observed by chance are shown in the table * significant at the 5% level. The test is 2-tailed.

number of passages		number of passages: 0	5	10
	20	.028*	.058	.208*
	10	.058*	.486	
	5	.058*		

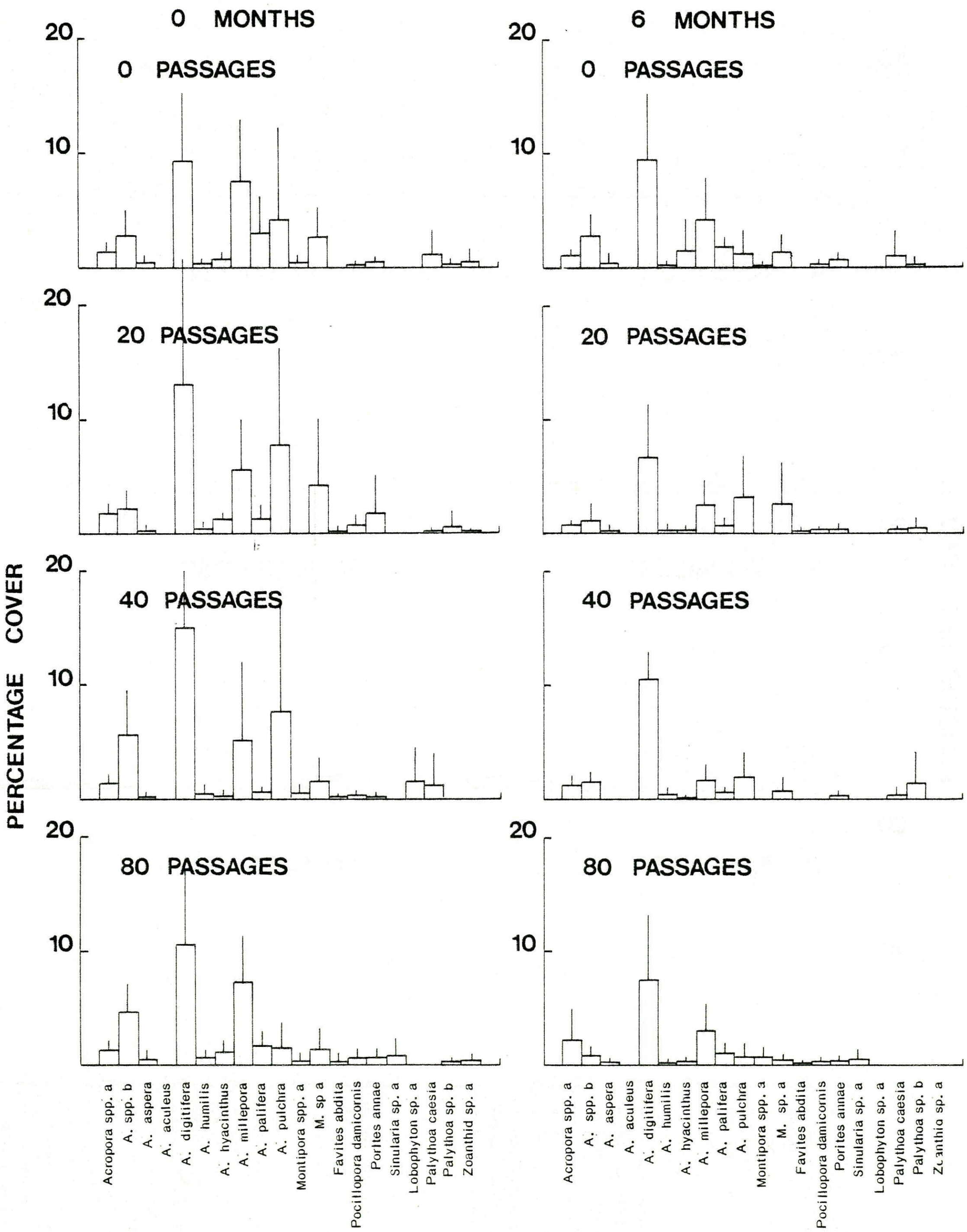
Figure 2.7 Mean (bar) and standard deviation (line) of the percentage cover of all but the extremely rare species (see section 3.3.5) found along the transects of the long-term trampling experiment in each treatment on all sample dates at the outer reef flat site.

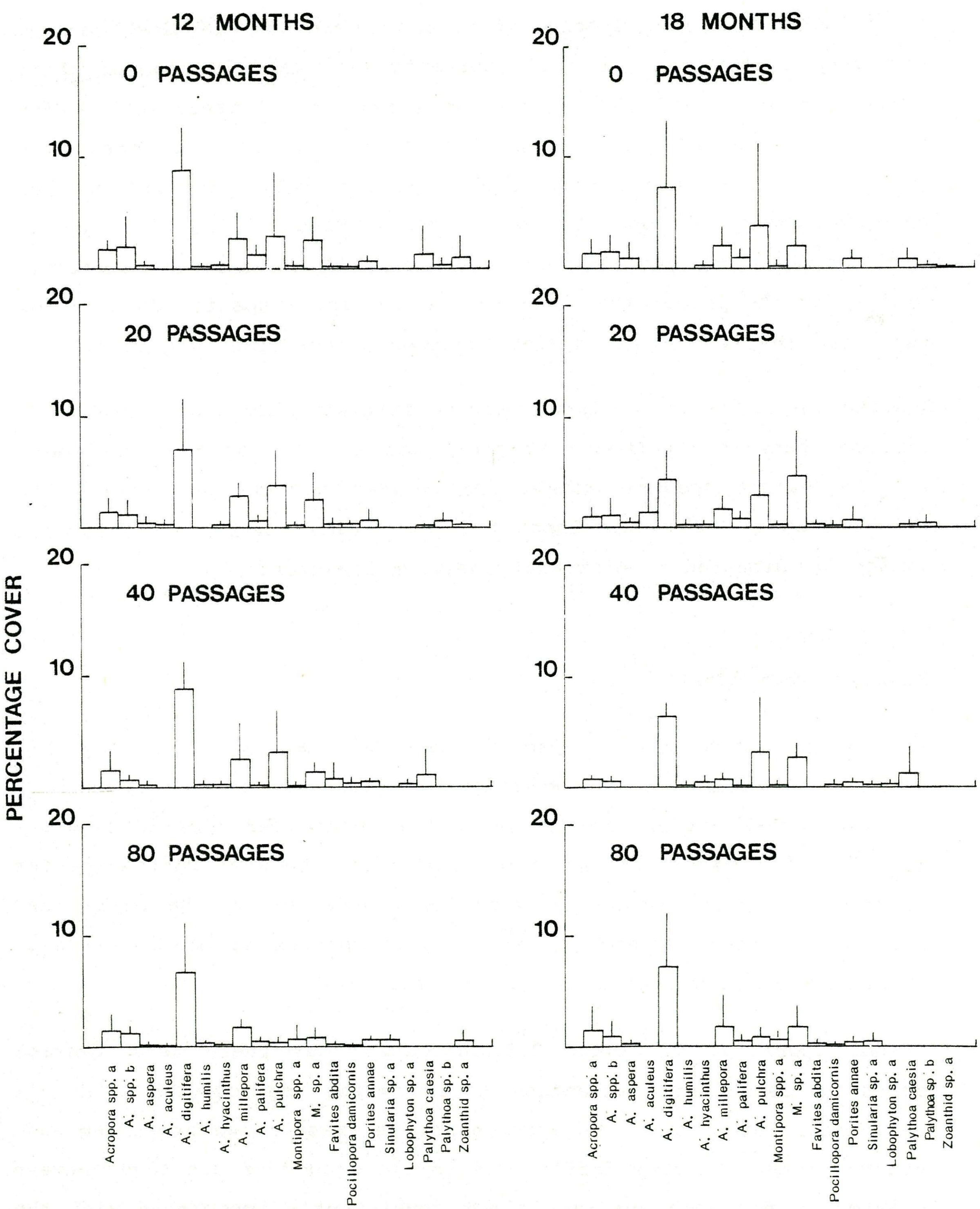




12 MONTHS
18 MONTHS
PERCENTAGE COVER
20
10
0 PASSAGES
5 PASSAGES
10 PASSAGES
20 PASSAGES
Acropora spp. a
A. spp. b
A. aspera
A. spp. c
A. sp. a
A. digitifera
A. hyacinthus
A. millepora
A. palifera
Pavona decussata
Montipora spp. a
Platygyra daedalea
Pocillopora damicornis
Porites annae
P. lutea
Sarcophyton trocheliophorum
Palythoa caesia
Tridacna maxima

Figure 2.8 Mean (bar) and standard deviation (line) of the percentage cover of all but the extremely rare species (see section 3.3.5) found along the transects of the long-term trampling experiment in each treatment on all sample dates at the reef crest site.





12 MONTHS
18 MONTHS
0 PASSAGES
20 PASSAGES
40 PASSAGES
80 PASSAGES
PERCENTAGE COVER
20
10
Acropora spp. a
A. spp. b
A. aspera
A. aculeus
A. digitifera
A. humilis
A. hyacinthus
A. millepora
A. palifera
A. pulchra
Montipora spp. a
M. sp. a
Favites abdita
Pocillopora damicornis
Porites annae
Sinularia sp. a
Lobophyton sp. a
Palythoa caesia
Palythoa sp. b
Zoanthid sp. a

species during the experiment have been graphically presented in Figure 2.7 and 2.8. The remainder will not be considered further as they each occur so rarely that their individual effect on the overall picture was not significant.

2.4.5a Outer reef flat

On the outer reef flat species of *Acropora* were individually the most abundant at the start of the experiment (Figure 2.7) however their percentage cover falls during the experiment in all treatments. With the clear exception of *Acropora palifera* this trend is most pronounced on the trampled transects particularly in the case of *Acropora aspera*, the most abundant species (Figure 2.7), which has an open arborescent growth form and generally grows in thickets. Changes in the percentage cover of the remaining species do not show any clear trends associated with treatments over time (Figure 2.7).

Despite the above trends there were no statistically significant differences between treatments at the start and end of the experiment for any single species except *Pocillopora damicornis* (Table 2.9). At the start of the experiment the percentage cover of *Pocillopora damicornis* differed significantly between treatments.

2.3.5b Reef crest

Species of *Acropora* were also the most abundant coral on the reef crest at the start of the experiment (Figure 2.8) however their percentage covers differ from those on the outer reef flat (Figure 2.7 and 2.8). In particular *Acropora digitifera* the most common species on the reef crest occurs in very low abundances on the outer reef flat and *Acropora aspera* the most common species at the latter site occurs in very low abundances on the reef crest.

Visual appraisal of Figure 2.8 indicates that there is a general trend of decreasing percentage cover during the experiment in all treatments for most of the species on the crest which are being considered here. However differences in the amount of decrease between treatments for each species is not consistently associated with the

Table 2.9 Results of Friedman's 2-way ANOVAs used to compare the percentage cover of species between treatments on the outer reef flat transects at the beginning and end of the long term trampling experiment. p is the probability that the differences between treatment groups were observed by chance χr^2 is the test statistic R=N=4 * significant at the 5% level.

Species	0 months		18 months	
	χ_r^2	p	χ_r^2	p
Acropora spp.a	0.8	>.9	2.0	>.6
A. spp.b	1.9	>.6	1.3	>.7
A. spp.c	1.5	.75	0.3	.9
A. sp.a	.7	>.9	3.1	>.39
A. aspera	0.1	>.9	4.9	>.19
A. digitifera	1.6	>.6	1.4	>.75
A. hyacinthus	3.8	>.32	2.5	>.5
A. millepora	1.9	>.6	.5	>.9
A. palifera	4.1	>.2	4.0	>.24
Pavona decussata	0.6	.93	2.4	.52
Montipora spp.a	0.7	>.9	2.2	>.52
Platygyra daedalea	3.6	>.3	4.0	>.24
Pocillopora damicornis	9.2	<.014*	3.1	>.4
Porites annae	1.0	>.8	1.1	>.8
P. lutea	1.1	>.8	1.5	.75
Sarcophyton trocheliophorum	1.8	.68	1.7	>.6
Palythoa caesia	1.8	.68	2.8	>.4

occurrence of trampling and its intensity. This fall in percentage cover is most pronounced for the commoner *Acropora* species such as *Acropora* spp.b, *A. digitifera, A. pulchra* and *A. millepora.*

Statistical analysis (Table 2.10) shows that the percentage cover of all the species being considered on the crest, with the exception of *Acropora palifera,* did not differ significantly between treatments at the beginning or end of the experiment. The percentage cover of *A. palifera* did differ significantly between treatments at the end of the experiment however pairwise comparisons show that the percentage cover of this species on the untrampled transects was only significantly greater than that on the transects trampled at medium inten-

Table 2.10 Results of Friedman's 2-way ANOVAs used to compare the percentage cover of species between treatments on the reef crest transects at the beginning and end of the long term trampling experiment. p is the probability that the differences between treatment groups were observed by chance. χr^2 is the test statistic R=N=4 * significant at the 5% level.

Species	0 months		18 months	
	χ_r^2	p	χ_r^2	p
Acropora spp.a	2.1	.65	0.6	.93
A. spp.b	2.7	.51	3.2	>.39
A. aculeus	0.0	1.0	0.7	.9
A. aspera	4.1	>.24	6.9	.07
A. digitifera	3.6	.36	1.0	>.8
A. humilis	0.4	>.93	0.5	>.93
A. hyacinthus	2.7	.51	3.4	>.36
A. millepora	0.3	.99	2.1	.65
A. palifera	3.9	.32	8.1	.03*
A. pulchra	0.6	>.93	0.2	>.99
Montipora sp.a	0.5	>.93	0.2	>.99
Montipora spp.a	0.3	>.99	0.9	.9
Favites abdita	0.5	>.93	1.7	>.68
Pocillopora damicornis	5.0	<.19	0.4	>.93
Porites annae	3.4	>.36	5.7	.14
Sinularia sp.a	0.5	>.93	0.6	.93
Lobophyton sp.a	0.4	>.93	0.5	>.93
Palythoa caesia	1.0	>.8	1.0	>.8
Palythoa sp.b	0.5	>.93	0.6	.93
Zoanthid sp.a	0.4	>.93	0.5	>.93

sity (Table 2.11). Given the large number of individual statistical comparisons and an absence of marked trends related to trampling in the percentage cover data for this species this result is likely to be due to chance rather than trampling effects.

2.3.6 Abundance of algae

On the outer reef flat the percentage cover of algae increased during the experiment in all treatments but at different rates (Figure 2.9). This increase was the largest on the untrampled transects and became increasingly smaller as the intensity of trampling increased to the highest treatment level. These trends suggest that trampling was

Table 2.11 Results of Mann-Whitney U-tests used to compare the percentage cover of *Acropora palifera* between treatments on the reef crest at the end of the long term trampling experiment. $n1=n2=4$. The probabilities that differences between treatment groups were observed by chance are shown in the table * significant at the 5% level. The test is 2-tailed.

number of passages		number of passages: 0	20	40
	80	.342	.342	.2>p>.104
	40	<.05*	.114	
	20	1.0		

Table 2.12 Results of Friedman's 2-way ANOVAs used to compare the percentage cover of algae between treatments at both sites of the beginning and end of the long term trampling experiment. p is the probability that the differences between treatment groups were observed by chance χ_r^2 is the test statistic R=N=4 * significant at the 5% level.

Species	0 months		18 months	
	χ_r^2	p	χ_r^2	p
Reef Flat	6.9	.068	5.7	.141
Reef Crest	0.9	.928	0.6	.928

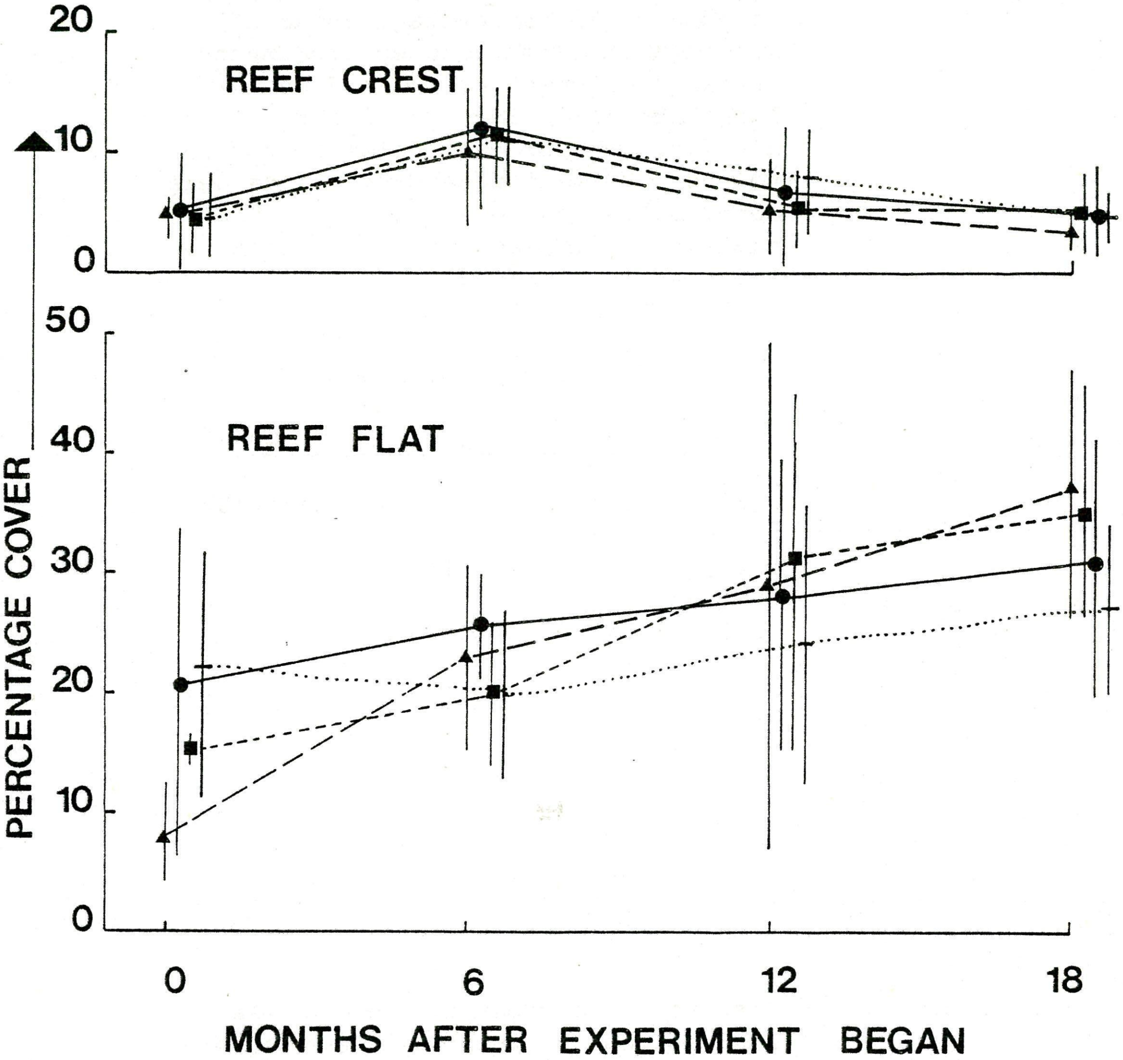


Figure 2.9 Mean and standard deviation of the percentage cover of algae found along the transects at both sites of the long-term trampling experiment in each treatment on all sample dates.

control (▲)

trampling treatments

intensity: level 1 (■)

level 2 (●)

level 3 (–)

inhibiting a natural rise in the abundance of algae at the site despite the fact that there were no significant differences between treatments in the abundance of algae at the end of the experiment (Table 2.12). In this respect it is noteworthy that the order of the mean percentage covers for the four treatments reverses during the experiment and the probability of the observed differences at the start of the experiment was low (Table 2.12). Both observations support the proposition that initial differences between treatment groups would have masked the statistical significance of trampling effects.

On the reef crest the abundance of algae is much lower than on the outer reef flat and it shows similar changes in all treatments during the period of the experiment (Figure 2.9). Additionally, the percentage cover of algae did not differ significantly between treatments at the beginning or end of the experiment at this site (Table 2.10).

2.3.7 Breaks in live coral

On the outer reef flat trampling at all intensities caused a significant increase in the breaks in live coral on all sample dates. The only exception was trampling at the lowest intensity which did not result in a significant increase in breaks on the second sample date (Figure 2.10, Tables 2.13, 2.14). However, there were no significant differences between the number of breaks caused by different trampling treatments during the experiment at this site (Table 2.14).

On the reef crest trampling only caused a significant increase in the breaks in live coral on the first and third sample dates (Figure 2.10, Tables 2.13, 2.14). On the second and last sample dates trampling did not produce significantly different numbers of breaks between treatments (Table 2.13). Additionally, on the first and third sample dates different levels of trampling did not cause significantly different numbers of breaks (Table 2.14).

At both the reef flat and reef crest sites the following trends occurred in the data.

1. The trampling performed at the beginning of the experiment resulted in higher numbers of breaks than trampling later in

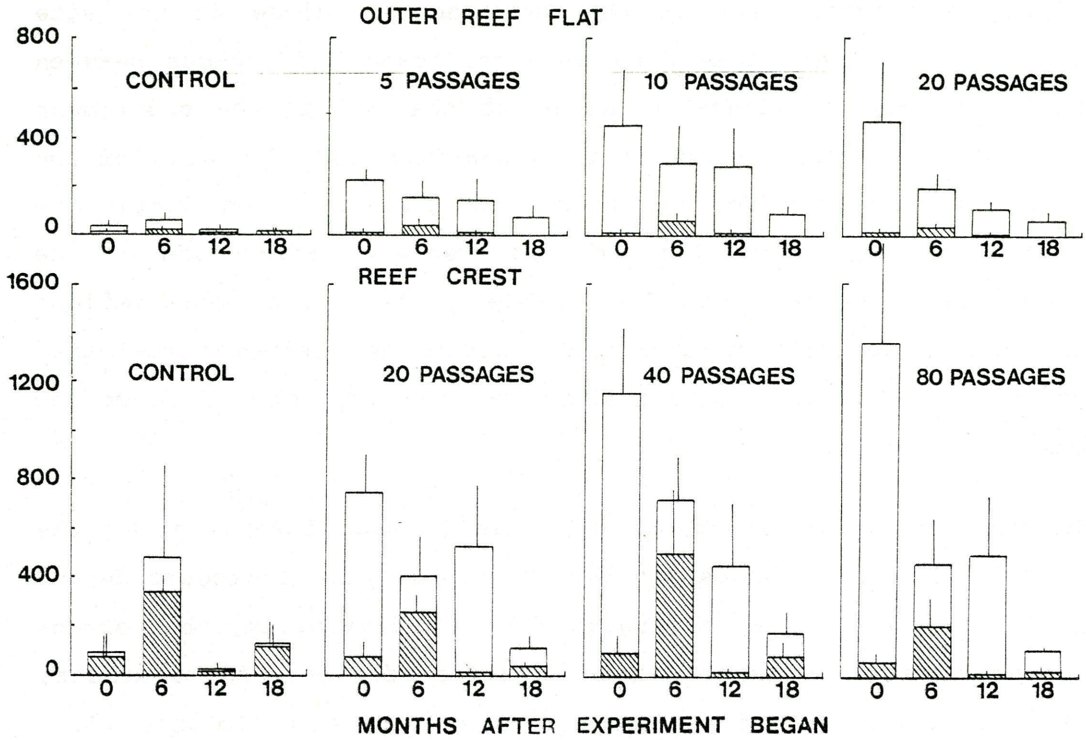


Figure 2.10 Mean (bar) and standard deviation (line) of the number of breaks in live coral along the pathways of the long-term trampling experiment in each treatment on all sample dates. Breaks before trampling are represented by the diagonally lined portion of the bar, breaks after trampling are represented by both the open and diagonally lined portions of the bar.

the experiment in all trampling treatments (Figure 2.10). This indicates that the immediate damage caused by trampling was greatest when the experiment began.

2. The numbers of breaks appear to be levelling off at the two higher treatment levels on the first sampling date (Figure 2.10, Table 2.14) which suggests that more damage occurs during the first half of the total passages constituting the highest trampling intensity than the second half. This is consistent with the results of the short term experiment in Chapter 3 which show that trampling at the lowest intensity is sufficient to detached most of the living coral which is not resistent to

trampling and that further trampling serves mainly to break up the pieces already detached. It follows that the number of breaks occurring during each passage will fall after most coral is detached and has been fragmented.

3. The numbers of breaks before trampling six months after the start of the experiment are higher than those at any other time, especially on the reef crest (Figure 2.10). This may have been caused by a period of very rough seas which occurred before the six month samples were taken. Photographic records indicate that the mobility of the boulders had increased in the experimental areas, especially on the reef crest.

Table 2.13 Results of Friedman's 2-way ANOVAs used to compare the numbers of breaks in live coral before trampling, after trampling and caused by trampling (after-before) during the long term trampling experiment at both sites. p is the probability that the differences between treatment groups were observed by chance. χr^2 is the test statistic R=N=4 * significant at the 5% level.

Sites and Data	Sample date (months)							
	0		6		12		18	
	χr^2	p	χr^2	p	χr^2	p	χr^2	p
<u>Reef Flat</u>								
Before trampling	5.1	.19	2.1	.649	4.4	>.24	5.0	>.19
After trampling	9.3	.012*	8.1	.633*	7.6	<.05*	9.3	.012*
After-Before	9.3	.012*	6.9	.068	7.6	<.05*	9.3	.012*
<u>Reef Crest</u>								
Before trampling	0.3	.992	4.8	.2	1.35	>.75	3.6	.36
After trampling	9.9	.0062*	5.1	.19	8.1	.033*	0.9	.9
After-Before	10.8	.0016*	1.5	.754	8.1	.033*	3.3	.389

Table 2.14 Results of the Mann-Whitney U-tests used to compare the number of breaks caused by trampling between treatments on the outer reef flat and reef crest during the long term trampling experiments. n1=n2=4. The probabilities that differences between treatment groups were observed by chance are shown in the table * significant at the 5% level. The test is 1-tailed.

Outer Reef Flat

Sample date (months)	0			6			12			18		
Number of Passages	0	5	10	0	5	10	0	5	10	0	5	10
20	.014*	.057	.557	.029*	.243	.243	.014*	.243	.057	.014*	.5	.075
10	.014*	.171		.029*	.171		.014*	.171		.014*	.243	
5	.014*			.1			.014*			.014*		

Reef Crest

Sample date (months)	0			12		
Number of Passages	0	20	40	0	20	40
80	.014*	.057	.557	.014*	.557	.243
40	.014*	.171		.014*	.243	
20	.014*			.014*		

2.4 DISCUSSION

2.4.1 Interpretation

At both sites human trampling caused the greatest amount of immediate physical damage to live coral at the start of the experiment which suggests that there was less coral present on subsequent sample dates that was vulnerable to trampling damage. This is supported by the observations that most living coral which is vulnerable to trampling at either site is broken off at the lowest trampling intensity and that it was not replaced by similar new growth during the 12 weeks between treatments. Clearly both communities have been altered by the long-term trampling in that the amount of physically delicate live coral was reduced.

Although the numbers of breaks cannot be directly compared between sites, as this parameter has a different relationship to actual physical damage at either site (Section 3.2.2, Chapter 3) it was clear that trampling caused less damage in relation to the background of natural damage on the crest site than on the outer reef flat site on two sample dates. Six months into the experiment during a period of rough weather and increased boulder mobility and on the final sample date trampling did not cause any increase in immediate physical damage on the reef crest.

Although trampling clearly broke up live coral at both sites the inert substratum was only broken up on the outer reef flat. The consolidated pavement of the reef crest was completely resistant to physical damage by trampling whereas a large proportion of the unconsolidated dead coral on the reef flat was rapidly destroyed by it. The accumulation of mobile coral rubble on the reef flat was partly due to this process and partly due to the break up of open arborescent colonies of *Acropora* species.

No rubble accumulated on the reef crest transects even though trampling did break up live coral. This was due to the facts that no inert substrate was broken up, the amount of detached coral was small compared to that on the reef flat (Section 3.2.2, Chapter 3) and what was detached had a high probability of being washed away in the turbulent reef crest conditions (Section 3.3.2, Chapter 3).

Trampling significantly altered the composition of the sessile community on the outer reef flat by reducing the abundance of corals with arborescent colonies, in this case mainly common *Acropora* species. Furthermore trampling at the highest intensity caused the greatest decline. In contrast, trampling did not change the abundance of any morphological category or species on the reef crest in spite of the fact that it did damage live coral in this area. Clearly the quantity of detached coral lost from the trampled transects did not constitute a significant amount of the live cover (also see Sections 3.2.2 and 3.2.3, Chapter 3).

The morphological classification system described in Section 2.2.4 and used to display the abundance data in Section 2.3.4 shows that there is a greater abundance of corals which are easily damaged by direct physical forces on the outer reef flat than on the reef crest. We would predict, therefore, that human trampling would cause more damage to the living reef flat community due to the physical destruction of these forms. The results support this prediction and show that even the lowest treatment on the reef flat, 5 passage/12 weeks, caused more damage than the highest treatment on the reef crest, 80 passage/12 weeks. The community on the reef crest site is able to tolerate at least 16 times the trampling intensity which causes significant damage to that on the reef flat site without showing any significant changes for 18 months. The question of predicting the vulnerability of a site based on our current results is taken up in Section 2.4.3.

Although the algal component of the sessile communities was not dealt with in any detail our results show that trampling had no effect on the abundance of macro-algae on the reef crest and strongly suggest that it inhibited a natural increase in th amount of algae on the reef flat. The factors responsible for this difference are undetermined but they are likely to be related to the difference species and growth forms found at each site. Those on the crest tended to be low and prostrate while those on the reef flat tended to be more upright.

The results also showed that there was a natural decline in the percentage cover of sessile animals at both sites. This decline was most pronounced amongst the corals with branching colonies on the reef flat and corals with digitate colonies on the reef crest. Natural physical disturbances such as increases in the movement of boulders at either site may have been responsible but there is no conclusive evidence available.

In addition to the preceding considerations, there are two groups of evidence indicating that trampling in the long term produces progressive changes which may not show up in the short term. Firstly the ditches and pathways caused by trampling on the outer reef flat transects became deeper and more extensive during the period of the experiment. Secondly the changes in the percentage cover of those elements of the reef flat community which were significantly affected by trampling namely mobile rubble, unconsolidated dead coral, open arborescent corals and algae, occurred more or less gradually during the experiment rather than instantly. Also it follows that if trampling continues for an extended period of time at a site such changes will slow down and cease as those corals which cannot withstand the trampling pressure are removed from the site. The structure of the remaining community and how closely it resembles the original will depend on the nature of the site and the intensity of use.

This is an important management consideration and the relationship between the nature of the site in terms of substrate structure and coral morphology, the intensity of use and the damage which occurs is considered in the following section.

To conclude this section the results of this experiment and their interpretation as discussed here have been assembled in summary form and presented in Table 2.15.

Table 2.15 Summary of results and conclusions of the long term trampling experiment.

Zone	Outer Reef Flat			Reef Crest		
Intensity of use for 18 months	5 to 20 passages every 12 weeks			20 to 80 passages every 12 weeks		
	algae	sessile animals	inert substrate	algae	sessile animals	inert substrate
Characteristics of Site	upright	branching forms and species predominating	sand, consolidated dead coral, and unconsolidated dead coral	prostrate	low and compact forms and species	consolidated dead coral
Immediate Impact of Trampling	?	live coral broken and damaged	some unconsolidated dead coral broken up, consolidated dead coral and sand undisturbed	none	some breakage of live coral	none
Longer term Effects of Trampling	natural rise in abundance of algae inhibited	abundance of open arborescent colonies reduced; increase in mobile rubble and creation of ditches and pathways	increase in mobile rubble and creation of ditches and pathways; reduction in unconsolidated dead coral	none	none	none
Relative vulnerability of site to trampling damage	high			low		

2.4.2 Preliminary prediction: site vulnerability

Figure 2.11 illustrates the relation between trampling intensity and damage expressed as a reduction in the percentage cover of a given morphological or substrate type. We have, as yet, insufficient data to precisely quantify this relationship thus the shapes of the curves are hypothetical. However, the following general qualities have been

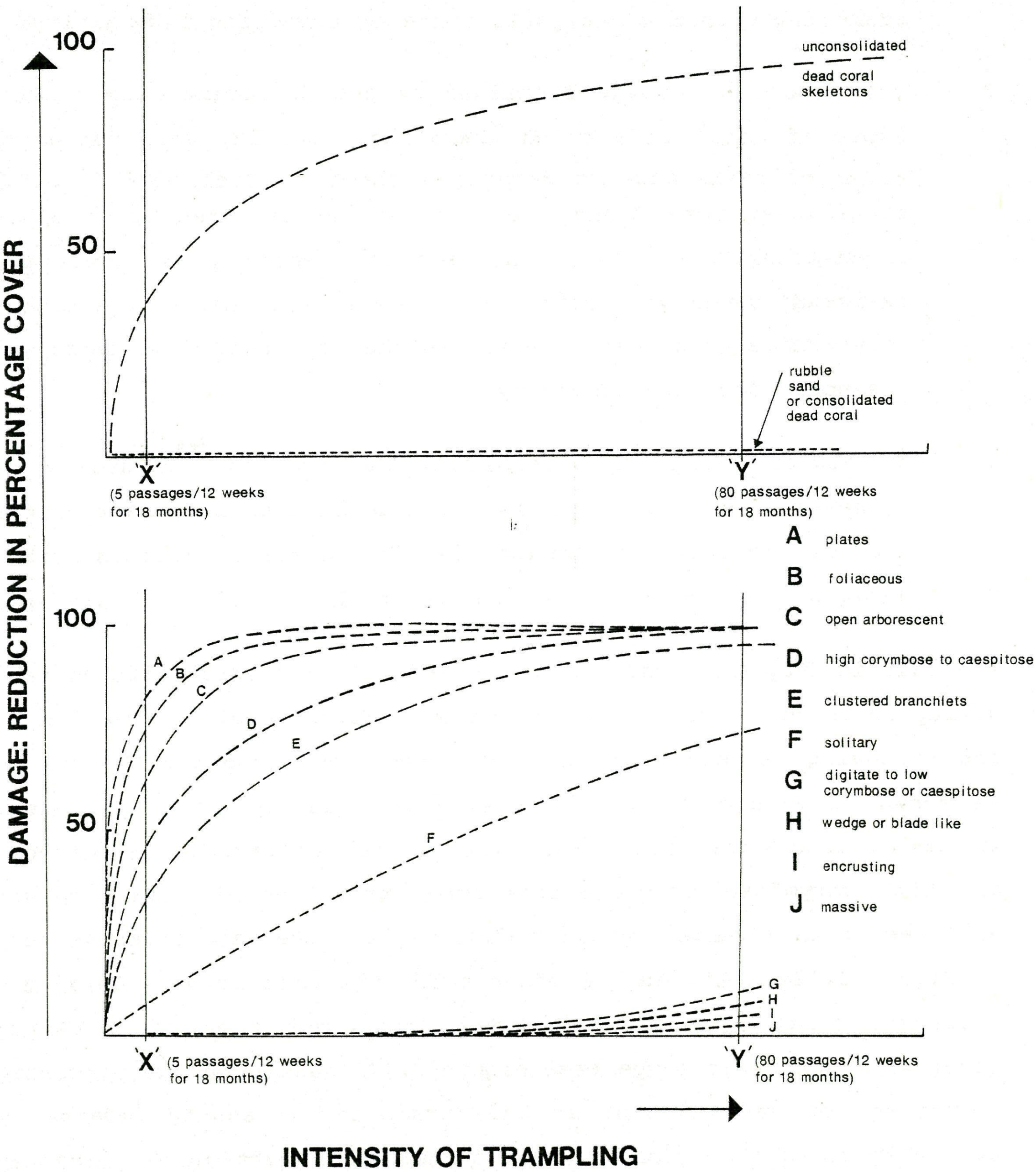


Figure 2.11 The relationship between damage, measured as the percentage reduction of percentage cover, and intensity of trampling for the different morphological categories of coral and the different substrate categories.

indicated by the empirical evidence of the long term trampling experiment and consideration of the mechanical properties of differently shaped coral skeletons.

1. As the intensity of trampling increases the amount of damage increases until there is total destruction except in the case of sand, consolidated dead coral and rubble. These three components of the reef flat community will not be destroyed by trampling within a realistic range of trampling intensities.

2. The amount of damage sustained by the different morphological types of coral at a given trampling intensity will follow the order of resistance to damage as shown in Table 2.5 (ie. less resistance, more damage) except at the extremes of trampling intensities. At low intensities of trampling we expect that resistant types will suffer no or an equally small reduction in cover while at higher intensities the less resistant types will disappear from the community.

3. At higher trampling intensities the increase in damage per increase in unit of trampling will decline as a greater proportion of the trampling impacts fall on material which is already damaged. The curves will, therefore, level off at this stage.

The relationship in Figure 2.11 can be used to predict site vulnerability in terms of the damage caused by a given level of trampling in the following manner. Consider two levels of trampling "X" and "Y" as shown in Figure 2.11. If a site is made up largely of unconsolidated dead coral and corals with plate, foliaceous, arborescent and high corymbose to caespitose forms trampling at this intensity will result in a large overall reduction in percentage cover as shown in Figure 2.12a. If, on the other hand, the site is made up of more resistant coral forms and substrates this reduction in percentage cover will not be as large (see Figure 2.12b) although the percentage reduction for each element at this trampling intensity remains the same (Figure 2.11). Figures c and d show the reduction in percentage cover at the two hypothetical sites at the higher trampling intensity "Y". Clearly site A is the most vulnerable and would be easily damaged by low levels of trampling.

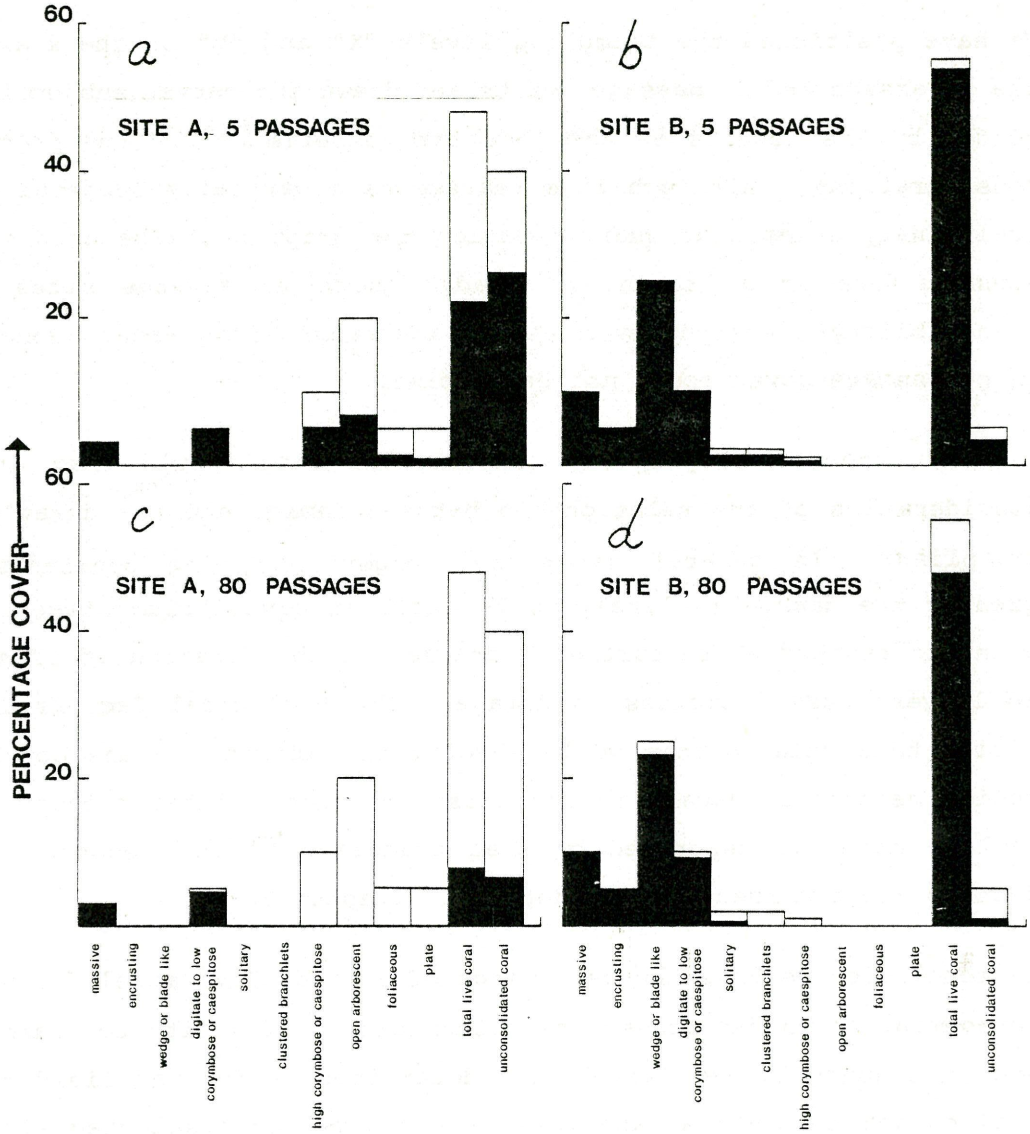


Figure 2.12 The predicted reduction in percentage cover at two different sites and two different trampling intensities based on the relationships depicted in Figure 2.11. Percentage cover before trampling (open bars) Percentage cover after trampling (closed bars) The trampling intensities are given as the number of passages over a given site every 12 weeks for 18 months.

We have positioned the trampling levels "X" and "Y" on the x axis at the 5 passage and 80 passage points and drawn the curves subjectively, guided by the results of the long term experiment and the preceding considerations. Although this represents a partially subjective and preliminary attempt at quantification the graph could be used in its present form as a "rough and ready" guide to arrange sites in a vulnerability hierarchy even though any predictions about reductions in percentage cover could not be precise.

Further attempts to properly quantify the graph would also involve consideration of the relationship between damage and the duration of trampling. In general terms the longer trampling continues the greater the damage is likely to be until an equilibrium stage or end point is reached where further increases in the duration of trampling no longer cause increases in damage. The biological factors determining this relationship would involve the ability of the corals to resist mechanical damage in the first instance and their capacity to replace material destroyed by that trampling in the second. These factors are examined in more detail in Chapter 5.

In conclusion we have the beginnings of a predictive model for use in management which can assess the vulnerability of a site to trampling. Once the quantitative details are determined by further field observations and theoretical analysis, the changes to a selected site can be predicted under a given trampling regime.

CHAPTER 3 SHORT TERM TRAMPLING AND DRIFT EXPERIMENTS

CHAPTER 3 SHORT TERM TRAMPLING AND DRIFT EXPERIMENTS

3.1 INTRODUCTION

The destruction of living and dead coral skeletons is a continuous natural process. The agencies of the initial destruction may be physical, primarily wave action, or biotic (Orme 1977). Bioerosion is one of the major processes of destruction and may occur as surface grazing by echinoids, molluscs and parrot fish and by boring of the skeleton by a wide variety of organisms (Hutchings 1983). Human trampling may be considered as a further agent of either physical or bioerosion but it is not known whether the nature of the breaks and size and nature of the fragments produced is similar to, or different from those produced by natural processes. Grain size of beach sediment produced by natural processes was found by Folk and Robles (1964) to range from coral blocks over 1m across down to fine coral grit. They term the sediments from branching corals as coral 'sticks' (64mm), coral 'joints' (0.25mm) and coral grit. The larger sediments are then broken down to smaller particles by physical, chemical and biological agencies and transported primarily by water movement (Orme 1977). Portions of detached coral that are still living may become lodged within their original colony or in some other location and depending on species and the size of the portion, continue to live and grow if they are not exposed to the air or covered with sand.

The first questions addressed in the work reported in this chapter are "What is the nature of the sediments produced by human trampling on branching corals at differing intensities, and how does this relate to the non-destructive measure of damage by counting breaks in live coral used in the long-term ampling experiments? (Chapter 2). As the long term experiment had to be recorded at intervals, the removal of fragments for measuring would have disrupted the results and so a separate short-term experiment described here was necessary. Initial observations showed that quite large numbers of live coral fragments were detached as a result of trampling. Since the fragments depend on becoming lodged in a suitable position for their continued survival, a second question arises as to whether they continue to be moved around on the reef flat or crest with the flow of ordinary tides? The experiments that attempt to answer these two sets of questions are presented and discussed in sequence.

3.2 SHORT TERM TRAMPLING EXPERIMENT

3.2.1 Methods

3.2.1a Site Selection

The transects were laid out in positions not previously used for trampling experiments, two of 5m on the reef crest and three 5m on the reef flat. The reef crest sites had between 20 per cent and 40 per cent cover of live coral and the outer reef flat transects were along the sides of pools where branching species were abundant and cover of live coral was about 60 percent.

3.2.1b Treatments

Transects of 80 and 20 passages were walked on the reef crest in November 1982 and one of 20 passages and two of 5 passages were walked on the outer reef flat in May 1983.

3.2.1c Recording

The percentage cover of live coral and the number of breaks in live coral were recorded in 25cm by 25cm quadrats placed continuously along each transect before the treatments were carried out. Only 19 quadrats were recorded in the 20 passage transect on the reef flat. After the transects had been trampled, the number of visible breaks were recorded in all except one of the 5 passage treatments on the outer reef flat and all the detached fragments were collected from each quadrat. These were sorted into 2cm size classes except for two classes (<1cm and 9cm - 10.5cm) which were only 1.5cm long. Three pieces from the reef crest which were over 9cm were recorded as such. The number of fragments in each size class were counted and weighed except the portions less than 1cm which were counted but were too light to be recorded on our scales. The coral fragments from the crest transects and the second 5 passage transect on the outer reef flat were taken to the laboratory for measurement while those from the other two reef flat transects were measured in the field. The material from the crest transect trampled 80 times and from the extra outer reef flat transect, which had been trampled five times, was separated by cutting where necessary into live and dead portions which were measured and weighed in the laboratory.

3.2.1d Analysis

Standard errors were calculated on the mean figures of all data, on each transect. The regression coefficients and their significance were calculated between the field counts of breaks and the actual number of coral fragments recovered from each quadrat.

3.2.2 Results

There was a significant correlation between the field counts of breaks and the number of fragments detached from the reef crest, especially at the higher intensity of trampling. This relationship was not significant on the outer reef flat (Table 3.1). A mean of

Table 3.1 Regression of field counts of breaks recorded after trampling, minus the number recorded just before trampling, on the number of pieces of coral recovered.

Zone and Treatment	R^2	Significance of regression
Reef Crest		
80 passages	0.79	0.001
20 passages	0.56	0.001
Reef Flat		
20 passages	0.14	n.s.
5 passages	0.01	n.s.

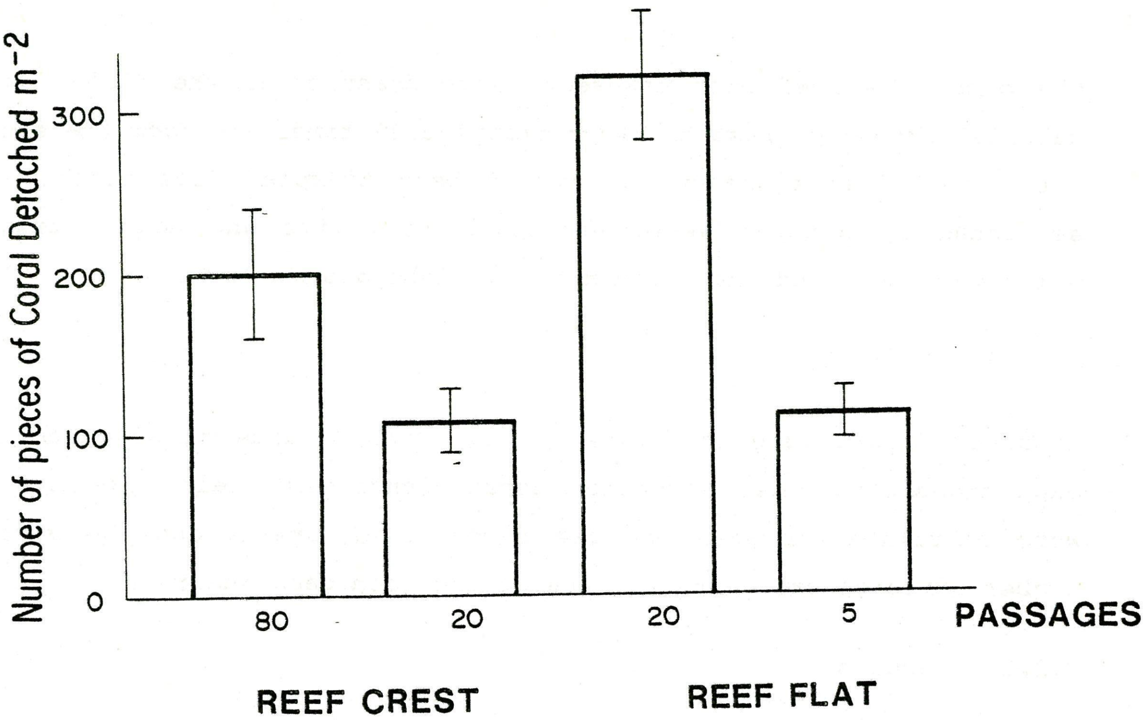


Figure 3.1 The number of pieces of coral m^{-2} detached by trampling on the reef crest and reef flat.

200 pieces of coral m^{-2} were detached from the 80 passage transect and just over 100 pieces m^{2} on the 20 passage transect on the reef crest (Figure 3.1). This compares with the 320 pieces of coral m^{-2} detached on the 20 passage transect on the reef flat and just over 100 pieces m^{-2} detached by 5 passages on the reef flat (Figure 3.1). It is noteable however that only $0.7kgm^{-2}$ was broken from its anchorage on both reef crest transects were as $5.7kgm^{-2}$ was detached from each transect on the reef flat (Figure 3.2). This compares with $12kgm^{2}$ of detached coral recorded by Woodland and Hooper 1977 after 18 passages on a similar reef flat habitat on the adjacent Wistari reef. Although the total amount of coral detached from the reef crest was much less than from the reef flat, over 90 per cent of it was living whereas only about 60 per cent of the coral detached from the reef flat was alive (Figure 3.3).

Examination of the distribution of the size classes in each treatment shows that pieces of coral with a maximum dimension of 34.5cm were detached on the reef flat whereas the maximum size on the reef crest was about 15cm (recorded as over 9cm) (Figure 3.4). The higher intensities of trampling produced more small pieces of coral at both

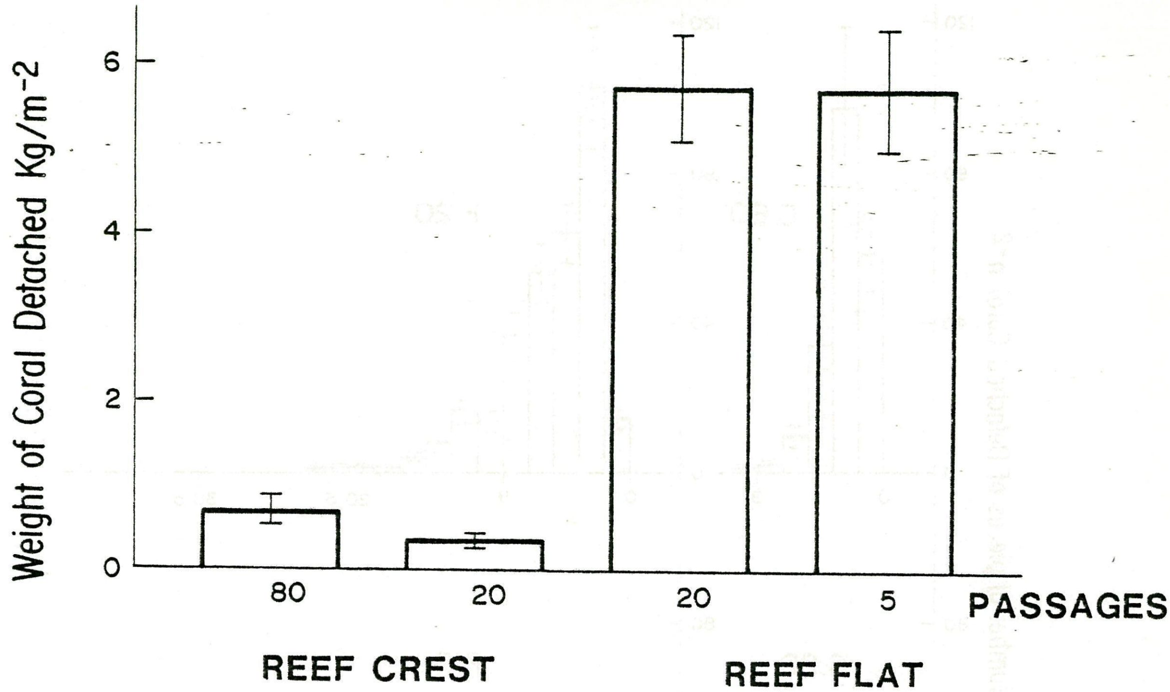


Figure 3.2 The weight of coral m^{-2} detached by trampling on the reef crest and reef flat.

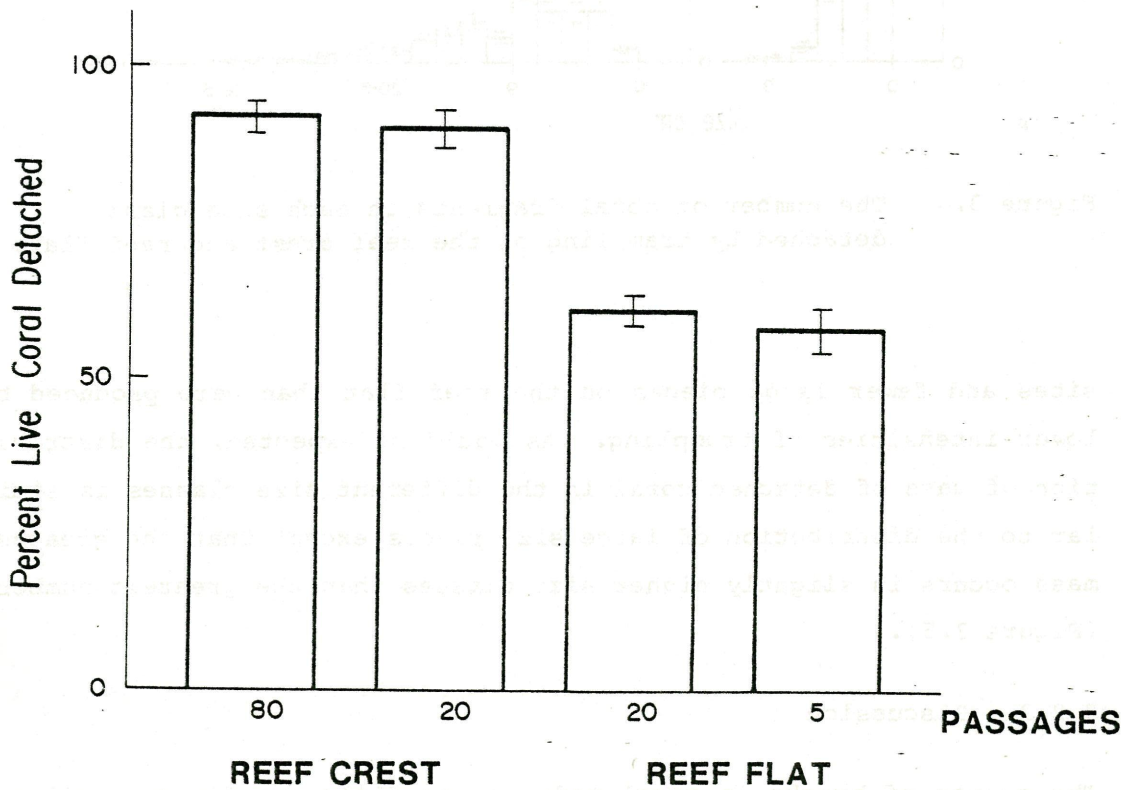


Figure 3.3 The percentage of live coral in the material detached by trampling on the reef crest and reef flat.

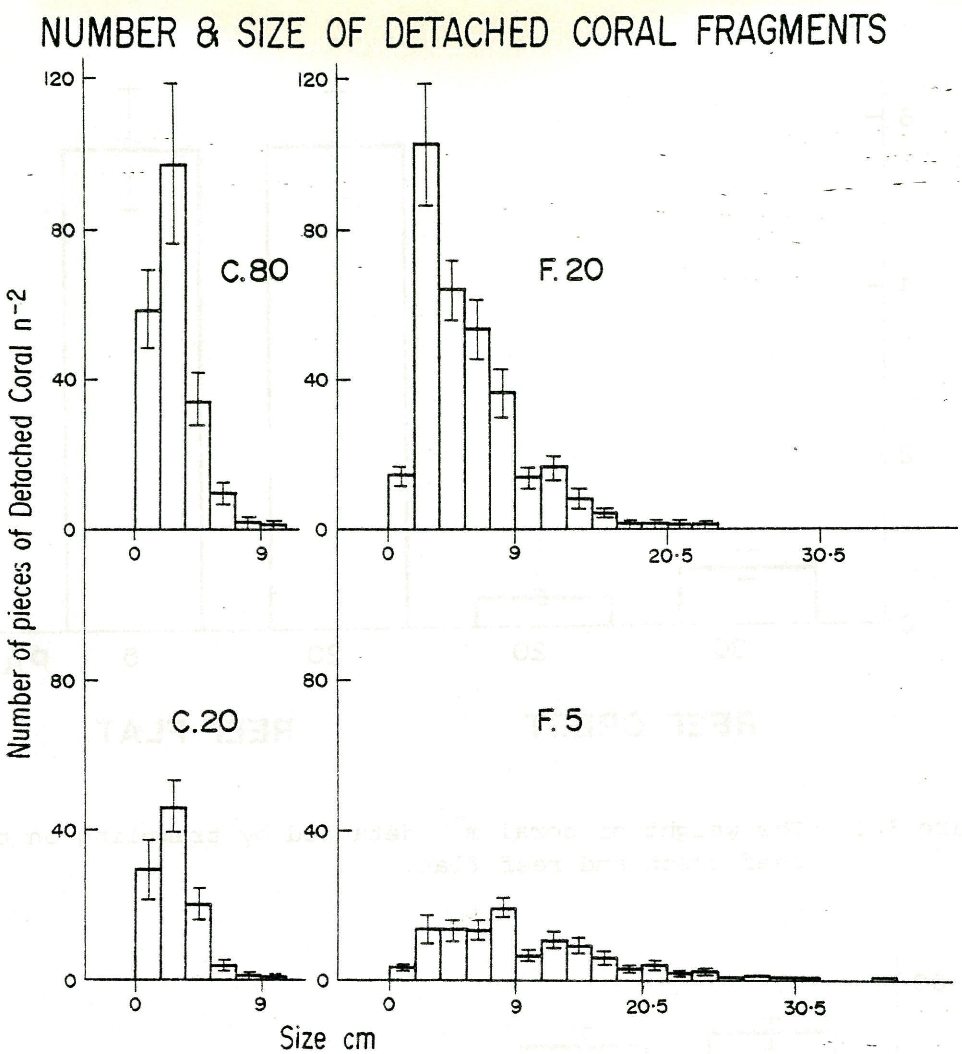


Figure 3.4 The number of coral fragments in each size class detached by trampling on the reef crest and reef flat.

sites and fewer large pieces on the reef flat than were produced by lower intensities of trampling. As would be expected, the distribution of mass of detached coral in the different size classes is similar to the distribution of large size pieces except that the greatest mass occurs in slightly higher size classes than the greatest numbers (Figure 3.5).

3.2.3 Discussion

The counts of breaks in coral made in the field are directly related to the number of pieces of coral detached from the reef crest and the measurements presented in Chapter 2 can be directly interpreted. This relationship does not hold on the outer reef flat and while the count of number of breaks clearly measure one aspect of damage the

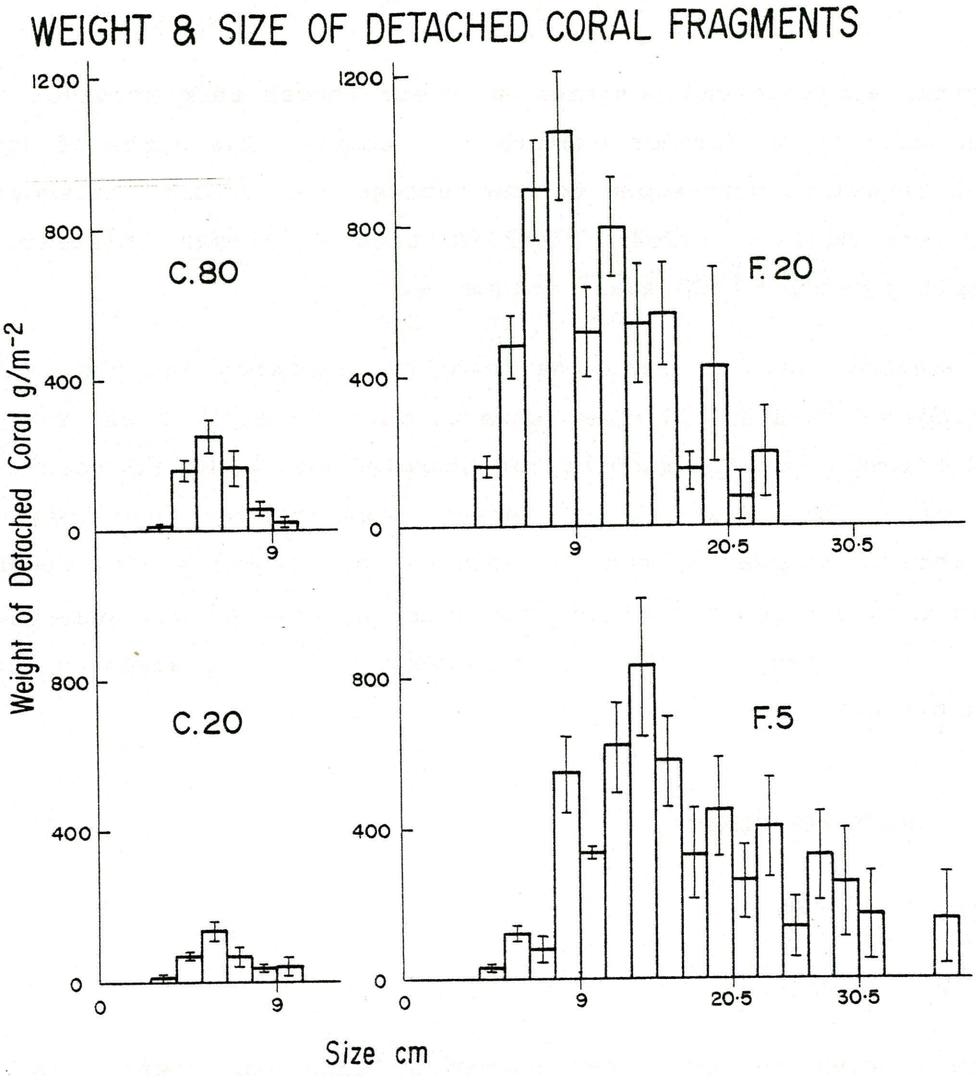


Figure 3.5 The weight gm^{-2} of coral fragments in each size class detached by trampling in the reef crest and reef flat.

significance of that data is harder to interpret. The reason is probably that many of the breaks that occur in reef flat corals cannot be seen as they occur deep within the coral matrix whereas the reef crest community is shallow and entirely visible. However the visible breaks are what the visitors will see as they walk through the outer reef flat pools and are therefore directly related to the perceived tourist impact.

In general, the numbers, weight and size of coral fragments detached in both habitats confirm that the outer reef flat corals are more easily damaged by human trampling than those on the reef crest. At low intensities of trampling (5 passages) the broken corals on the outer reef flat often remained interlocked and more or less in their original attitude and position so their longer term survival may be quite good if no further disturbance occurs. The sizes of detached coral fragments correspond to the "sticks" and "joint" categories of Folk and Roble's (1964) classification. Higher intensities of trampling produce more small fragments.

The eventual fate of both the detached fragments and the remaining portions of damaged colonies needs to be understood if we are to make predictions about the recovery of trampled areas of reef corals. The survival of both portions was investigated in fixed positions and is reported in Chapter 5, but the survival of fragments also depends on where they are positioned and the drift experiment was undertaken to find the potential for their movement when placed in exposed situations.

3.3 DRIFT EXPERIMENT

3.3.1 Methods

3.3.1a Material

Three species of coral were chosen for this experiment. They were *Acropora millepora, A. palifera* and *Pocillopora damicornis*. The skeletons were cleaned and cut into 2cm, 4cm and 8cm sizes. These are the same species and sizes that were used in the damage and recovery experiments reported in Chapter 5. There were thus three sizes and three species making nine combinations in all. A total of 54 size and species sets (nine fragments in each) were prepared and painted in different colour codes for each species/size combination. Three sites were selected on the reef crest and the outer reef flats (six in all). Those on the outer reef flat had relatively smooth surfaces of branching coral and those on the reef crest had surfaces of level consolidated coral where the fragments would be exposed to water movement. This is the extreme location as most fragments detached by trampling would fall into more protected positions. Nine differently coded sets (replicates) were placed with 50cm intervals between each piece along a fixed transect at each of the six sites in November 1982. The sizes and species positions within each set were randomised.

3.3.1b Recording and analysis

The position of each fragment was recorded each day for six days (11 tides). The accumulated distance moved by each fragment at each recording was the basis for an analysis of variance and the least significant difference was calculated for each recording.

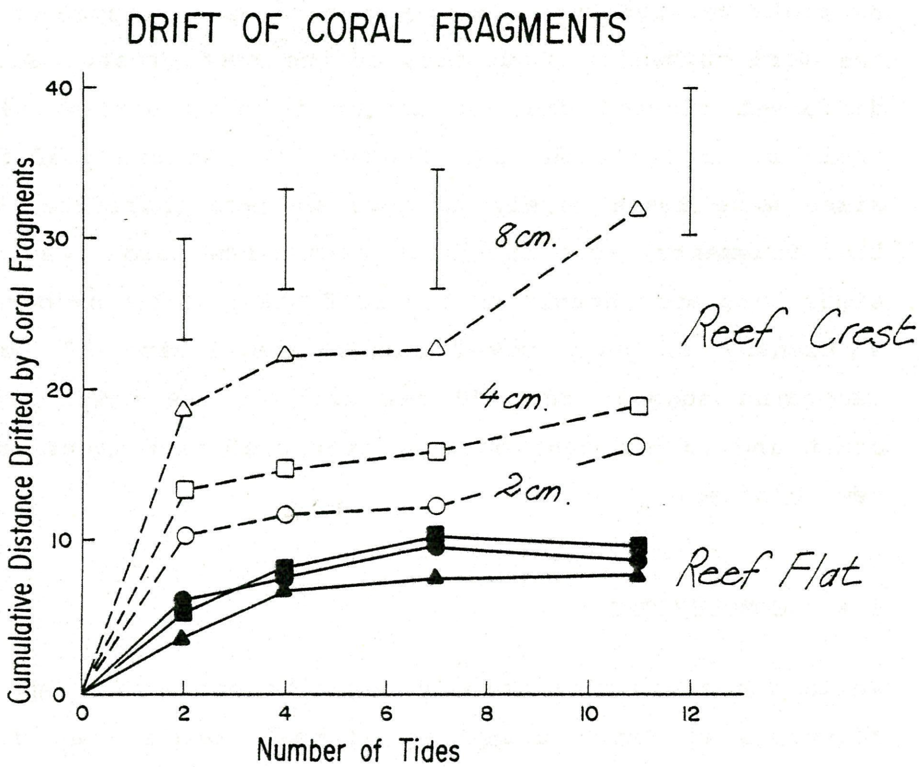


Figure 3.6 The cumulative distance drifted by coral fragments on the reef crest and reef flat.

3.3.2 Results

The accumulated distance moved by the coral fragments was greater on the reef crest than on the outer reef flat (Figure 3.6). On the crest the larger sizes moved the greatest distance whereas the smaller sizes moved further on the reef flat. There was no significant difference between the distances moved by the different species. At the last recording, 24 pieces (10 per cent) on the reef crest had remained stationary or were only recorded as moving 1cm, within the range of error of recording and 45 pieces (19 per cent) remained stationary or were recorded as only moving 1cm, on the outer reef flat.

3.3.3 Discussion

As would be predicted the movement of coral fragments was greater in the more turbulant conditions of the reef crest. Surprisingly, the different species did not appear to move differently in spite of their range of forms (See Chapter 5). On the reef flat the larger sizes were least likely to move and are therefore, in the case of live fragments, more likely to form a new colony whereas the smaller sizes were more stable on the reef crest. The numbers that remained stationary or only moved within the limits of accuracy of the recording suggest that 10 per cent of the coral fragments on the crest and 19 per cent on the outer reef flat might survive and form new colonies.

3.4 CONCLUSIONS

While these experiments only describe one small aspect of the consequences of human trampling on reef corals they do qualitatively support the hypotheses that the processes are similar to other forms of physical and bioerosion. Much more work is required to examine the quantitative nature of the effects and the implications of their temporal and spatial distribution which are probably quite different from natural processes.

CHAPTER 4 RECOVERY EXPERIMENT

CHAPTER 4 RECOVERY EXPERIMENT

4.1 INTRODUCTION

The experimental exclusion of herbivores or carnivores from areas in natural or man-managed communities is a well established technique to determine the effect these biological agents have on the other community members (eg. see Paine 1977, Watt 1957). Physical barriers are employed to restrict the access of the animals to several areas within the community and species numbers and abundances inside and outside the exclosures are monitored. Any differences over time indicate the impact these animals have on their communities.

Heron Island supports a P & O tourist resort which was first established on the cay in the nineteen forties and now has the facilities to accommodate up to 200 guests. Organized guided reef-walks (Plate 4.1) have been conducted on the reef flats around the cay for more than 20 years and during the seventies, at least, these walks have taken place on an area of reef flat directly opposite the outdoor resort bar (Figure 4.1). The number of people on the walks varies from 10 to 40 and they are held, approximately, on 10 days in every 14; bad weather and unsuitable tides preventing daily walks.

The boundaries of this trampled area are not sharply defined as independent walkers frequently move in and out of the general area and the tour groups which have a tendency to spread out, do not follow exactly the same path each day. Furthermore, the composition of the sessile communities on the intertidal reef flat surrounding the island are not homogenous, thus differences between the guided walk area and those adjacent could be due to environmental factors not associated with trampling. Accordingly the analytical approach (Section 1.4) was not used to determine the impact of these guided walks as two of its basic assumptions were violated. Instead, an experimental approach employing the exclusion technique was employed to address this question.

Our recovery experiment has been designed to test the following hypothesis. Human trampling resulting from the guided reef walks conducted by the Heron Island resort has altered the sessile com-

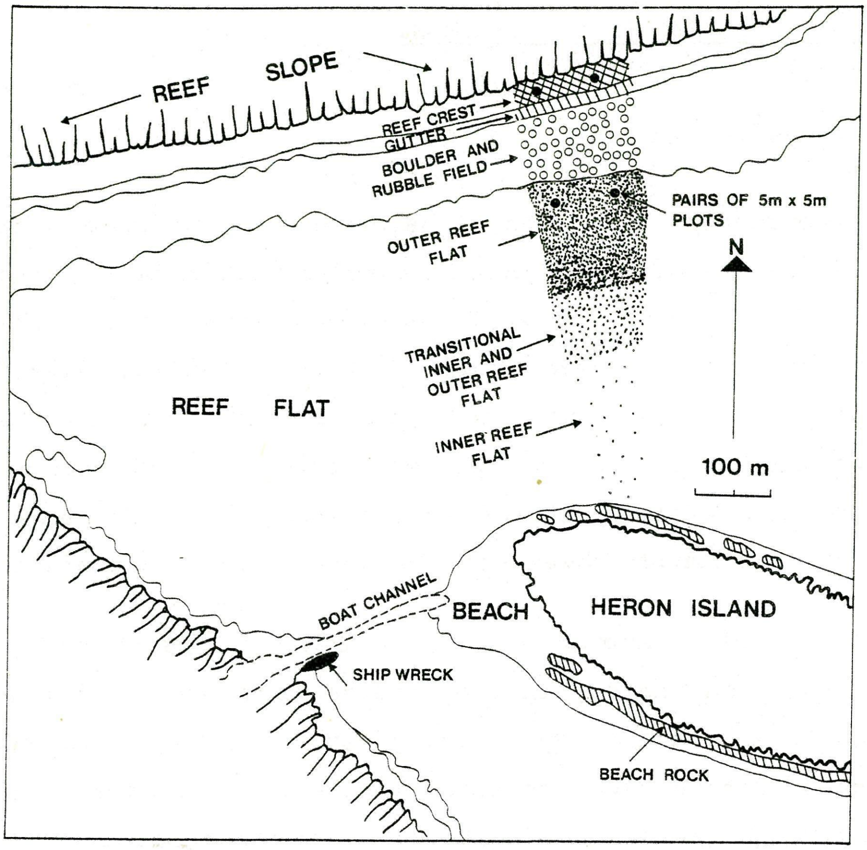


Figure 4.1 A section of Heron Island reef flat showing the area to the north of the cay which is used by the P.O. tourist resort for guided reef walks. The stippling shows the extent of the area and the zones within it. The location of the pairs of experimental plots are also marked.

munities growing on the continuous dead coral surfaces (Plate 4.2) in the outer reef flat and reef crest areas regularly traversed by those walks (see Figure 4.1).

4.2 METHODS

4.2.1 Field layout

Four pairs of 5m x 5m plots were marked out on the reef between the 10th and 14th May 1982 in the positions shown in Figure 4.1. People were excluded from one plot in each pair (Figure 4.2) by a low fence constructed of galvanized angle iron stakes with a 4mm stainless steel cable strung between them (Plate 4.2). The stakes were ham-

Plate 4.1 A guided reef-walk from the Heron Island Resort

Plate 4.2 An exclosure plot on the reef crest

mered into the reef and range in height from 20cm to 40cm above the substrate. Signs resistant to u.v. light which read

PLEASE DO NOT ENTER

recovery plot, research by GBRMPA and Griffith University

were attached to each of these exclosure plots.

The other plot in each pair remained accessible to reef walkers and was marked at the corners with tent pegs hammered down into the substrate inconspicuously. Leaflets explaining the purpose of the plots were left at the resort for general circulation.

4.2.2 Data collection and processing

Ten 1m x 1m quadrats were randomly allocated within each of the plots (see Figure 4.2) and are being photographed with colour transparency film at yearly intervals to provide permanent photographic samples.

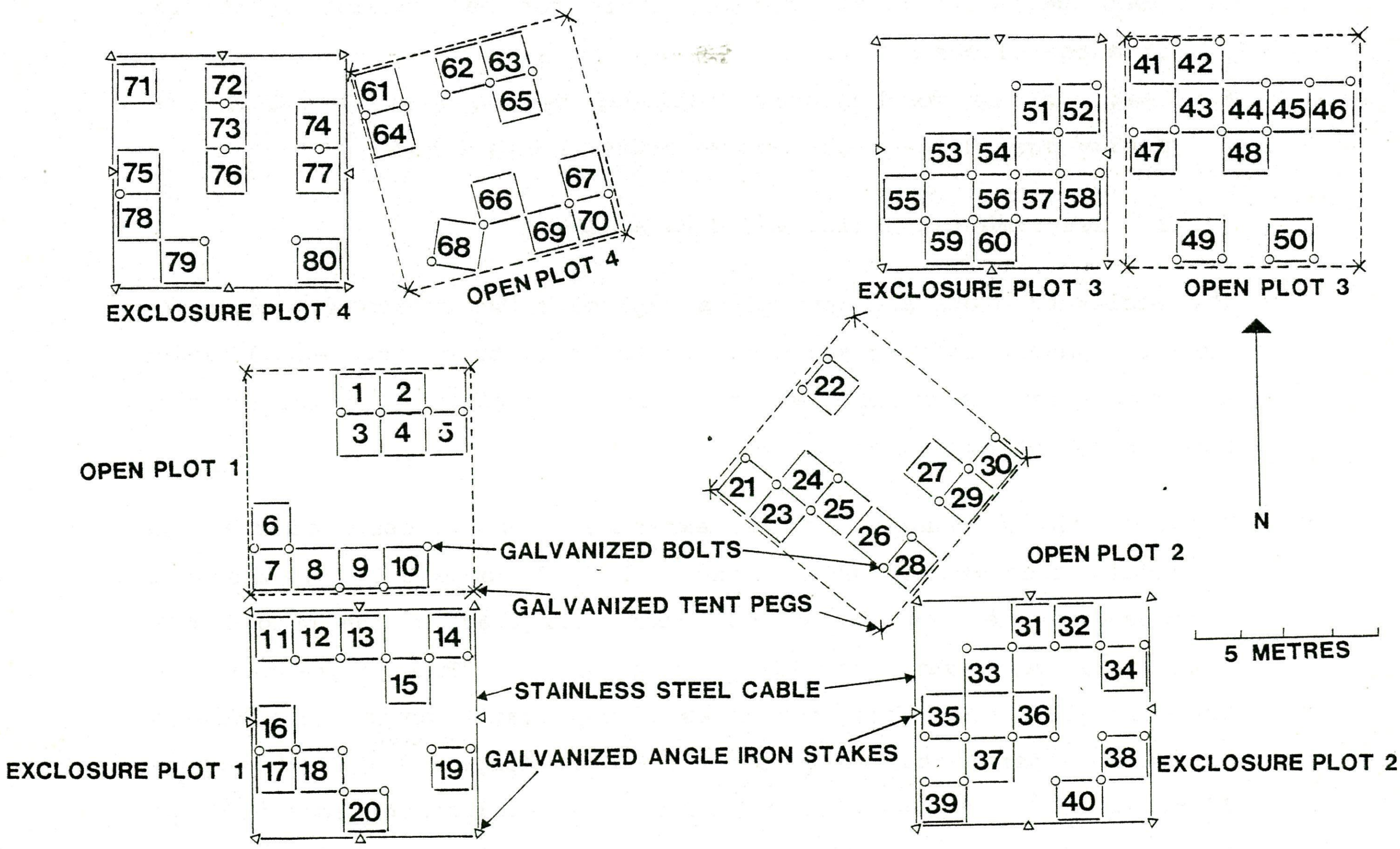


Figure 4.2 The meter square photographic quadrats within the eight experimental plots. The relative positions of the plots within pairs is shown to scale but the positions of the pairs in relation to one another is not.

The plots have been sampled twice, initially on the 23rd and 24th May 1982 and one year later on the 25th and 26th of May 1983.

The percentage cover of each component of the community is calculated for each quadrat by superimposing a grid of 100 evenly spaced points onto a life-sized projection of each transparency and recording the identity of the taxa falling under each point. The percentage cover for each plot is then calculated from the figures from the ten quadrats.

This data is being presented for the following components of the community:

1. total live coral
2. total unoccupied dead coral substratum
3. sessile invertebrates other than coral
4. algae (not including coralline red algae
5. each genus of coral (species could not be reliably identified from the slides)
6. each of the morphologies displayed by the sessile animal community according to the scheme presented in 2.4.2

4.2.3 Experimental design and data analysis

The exclosure plots and open plots represent two treatments, no. exposure to human trampling and exposure to human trampling respectively, and each plot is considered as a replicate giving a total of four replicates for each treatment.

Prior to the setting up of the experiment it was observed that the physical structure of the living and dead components of the communities on the reef crest and outer reef flat in the guided reef walk area were very similar (Table 4.1). This suggested that treating plots from these two zones as replicates would not introduce excessive experimental variation. The percentage cover data from the first sampling of the plots confirmed this subjective assessment and indicated that the generic composition of the live coral communities from these zones was also very similar (see Appendix 4.2).

The percentage cover data produced by this experiment was not normally distributed and the non-parametric Mann-Whitney U-test was used to test for differences between treatments. Although the plots were paired, a test for two related samples could not be used due to the small replicate number.

Table 4.1 The different reef zones traversed by the guided reef walks from the tourist resort.

Zone	% of area traversed by guided walks	Physical Structure
Inner reef flat	22	Broad expanses of sand surrounding clumps of algae and dead or live coral.
Transitional inner/outer reef	14	Semi-continuous dead coral not consolidated into a pavement, many pools and sand channels, massive and stoutly branching corals common.
Outer reef flat	34	Low, compact coral colonies on more or less level area of semi - to completely consolidated coral pavement, some sand pools with more upright coral colonies.
Boulder and rubble field	19	Boulders and heaps of coral rubble on a consolidated coral pavement.
Gutter	3	Bare consolidated coral pavement forming a depression between the reef crest and boulder field
Reef crest	8	Low, copact coral colonies on a level consolidated coral pavement.

4.3 RESULTS

Over 70% of the substratum was dead coral in both treatments at the start of the experiment and 12 months later (Figure 4.). Scleractinian corals occupied between 15% and 20% of the remaining substratum, algae between 4% and 8% and other sessile invertebrates less than 1%. Inspection of Figure 4.3 shows that there are no trends in changing abundances associated with the treatments for these four categories over the first year of the experiment. Additionally there are no significant differences between treatments at either sample dates for these four community components (Appendix 4.1).

Twenty-four individual genera were recorded in the plots (Table 4.2) and 18 of these attained a mean percentage cover of 0.2% or more in at least one of the treatments on the initial or 12 monthly sample date (Appendix 4.2). Twelve of these 18 genera were scleractinian corals and the genus *Acropora* was clearly the most abundant (Figure 4.).

There were no significant differences between treatments for the percentage cover of any of the 24 genera or unidentified corals, drift algae and unidentified algae at either sample date (Appendix 4.2). Furthermore as can be seen in Figure 4.3 the structure of the live sessile community represented as the percentage cover of the 18 more common genera does not show any clear changes over the first year of the experiment which can be associated with the treatments.

The unoccupied substratum in the zones where the plots are situated is made up of partly or completely consolidated dead coral which provides a rough, but essentially level, surface which easily supports the weight of human walkers without damage. The structural morphologies displayed by the corals and sessile invertebrates in these areas are various but generally low and compact rather than upright and open. The general physical aspect of this area suggest robustness in the face of direct mechanical disturbances. This is supported by Figure 4.4 which shows that most of the sessile animals in the plots have morphologies, following the classification system used in section 2.2.4, that will not be easily damaged by trampling.

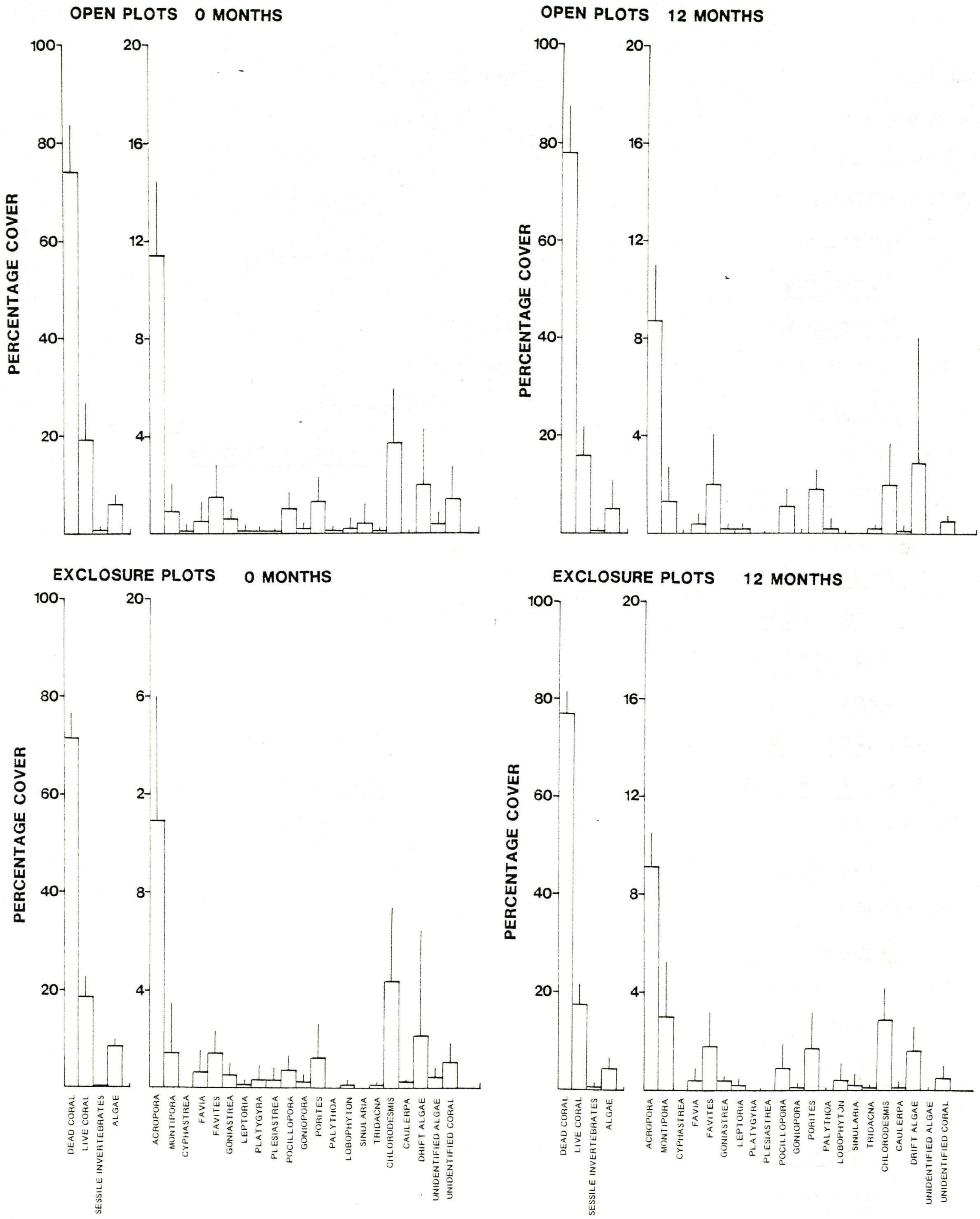


Figure 4.3 The mean (bar) and standard deviation (line) of the percentage cover of the 18 common genera and other community components in the exclosure and open plots of the recovery experiment. Data for the 1st (0 months) and second (12 months) sample dates are given.

Table 4.2 Genera found in the plots

Cnidaria

Anthozoa

Hexacorallia

Scleractinia

Acroporidae

Acropora

Montipora

Agariciidae

Pavona

Faviidae

Cyphastrea

Favia

Favites

Goniastrea

Hydnophora

Leptoria

Platygyra

Plesiastria

Fungiidae

Fungia

Mussidae

Lobophyllia

Pocilloporidae

Pocillopora

Stylophora

Porithdae

Goniopora

Porites

Zoanthidea

Palythoa

Octocorallia

Alcyonacea

Alcyoniidae

Lobophyton

Sinularia

Mollusca

Bivalvia

Tridacnidae

Tridacna maxima

Chlorophyta

Chlorodesmis

Caulerpa

Halimeda

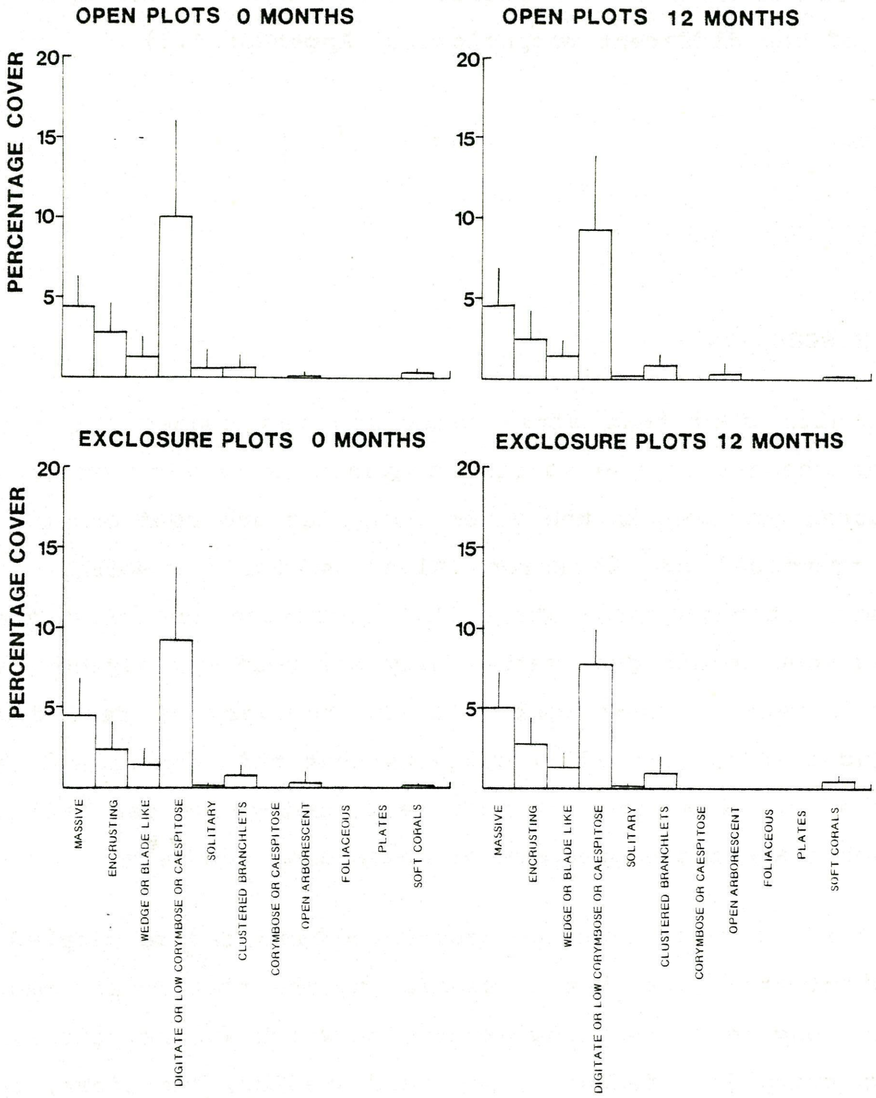


Figure 4.4 The mean (bar) and standard deviation (line) of the percentage cover of the morphologies displayed in the sessile animal community in the exclosure and open plots of the recovery experiment. Data for the 1st (0 months) and second (12 months) sample dates are given.

Digitate or low corymbose colonies are the most common in the plots followed by the more structurally resistant massive, encrusting and wedge or blade like branched colonies (Figure 4.4). The less resistant forms are rare.

Figure 4.4 shows that the abundances of the various morphologies do not show any changes associated with the treatments in the first year of the experiment. Additionally there were no significant differences on either sample date between treatments in the mean percentage covers of the different morphologies (Appendix 4.3).

4.4 DISCUSSION

The results show that after trampling has ceased for a year there were no changes in the sessile communities growing on the continous dead coral surfaces in the outer reef flat and reef crest areas regularly traversed by the Heron Island guided reef-walks. We cannot conclude at this early stage that trampling has not had any effect here as some corals grow very slowly and recovery may not be detected within a year. Other work with the recovery of reef flat systems (Yamaguchi 1975, Loya 1976) suggests that this experiment needs to be conducted for a minimum of four years before we can make conclusive statements about the presence or absence of recovery.

However it is clear that the sessile communities we sampled here have a physical structure that is similar to the reef crest community used for the long term trampling experiment which was relatively resistant to high trampling pressure. We would predict, therefore, that at the present intensity of use where the same pathway is very unlikely to be trampled each day (consider 30 people per day wandering within the areas shown on Figure 4.1) that this community is not being extensively altered by trampling.

As can be seen in Figure 4.1 the reef walks traverse several different reef zones which have different physical structures and sessile communities as listed in Table 4.2. As explained in Section 2.2.1 the sessile communities in the inner reef flat and in the boulder field are not vulnerable to human trampling. Reference to Table 4.2 shows, therefore, that approximately one quarter of the area where sessile communities are trampled contains a sessile community which is different to that sampled by the plots. The coral colonies are not as low and compressed and the unoccupied substratum is not level.

This suggests that this area may be more readily damaged by trampling. We note, however, that the substrate does, in the great majority of cases, support the weight of human walkers and that visual appraisal indicates that the majority of species in the area have massive colonies or ones with knotty wedge-like branches. This area will not be so easily damaged by trampling as the outer reef flat community in the long term trampling experiment and may actually be as robust as the sessile communities containing lower more compressed colonies.

CHAPTER 5 DAMAGE AND RECOVERY AT THE SPECIES LEVEL

5.5 SURVIVAL AND GROWTH EXPERIMENT WITH CORAL FRAGMENTS

5.5.1 Aim

5.5.2 Methods

5.5.3 Results

5.5.3a Survival of fragments

5.5.3b Growth of fragments

5.6 DISCUSSION

5.6.1 Resistance

5.6.2 Tolerance

5.6.3 Resilience

5.6.4 Strategy

CHAPTER 5 DAMAGE AND RECOVERY AT THE SPECIES LEVEL

5.1 INTRODUCTION

5.1.1 General model

Whichever means are chosen to manage a resource the objectives of management have to be defined. In the case of a coral reef flat used for recreation the management objectives for a site are most likely to be expressed in terms of ecological measures such as cover of coral, number of certain sized colonies per meter of pool edge or number of species per unit area. However, when managing a biological resource it is not possible to set a single number as a management target because populations of organisms are subject to continuous changes and it is against this fluctuating background that targets have to be defined and the impact of use assessed.

There are then two qualities that need to be investigated. One is the natural variation in coral populations and colonies, and the other is the stability or response of those populations to human impacts. Natural variation of sessile communities has been the subject of a number of studies (eg. Kay & Keough 1981, Connell 1983) and extreme conditions such as hurricanes have caused between 71% and 100% reduction in the cover of corals in study sites on the Heron Island reef (Connell 1983). However moderately severe storms only reduced coral cover by 11% in Hawaii (Dollar 1975 quoted by Highsmith 1982). As in many terrestrial habitats, it is against this background of occasionally severe disruption and more frequent less intense disturbances (Connell 1983) that the continuous impact of visitors trampling on the reef has to be viewed. If a trampling event can cause as much destruction as a severe storm and the trampling is repeated continually then the impact on the environment is a matter of grave concern, at least for the manager trying to provide a fulfilling experience for the reef visitors.

The approach adopted for the work reported in this chapter is essentially a reductionist one that may be interpreted in relation to natural changes in coral populations where these are known. Interactions between animals and plants have been considered in three stages (Liddle in press) and the same stages can be used in the study of human trampling on corals. The first stage, designated as alpha processes involve the signals that are received by the animal (visitor) and convey both the information that determines where they would walk and the beauty which is the primary aim of the visit. This stage has not been investigated in this study. The beta processes are defined as the period of contact and the immediate consequences thereof and the gamma processes are the response of the plant (or coral) to the changes produced by the beta processes. These last two processes assessed by means of immediate damage in the corals, or their resistance; their survival after damage (tolerance) and their ability to grow back to the original condition (resilience).

These three qualities were defined more precisely by Kay & Liddle (1983).

Resistance, the amount of force or number of impacts required to produce breaks in the coral skeleton or a specified amount of polyp damage and death.

Tolerance, the probability of survival of a fragment or colony after a given amount of damage.

Resilience, the ratio of growth rate of a colony or fragment after a given amount of damage to the growth rate of an undamaged colony or fragment.

These terms have been used many times in the extensive literature on stability and disturbance and while we do not propose to review this literature it is pertinent to consider two examples. Our usage is nearest to that of Grime (1979) who distinguishes 'between inertia, ie. resistance of the undisturbed vegetation to change ... and resilience, ie. the ability to recover rapidly from disturbance'. Qualities which he considers increase and decrease respectively during the course of succession. Westman (1978) uses the terms in a very similar manner except that he includes 'amplitude' as a part of resilience (Table 5.1) whereas we use the term tolerance to define a rather similar quality which we do not consider as an aspect of resilience although the two processes will take place at the same time and may interact.

Table 5.1 Characteristics of resilience and examples of their application modified from Westman (1978)

Characteristic	Definition	Example 1: A metal coil	Example 2: Ecosystem subjected to oil spill	Liddle and Kay
Inertia	resistance to change	force needed to stretch coil a given distance	amount of oil that must accumulate over a given area in a given time period to cause a given level of ecosystem damage (such as local extinction of species X & Y)	resistance
Elasticity	rapidity of restoration of a stable state following disturbance	time required to spring back to initial size after stretching a given	time required to recover initial structure or function following ecosystem damage (eg. restoration of populations X & Y)	resilience
Amplitude	zone from which the system will return to a stable state deformed	distance beyond which coil cannot be stretched without being permanently	maximum amount of oil that can accumulate in an area such that damage sustained can be fully repaired (eg. restoration of populations X & Y)	tolerance limits
Hysteresis	degree to which path of restoration is an exact reversal of path of degradation	degree to which region temporarily occupied by coil in springing back differs from region through which coil moved during stretching	degree to which pattern of secondary succession is not an exact reversal of the pattern of retrogression experienced following impact (eg. were the last species to die the first ones to return?)	Not defined
Malleability	degree to which stable state established after disturbance differs from the original steady state	degree to which stretched coil remains stretched after deforming force is removed	degree to which new climax ecosystem resembles the initial climax state (eg. how closely do the species composition and equitability of new climax state resemble the old?)	Not defined

The overall effect of human trampling on an area will depend on the variations in the responses of the species in that area. Given a knowledge of the behaviour of species or species groups, which are common in the area being considered the overall effect of reef walkers could be predicted. The measurable quantities that can be used to define resistance, tolerance and resilience of corals are:

1. the result of direct physical forces on colonies causing a) damage to the skeleton; and b) damage to the polyps (resistance);

2. the survival (tolerance) and growth rate (resilience) of fixed coral colonies which have been damaged;

3. the survival (tolerance) and growth rate (resilience) of detached coral fragments;

4. growth rate of undamaged colonies (standard or control);

5. settlement of spat creating new colonies (resilience of population).

The resistance, tolerance and resilience model provides a simple language and quantitative base, firstly, for assessing and comparing various species or patterns in response to trampling at the colony level and, secondly, for part of the model describing the effect of trampling on reef flats of various compositions. This model can be summarised by the following preliminary equation.

$$C_t+1 = A^x d + B^y e$$

C_{t+1} = cover of selected coral species one unit of time after trampling at a specific intensity.

A = the amount of attached coral remaining in area after damage (the result of its resistance).

B = the detached portions that remain on the path and the amount of coral fragments washed in after damage.

x = the survival rate (tolerance) of A

y = the survival rate (tolerance) of B

d = the recovery rate (resilience) of A

e = the recovery rate (resilience) of B

5.1.2 Resistance of corals

Each species of biological organism has a certain range of size and form. The actual form of an individual is dictated by its genetic make-up and by its interaction with the environment. Corals are no exception to this rule, although the range of form of the colonies of corals grouped in any one species is often much greater than most non-colonial animals. The physical shape of a colony is maintained by its aragonite skeleton and has been reached by an interaction between the genetic control of the growing polyps and the environment, including the physical forces of moving water (Vosburgh 1976, 1982; Chamberlain & Graus 1975; Bottjer 1980; Chamberlain 1978; Graus, et al 1977) and, in turbulent conditions, air flow (Chamberlain 1978), predatory animals (Hutchings 1983) and the physiological effects of prolonged exposure to air and rainwater.

The resistance of a coral to the physical forces that are imposed on it depends on its shape and size, and the mechanical properties of the coral material (Chamberlain 1978; Vosburgh 1982). It seems probable that the same factors will affect the resistance of coral to trampling, although the mechanical forces may be applied in a different direction from those normally applied by hydraulic factors, and are likely to be concentrated on quite small areas of the skeleton.

The dynamic forces exerted by the human foot in normal walking on a level surface may be up to 57 000 g cm^{-2} (Harper, Warlow & Clark 1961). In general, the massive (or encrusting) forms of coral are better able to withstand mechanical stresses than branched colonies, their advantage being in the form rather than the properties of the material (Chamberlain 1978). Branched colonies which have shorter branches will be subject to lower bending moments at similar imposed forces than those with longer branches. Corals with thicker branches will be able to resist greater strain than those with thinner branches if all other factors are equal. Those corals that have holes in their skeletons due to boring bivalves or worms will also have reduced strength due to these holes.

For the purpose of our investigation we have redefined meausres of the resistance of coral to trampling (Kay & Liddle 1983) as the amount of force required to produce breaks in the coral skeleton or the amount of polyp damage or death caused by a constant number of impacts. Of these two approaches, the first specifies a certain amount of damage and a variable amount of force which is required to cause that damage in different coral colonies, (and the second specifies a constant amount of force and a measurement of the variable amount of damage caused by that force to the different coral colonies). The first experiment described here follows the first form, with constant damage and variable force, and the experiment on massive coral, takes the second form, with constant force and variable damage.

5.1.3 Tolerance (mortality after damage) of corals

The survival of damaged coral presumably depends upon the extent and nature of the damage, the local environment and the species involved. Tolerance may depend on the ratio of area of damage to area of whole colony because larger remaining living area will have more resources for repair (Connell 1973). Death may be due to long exposure to air, either in sun or heavy rain, by floods of fresh water, especially if accompanied by heavy sedimentation, by stoppage of normal water circulation and by severe wave action during storms (Stoddart 1969). Local death due to competition or natural enemies (Connell 1973). His records over a period of 6 to 8 years indicated that colonies over 81cm^2 rarely died but the smaller colonies between 1 and 40cm^2 have a 44% death rate per year and the south crest and on the inner reef flat of Heron Island, however, on the north crest which is very exposed the percentage rose to 63%.

Tolerance of coral seems only to have been measured for detached fragments, either accumulations of storm damaged fragments or artificially detached coral, usually attached to a grid on the reef or sea floor. Knowlton et al (1981) followed survivorship of colonies of *Acropora cervicornis* detached by a Carribean hurricane and found that 98% of the colonies died after 5 months. 46% of the large (<37.6cm) fragments called *Acropora palmata* detached during a hurricane, survived for a period of four months and in the same investigation the survival rate of all species was recorded as 39% (Highsmith et al 1980). They also found that surival was strongly size dependent, a feature which appeared in Connell 1973 data for long term survival of colonies on Heron Island Reef (see analysis in Highsmith 1982). Two common Hawaiian species *Porites compressa* and *Mantipora verrucosa* were transplanted by Maragos (1974) to grids in 3 locations and monitored for 18 months. The results showed that survival was very dependent upon the type of site with greatest tolerance in the calmest, least polluted situation where over 80% survived, although they did have all algal growth removed from their surfaces during the 18 month period.

5.1.4 Resilience (recovery after damage) of corals

Resilience or recovery after damage also seems to have only been measured on detached fragments and not on the remaining portions of attached colonies. However, undamaged colonies may grow up to 25cm year^{-1} (J. Oliver Personal Communications) but this depends very much on where it is growing. *Acropora palmata* has been recorded to grow 8cm year^{-1} (Bak 1976, Gladfleter et al 1978) but one of our test species *Pocillopora damicornis* is recorded as having determinate growth with the rates declining as the colonies become larger (Moragos 1972, Loya 1976). This phenomena has lead Highsmith (1980) to predict that "long-term reef calcification rates may be higher in location with periodic disturbances of low to moderate intensities". However this is dependent upon settlement of larvae and new young colonies with high growth rates. Growth rates of detached portions were shown to be very dependent upon location and species (Maragos 1974).

It should be pointed out that much of the recovery literature deals with recolonisation and subsequent community growth and diversification after natural disturbance rather than the resilience of colonies or fragments after being damaged.

5.1.5 The experiments

The experiments described in this chapter were undertaken to provide data for the model. As one experiment may provide information for more than one quality the methods and results of all experiments are described together and the discussion is then ordered according to the relevant qualities. For example, in the case of resistance, data was derived from the long term experiments (Chapter 2) and the separate experiment and *Porites lutea* and from the laboratory experiment.

Four species were chosen for these experiments, *Acropora millepora*, *Pocillopora damicornis*, *Acropora palifera* and *Porites lutea*. *Acropora millepora* has a corymbose colony morphology, *Pocillopora damicornis* has colonies with clustered branchlets, *Acropora palifera* has short knotty or wedge shaped branches and *Porites lutea* has massive colonies. According to the morphology classification scheme described in Chapter 2 these species, presented in the order above, range from rather high vulnerability to trampling damage to very low (Table 2.5). Additionally they are all common reef flat species along the Great Barrier Reef.

5.2 BREAKING EXPERIMENT

5.2.1 Aim

In this experiment, we have measured the breaking strength of the branches of three species of coral, *Acropora millepora*, *A. palifera* and *Pocillopora damicornis*. Our aim was to determine the actual strength of the coral skeleton and to find the effect of the different cross section areas of the branches on their resistance to breaking. The massive coral *Porites lutea* was not used in this experiment.

Plate 5.2 Profiles of branches of *Acropora millepora*, *Pocillopora damicornis*, *Acropora palifera* and *Porites lutea* in silhouette shown after breakage from parent colony.

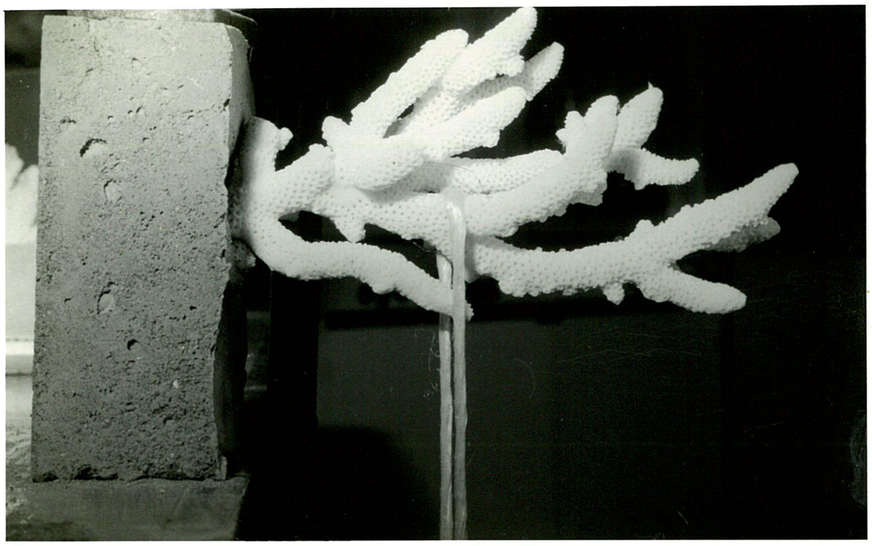


Plate 5.1 A section of colony of *Acropora millepora* set in rectangular block for branch-loading experiment.

5.2.2 Methods

Portions of colonies of the three species of branching coral were cleaned, dried, and their bases set in rectangular, cement blocks (Plate 5.1). This held the branches firmly at a known point along their length and allowed them to be positioned so that the branch being tested was horizontal. A container was suspended at a point 5cm from the base of the branch so that the branch formed a cantilever beam. Sand was then poured slowly into the container until the branch broke. With the stronger corals, it was necessary first to add lead weights to the container before sand was poured in. The weight of the container (the load), the distance from the point at which the container was suspended to where the break occurred on the branch, and the cross-sectional area at the break, with and without holes caused by boring bivalves, were all recorded.

5.2.3 Results and calculations

The records of all measurements are given in Appendix 5.1. The mean load required to break the branches was highest for *Acropora palifera* and lowest for *A. millepora* (Fig. 5.1a). The cross-section area of the branches at the point of break which was approximately at right angles to the branch in all cases, also followed the same order of magnitude (Fig. 5.1b). In both cases, the difference between the two *Acropora* species was statistically significant, but *Pocillopora damicornis* was only significantly different from *A. millepora* (Table 5.2).

Table 5.2 Probability (p) of differences between the load at breaking point and cross-section area of the different species (t test) NS: not significant at 5% level

	Acropora millipora	*Pocillopora damicornis*
<u>Load at breakage</u>		
Pocillopora damicornis	0.001	-
Acropora palifera	0.001	NS
<u>Cross-section area</u>		
Pocillopora damicornis	0.001	-
Acropora palifera	0.01	0.01

So that the effect of colony form and skeleton strength on the coral's resistance to damage could be further understood and used for predictions on other corals, the relationship between the weight required to break the branches and their remaining cross-section area was investigated (Fig. 5.2). While there was a statistically significant correlation for all the data combined, they only held good for *Acropora millipora* and *Pocillopora damicornis* when analysed separately (Table 5.3). Adjustment of the cross-section area to what it would have been if the holes caused by the borers had not been present improved the amount of variance accounted for by the

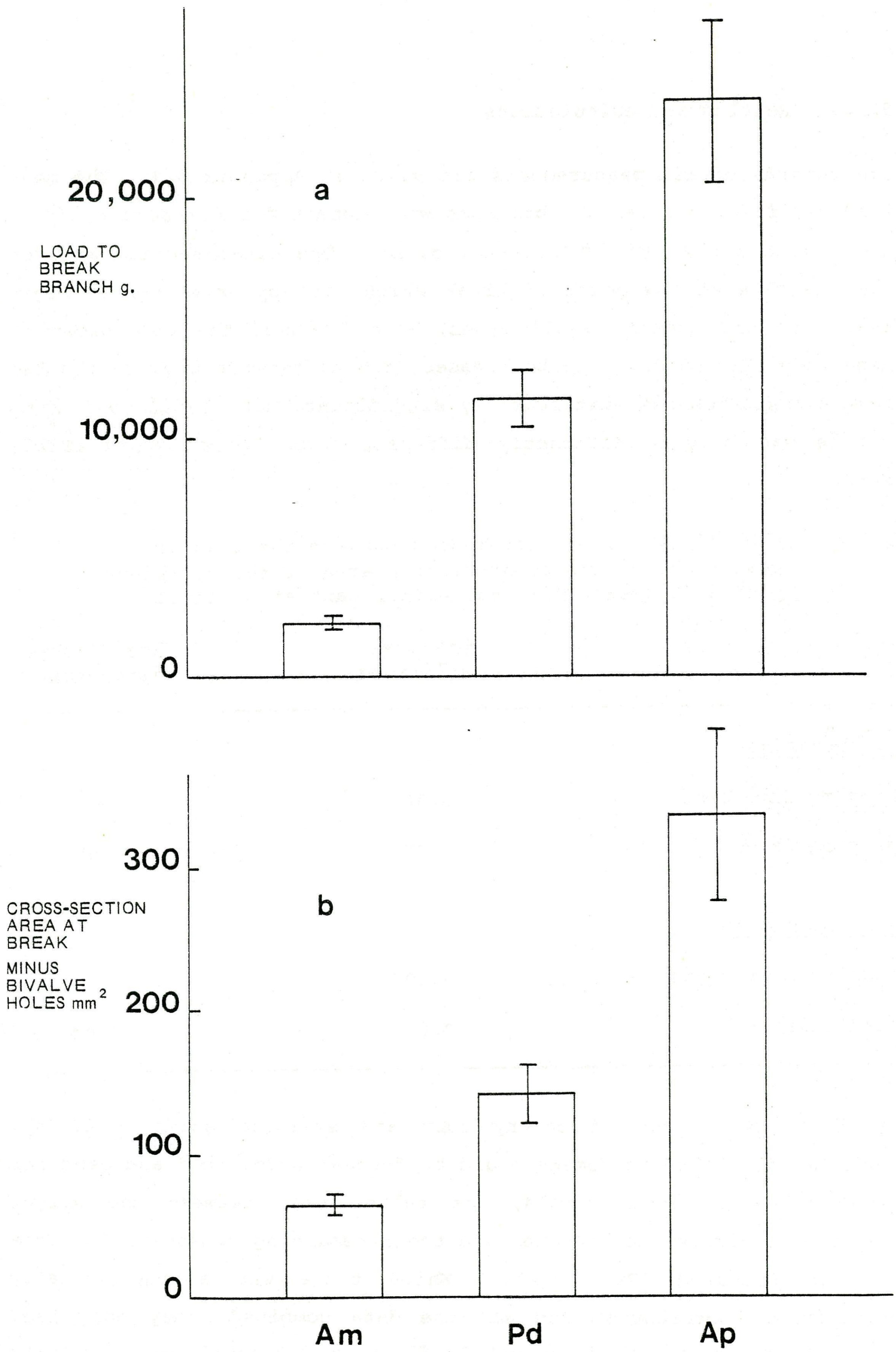


Figure 5.1 a) Load at time of break; b) Cross-section area at point of break. Am, *Acropora millepora*; Pd, *Pocillopora damicornis*; Ap, *Acropora palifera*. I, two standard errors.

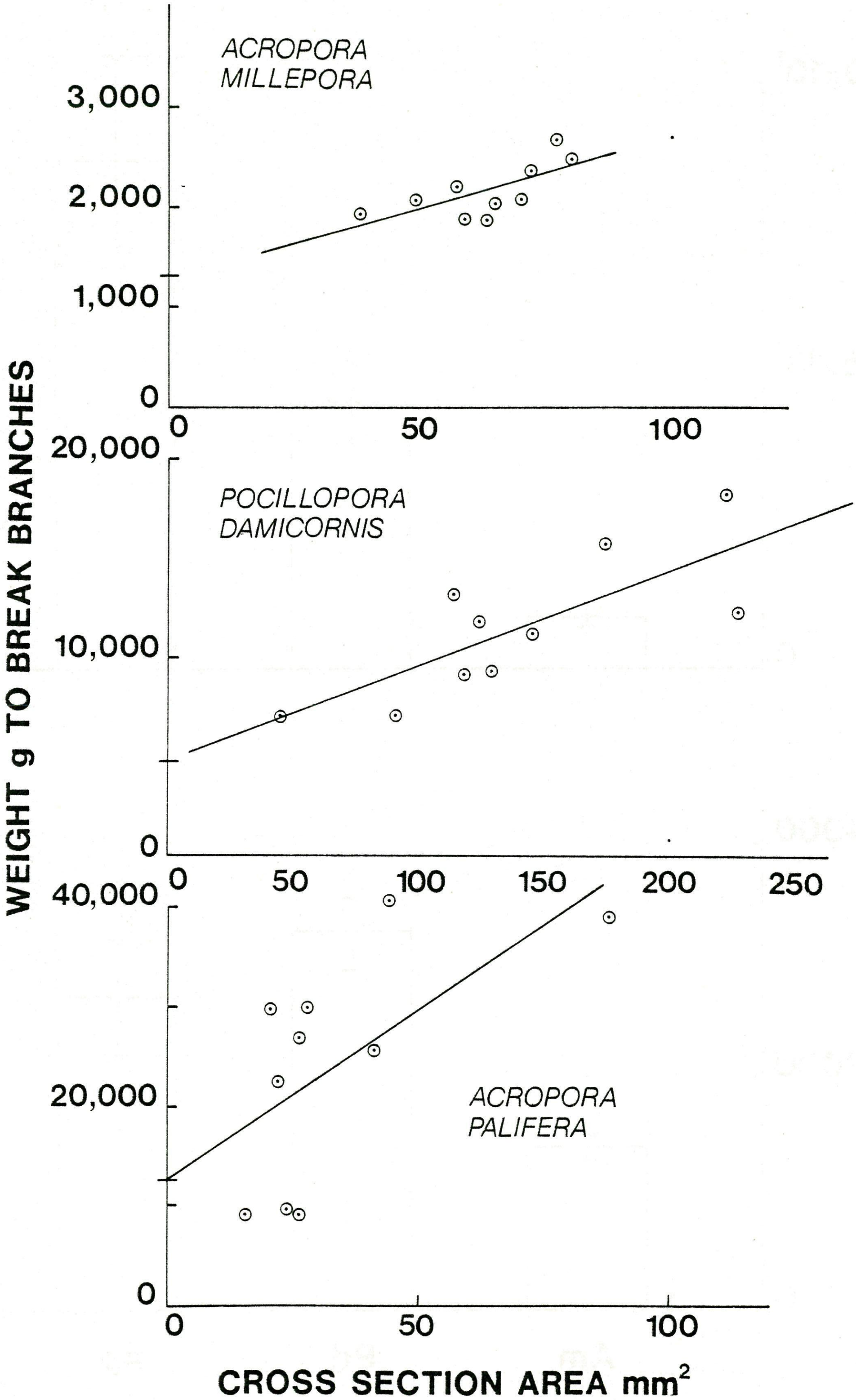


Figure 5.2 The relationship between the area of cross-section minus the area of any included bivalve holes, at position of break with the load that was required to break those particular branches in grams. A, *Acropora millepora;* B, *Pocillopora damicornis;* C, *Acropora palifera.*

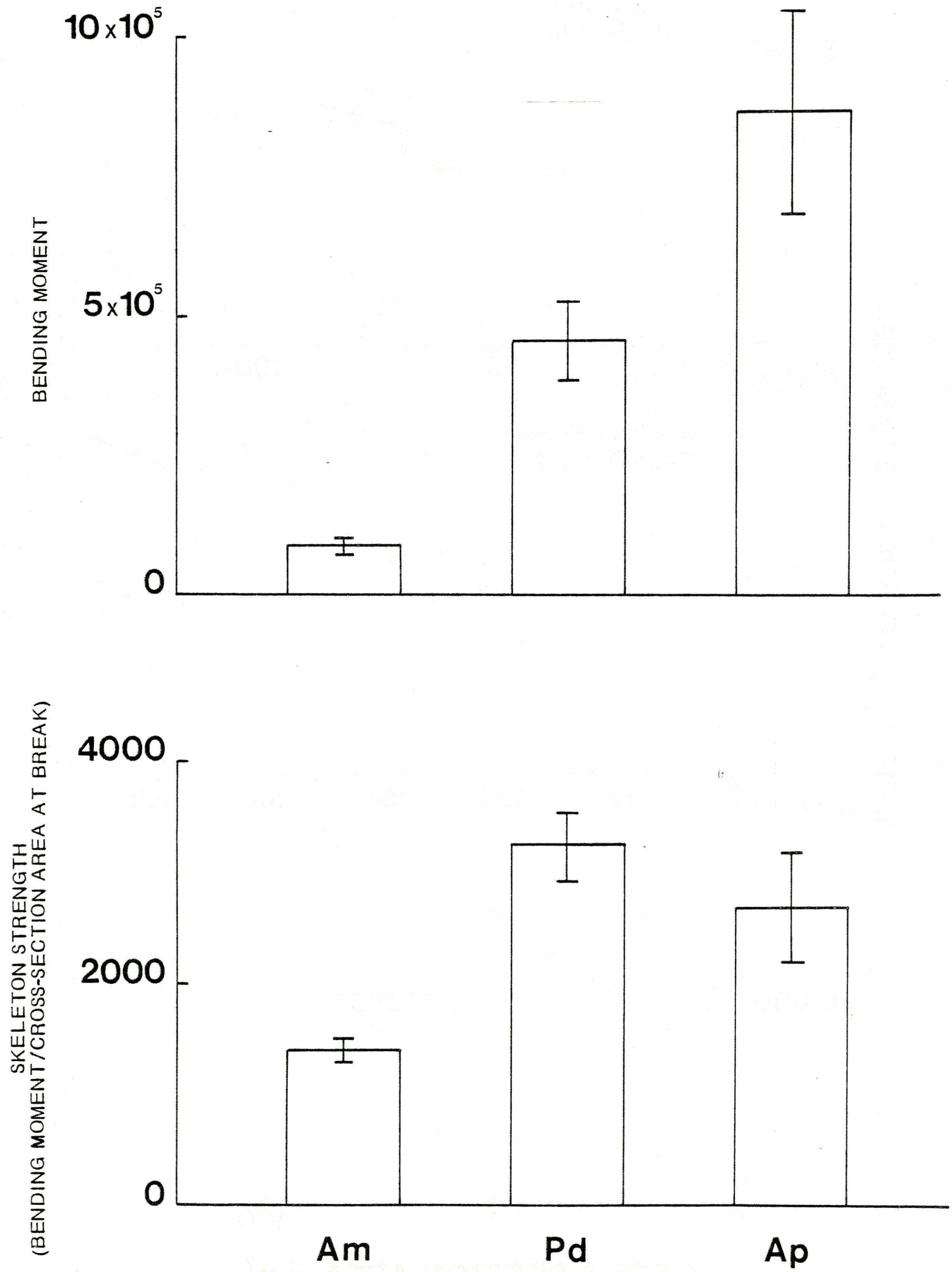


Figure 5.3 Bending moment and force applied at the time of break divided by the cross-section area. Am, *Acropora millepora*; Pd, *Pocillopora damicornis*; Ap, *Acropora palifera*. I, two standard errors.

Table 5.3 r values and probability of regression equations.

Y axis	X axis	r^2	Probability	Constant	Regression coefficient
All species					
Weight	Distance to break	0.00034	0.92	13318	-17.82
"	Cross-section area	0.68*	< 0.0000	2671	55.23
"	Distance (D) plus cross-section (C)†	0.69*	< 0.0000	6184	-95.88 (D) 55.88 (C)
Acropora millipora					
Weight	Distance to break	0.36	0.066	1583	15.25
"	Cross-section area	0.45*	0.034	1295	14.36
"	Distance (D) plus cross-section (C)†	0.46	0.114	1304	4.82 (D) 11.13 (C)
Pocillopora damicornis					
Weight	Distance to break	0.28	0.114	5249	164.75
"	Cross-section area	0.61*	0.008	4654	48.62
"	Distance (D) plus cross-section (C)†	0.61*	0.038	4719	-3.49 (D) 49.11 (C)
Acropora palifera					
Weight	Distance to break	0.07	0.45	16051	233.72
"	Cross-section area	0.40	0.051	12677	34.11
"	Distance (D) plus cross-section (C)†	0.40	0.17	11379	47.82 (D) 33.05 (C)
MODIFIED DATA FOR WHOLE OF CROSS-SECTION AREA					
All spp					
Weight	Cross-section area	0.68*	< 0.0000 (No change)	2281	55.77
Pocillopora damicornis					
Weight	Cross-section area	0.70*	0.0026 (Better)	2863	55.7
Acropora palifera					
Weight	Cross-section area	0.39	0.055 (Worse)	12720	33.81

* indicates statistically significant equations $p < 0.05$

† The two factors combined in multiple regression equation

regression in the case of *Pocillopora damicornis*, but reduced it for *Acropora palifera* (Table 5.3). When the distance between the suspension point and the point at which the branches broke was added to the equation, there was a slight improvement in the variance accounted for in all species (Table 5.3).

Calculations were made of the strength of the branches, allowing for the distance between the suspension point and the point of the breaks,

Load x distance = bending moment A.

and the strength of the material making up the skeleton

Bending moment/cross-section area at break B.

The branches of *Acropora palifera* were stronger than those of *Pocillopora damicornis* and *Acropora millepora* (Fig. 5.3a), but the skeleton strength was similar between *Acropora palifera* and *Pocillopora damicornis* (Fig. 5.3b), and lower for *Acropora millepora*, which was significantly different from the other two species (Table 5.4).

Table 5.4 Probability (p) of differences between the bending moment (load at breaking point) and bending moment/cross-section area of the different species (t test). NS, not significant at the 5% level.

	Acropora millipora	*Pocillopora damicornis*
<u>Load at breakage</u>		
Pocillopora damicornis	0.001	-
Acropora palifera	0.01	NS
<u>Cross-section area</u>		
Pocillopora damicornis	0.001	-
Acropora palifera	0.05	NS

5.3 TRAMPLING EXPERIMENT WITH *PORITES LUTEA*

5.3.1 Aim

This experiment was designed to determine the damage caused by different levels of trampling on the massive colonies of *Porites lutea* and the subsequent survival and regrowth of damaged polyps.

5.3.2 Methods

5.3.2a Field layout and experimental design

Sixteen irregularly hemispherical colonies of *Porites lutea* were selected in an irregular shallow channel running from the inner to outer reef flat in an area on the southwest side of the island 200 metres east of the wreck (Figure 1.9). These were divided into 4 groups of four which were situated at different distances from the island. A control and three trampling treatments were chosen for the experiment as described in Table 5.5. A colony within each group was randomly allocated to one of these treatments giving four replicates in all.

Table 5.5 The experimental treatments in the trampling experiment with *Porites lutea*

Treatment	Number of Footsteps
Control	0
Low Impact	5
Medium Impact	20
High Impact	80

Four high tensile nails 2cm in length were hammered into each colony at the corners of a square approximately 25cm by 25cm. These areas were as near to the horizontal plane as the topography of the colony surfaces permitted. Each colony was then subjected to the selected treatment by stepping onto the squares and then off, that is walking over the colony the required number of times. The experiment was set up on the 19th and 20th of May 1983 and measurements were made immediately after trampling, 3 or 4 days later and 71 to 74 days later.

5.3.2b Data collection and analysis

Measurements were made by placing ten 20 cm transects about 1cm to 1.5cm apart across the impact area within the nails and measuring the intercept length of the various categories of surface condition (see Table 5.6 and Plate 5.3) along each one. For each colony these measurements were used to calculate the percentage of the impacted area which was in a given condition.

The data from the experiment was not normally distributed so non-parametric tests were used for analysis. Additionally the four groups of colonies were treated as blocks due to the gradient in environmental parameters moving from inner to outer reef flat along the sandy channel.

5.3.3 Results

The immediate result of trampling on the colonies was the production of copious mucous by the polyps which were disturbed. The sand which had been kicked up by the trampling activity was then trapped by this mucous on the area which had been stepped on. After two or three days this sand and mucous layer broke up revealing damaged polyps, lesions in the tissue between polyps and bleached empty corallites. Trials with test colonies showed that the thick layers of sand still remaining at this stage covered empty corallites. Table 5.6 provides a description of the conditions of the colony surfaces encountered in the experiment.

The impact area differed significantly between trampling treatments with that for the high impact treatment being largest and that for

Plate 53 A Porites lutea colony after trampling.

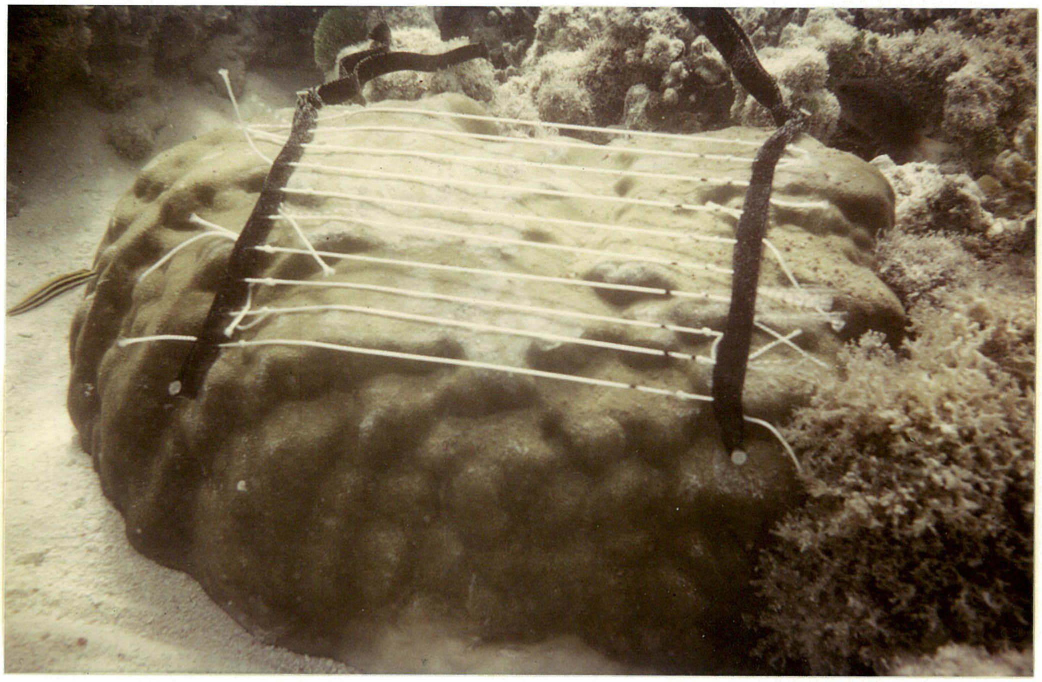


Table 5.6 The appearance and condition of the surface of *Porites lutea* colonies

Surface Condition	Description
Undamaged	Surface unobscured, no breaks or lesions in tissue of polyps or that between them.
Impact area	Sand trapped in mucous obscuring polyps.
Damaged	Breaks in live tissue between polyps which is often completely removed. Polyps very withdrawn into corallites and often visibly damaged with tentacles missing.
Dead	Either corallites are visibly empty or covered by sand mucous and filamentous algae.
Freshly scarred	Surface of colony bitten and scraped by parrot fish.
Smothered	Sand collected in depressions with no living tissue beneath.

the low impact treatment being smallest (Figure 5.4, Tables 5.7 and 5.8). However the short term damage resulting from the trampling was not always significantly different between treatments. The amount of damaged but living surface tissue recorded after three of four days did not differ significantly between treatments despite the trend in the data suggesting that a greater number of footsteps causd more of this type of damage (Figure 5.4, Tables 5.7 and 5.8). Also the proportion of the surface which was totally dead at this stage was equivalent for the low and medium impact treatments although it was clearly significantly greater in the high impact treatment (Figure 5.4, Tables 5.7 and 5.8). The surfaces of the untrampled colonies were not damaged in the ways considered above (Figure 5.4) however the proportion of dead surface in the low impact treatment was not quite significantly greater than that in the control treatment (Table 5.8).

After 71 to 75 days most of the damaged but living colony surfaces had healed (Figure 5.4) and the amount of undamaged colony surface

Table 5.7 Results of Friedman's 2-way ANOVA comparing surface condition between treatments. X^2r is the test statistic, p is the probability that the differences between treatments were observed by chance N = R = 4

Surface Condition	Days after Trampling: 0		3 or 4		71 to 74	
	Xr^2	p	x^2r	p	x^2r	p
Undamaged	12	.000072*	12	.000072*	7.1	>.054 <.068
Impact area	12	.000072*	—		—	
Damaged	—		11.1	.00094*	—	
Dead	—		10.43	.0027*	9.87	<.0069*
Freshly scarred	5.4	.158	3.3	.398	8.3	<.0033*
Smothered	0.6	.928	0.9	.9	2.4	.524

* significant at the 5% level

was equivalent between the control treatments and the lower two impact treatments (Tables 5.7 and 5.8). It was however, still significantly reduced in the high impact treatment compared to the other three due to the presence of relatively large areas of sand and algae encrusted skeleton on the high impact colonies which made up a significantly greater proportion of the colony surfaces in this treatment compared to the other three treatments (Figure 5.4, Tables 5.7 and 5.8).

These areas were also present on the colonies of the lower two impact treatments but only on the colonies of the medium impact treatment was the percentage of the surface they made up significantly greater than that on the control colonies (Figure 5.4, Tables 5.7 and 5.8).

Table 5.8 Results of Mann-Whitney U-tests comparing the percentage of the colony surface in a given condition between pairs of treatments at different sample dates. n1 = n2 = 4. U is the test statistic and p is the probability that the differences between treatments were observed by chance.

		Treatment Comparison											
Days after Trampling	Surface Condition	C vs 5		C vs 20		C vs 80		5 vs 20		5 vs 80		20 vs 80	
		U	p	U	p	U	p	U	p	U	p	U	p
0	Undamaged	0	.014*	0	.014*	0	.014*	0	.014*	1	.029*	0	.014*
	Impact area	0	.014*	0	.014*	0	.014*	0	.014*	1	.029*	0	.014*
3 and 4	Undamaged	0	.014*	0	.014*	0	.014*	2	.057	0	.014*	0	.014*
	Damaged Δ	0	.028*	0	.028*	0	.028*	2	.114	1	.058	4	.342
	Dead	2	.057	0	.014*	0	.014*	6	.343	0	.014*	0	.014*
71 to 75	Undamaged	5	.243	5	.243	0	.014*	8	.557	0	.014*	0	.014*
	Dead	6	.343	0	.014*	0	.014*	0	.014*	0	.014*	0	.014*
	Freshly scarred Δ	.057	.2	6	.686	0	.028*	5	.486	0	.028*	0	.028*

* significant at the 5% level;

Δ indicates tests are 2-tailed, otherwise they are 1-tailed.

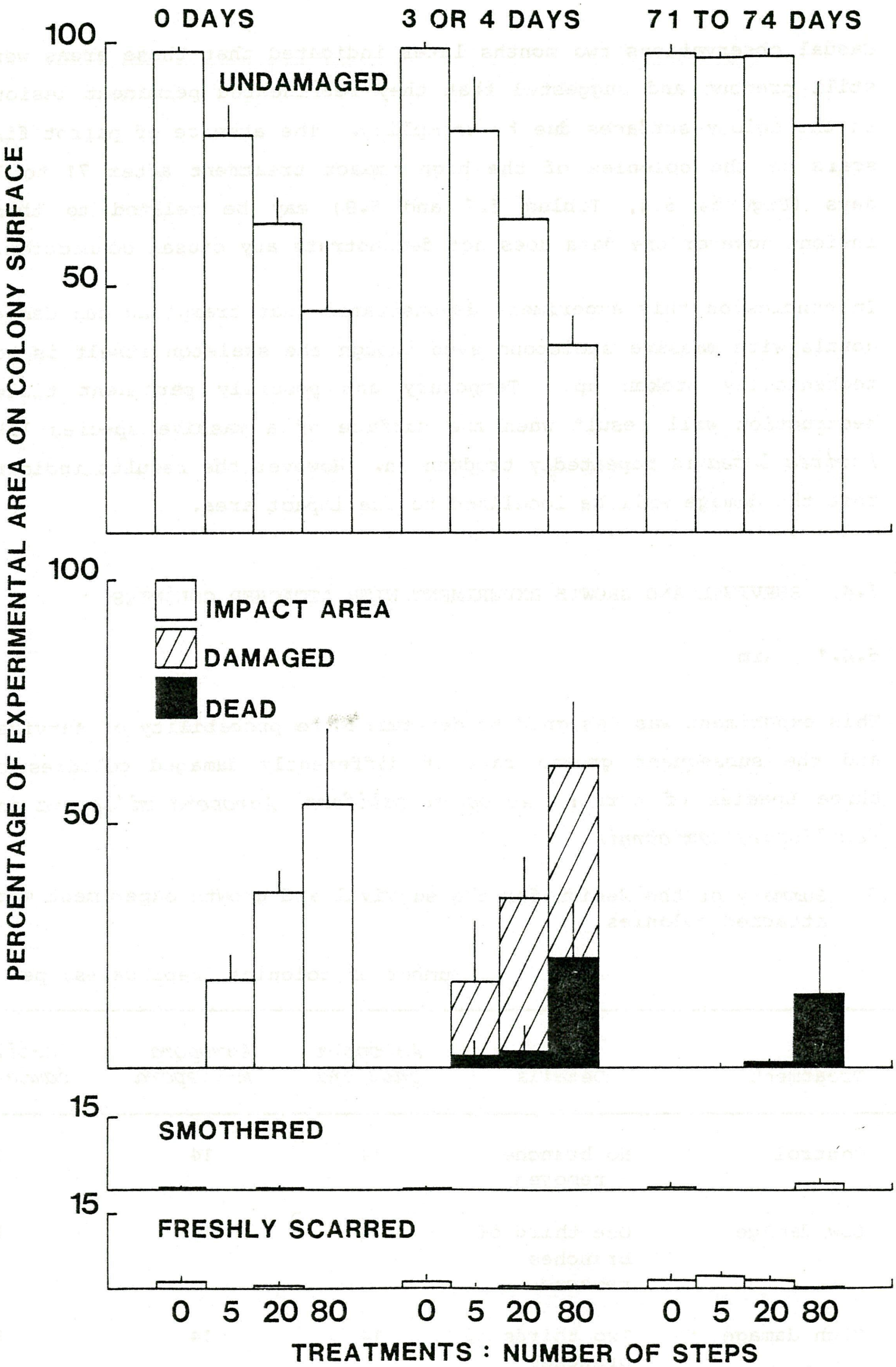


Figure 5.4 The percentages of the experimental areas on the surfaces of the *Porites lutea* colonies in a given condition during the experiment.

Casual observations two months later indicated that these areas were still present and suggested that they represented permanent lesions in the colony surfaces due to trampling. The absence of parrot fish scars on the colonies of the high impact treatment after 71 to 75 days (Figures 5.4, Tables 5.7 and 5.8) may be related to these lesions however the data does not demonstrate any causal connection.

In conclusion this experiment demonstrates that trampling can damage corals with massive skeletons even though the skeleton itself is not mechanically broken up. Temporary and possibly permanent tissue destruction will result when the surface of a massive species like *Porites lutea* is repeatedly trodden on. However the results indicate that the damage will be localized to the impact area.

5.4 SURVIVAL AND GROWTH EXPERIMENT WITH ATTACHED COLONIES

5.4.1 Aim

This experiment was designed to determine the probability of survival and the subsequent growth rate of differently damaged colonies of three species of coral: *Acropora palifera, Acropora millepora* and *Pocillopora damicornis.*

Table 5.9 Summary of the design for the survival and growth experiment with attached colonies

			Number of colonies (replicates) per species		
Code	Treatment	Details	*Acropora palifera*	*Acropora millepora*	*Pocillopora damicornis*
C	Control	No branches removed	14	14	14
1	Low damage	One third of branches removed	14	14	14
2	High damage	Two thirds of branches removed	14	14	14
3	Complete damage	All branches removed	14	14	14

5.4.2 Methods

5.4.2a Field methods and experimental design

On the outer reef flat in an area adjacent to the long-term trampling transects (Figure 1.9) 56 colonies of each species were selected for the experiment. They ranged in horizontal breadth and width from 15cm to 30cm and were not exposed to the air during low spring tides. All colonies appeared healthy and undamaged at the start of the experiment.

The design for this experiment is summarized in Table 5.9. There were four treatments representing a control and three levels of damage and 14 replicates for each treatment which were allocated to colonies in the field in the following manner. The first four colonies which were encountered were allocated to treatments C, 1, 2 and 3 respectively according to the order in which they were found. This pattern was then repeated for each group of four colonies after that until all 56 colonies had been located for each species.

When each colony was selected it was damaged appropriately and tagged with a dymo tape label secured to its base with 25lb breaking strain fishing line. In the high and low damage treatments the branches which were removed were selected so that those remaining were distributed evenly over the colony. A heavy hammer and chisel were used to knock branches off *Acropora palifera* colonies and a pair of scissors or a light hammer were used to remove branches from *Acropora millepora* and *Pocillopora damicornis* colonies.

The experiment was set up during the second week of December 1982 and the survival of the colonies and the percentage of the skeleton which had been covered by new tissue after it had been exposed by the damage treatments was recorded two months later during the second week of February 1983. The latter measurement was made subjectively by estimating the proportion of each broken stump which was covered by living tissue.

In addition the growth of branches on five of the colonies in the control, low damage and high damage treatments were recorded for each species as follows. At the beginning of the experiment a piece of fishing line (about 10lbs breaking strain) was tied firmly around the selected branch and the distance between the tip of the branch and the fishing line was meaured with a pair of plastic calipers. This measurement was made again 10 months later during the second week of October 1983. The difference between the two measurements was expressed as the growth of the branch for 10 months.

On each colony four intact branches were chosen for growth measurements and in the case of damaged colonies four broken branches were considered as well. The most easily measured branches were selected with the restriction that the growing end was not obstructed and where possible that each branch came from a different quarter of the colony. The design of this part of the experiment is shown in Table 5.10.

5.4.2b Data processing and analysis

For each colony involved in the growth measurements an average growth rate was calculated for intact branches and one for damaged branches using the data from the four individual branches. This average growth rate is used to calculate the means and standard deviations in all treatments and for the statistical comparisons between groups reported in the following section.

The data produced by this experiment was not always normally distributed so a non-parametric test the Mann-Whitney U-test (Siegel 1956) was used for analysis.

5.4.3 Results

All of the colonies which could be found two months after the experiment began were alive (Table 5.11) and appeared to be healthy with two exceptions. One *Acropora millepora* colony in the high damage treatment was broken up into several smaller pieces and 80% of another *A. millepora* colony in the complete damage treatment had died. Nevertheless the results show that colonies of the three species have a 100% probability of survival when subjected to damage in the range covered by this experiment.

Table 5.10 Summary of the design for the part of the survival and growth experiment with attached colonies which investigates growth rates

Treatment	Number of colonies per species	Number of branches measured per colony: Undamaged	Number of branches measured per colony: Broken
Control	5	4	
Low damage	5	4	4
High damage	5	4	4

Table 5.11 Results from the survival and growth experiement with attached colonies showing the percentage survival of undamaged and damaged colonies two months after the damage was inflicted.

	Number of colonies found				Percentage of colonies which survived			
Treatment:	C	1	2	3	C	1	2	3
Acropora palifera	14	14	14	14	100	100	100	100
Acropora millepora	13	14	12	13	100	100	100	100
Pocillopora damicornis	14	12	13	12	100	100	100	100

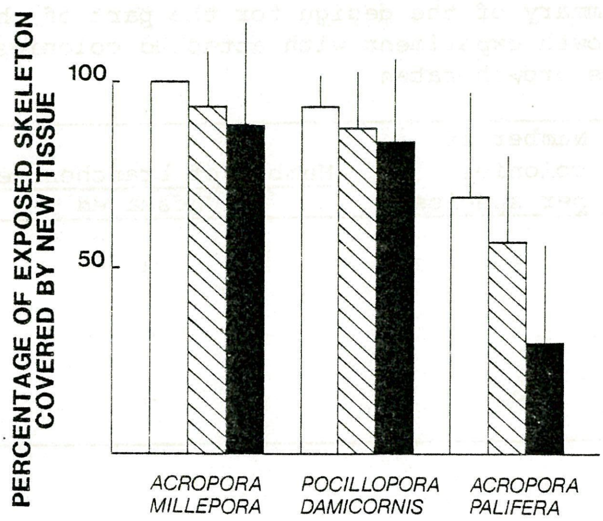


Figure 5.5 Mean (bar) and S.D. (line) of the percentage of the exposed skeleton which had been covered by new tissue growth two months after the damage was inflicted in the survival and growth experiment with attached colonies.

bars		treatment
open	:	low damage
diagonal lines	:	high damage
solid	:	complete damage

In contrast the data in Figure 5.5 suggests that the three species were unable to heal the damaged portions of their colonies equally fast and that the rate of healing was slower in the higher damage treatments. The mean percentage of exposed skeleton which was covered by new tissue growth in two months was greatest for *A. millepora* followed by *P. damicornis* then *A. palifera* in all damage treatments (Figure 5.5). Also for all three species this percentage was highest in the low damage treatment and lowest in the complete damage treatment (Figure 5.5). Overall, results of the statistical comparisons shown in Table 5.12 support these trends although differences between means were not always significant.

Appraisal of the growth rate data depicted in Figure 5.6 suggests that the growth of intact branches on colonies of *Acropora palifera* and *Acropora millepora* was not decreased by either of the damage treatments and that there were no differences between the two species

Table 5.12 Results of Mann-Whitney U-tests used to compare the percentage of exposed skeleton which has been covered by new growth between species and treatment groups. U is the test statistic, p is the probability that the differences between species were observed by chance.

COMPARISON						
	Acropora palifera vs *Acropora millepora*		*Acropora palifera* vs *Pocillopora damicornis*		*Acropora millepora* vs *Pocillopora damicornis*	
Treatment Group	U	p	U	p	U	p
Low damage	28	<.002*	57	.1>p>.05	28	<.002*
High damage	0	<.002*	24	<.002*	84	>.1
Complete damage	33.5	<.02*	20.5	<.002*	58	>.11
	Low damage vs high damage		Low damage vs complete damage		High damage vs complete damage	
Species	U	p	U	p	U	p
Acropora palifera	70	>.1	33	<.02*	45.5	<.02*
Acropora millepora	49	.1>p>.05	56	.1	96	>.1
Pocillopora damicornis	67	>.1	53	>.1	64	>.1

* significant at the 5% level. The test is 2-tailed;

n1 and n2 range between 12 and 14 and are listed in Table 5.11

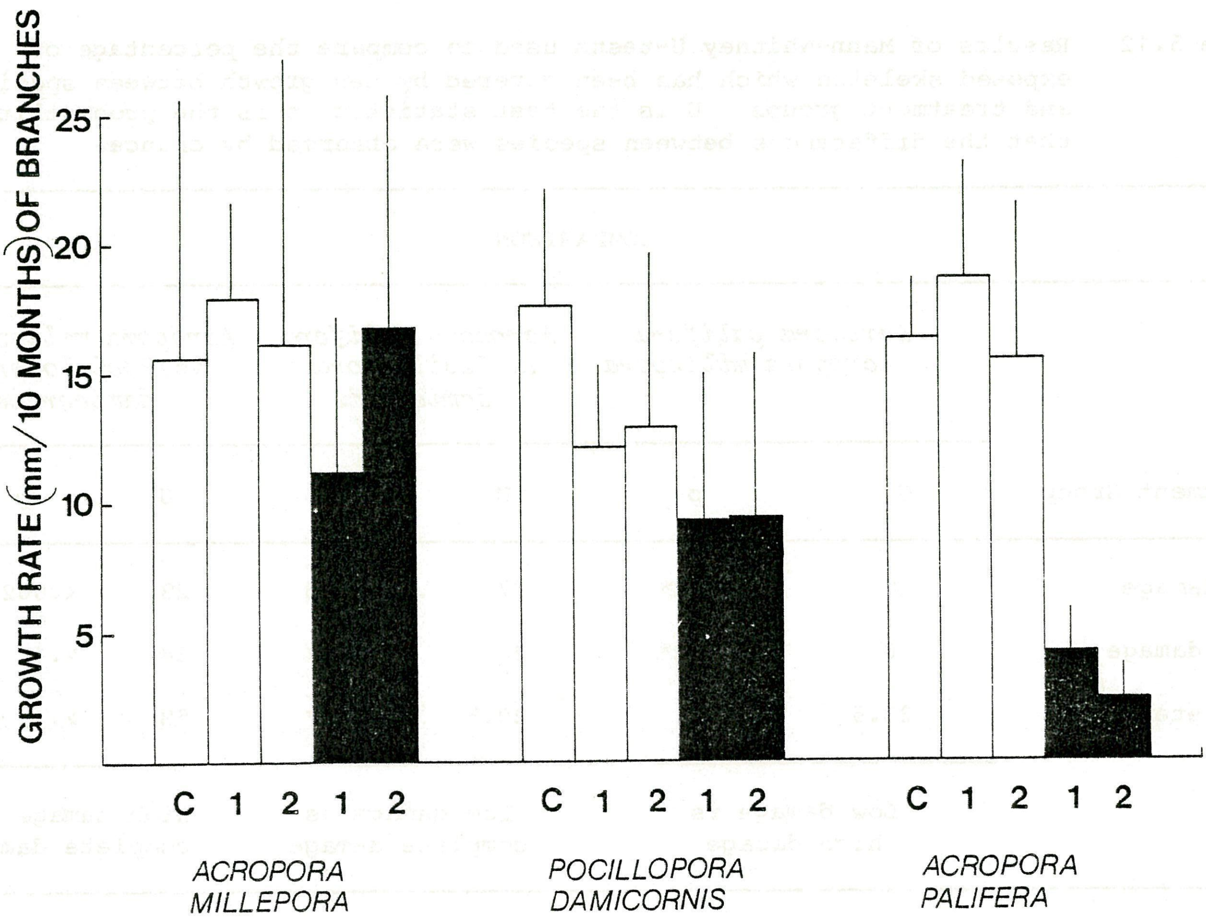


Figure 5.6 Mean (bar) and S.D. (line) of growth rate (mm/10 months) of undamaged and damaged branches on coral colonies in the survival and growth experiment with attached colonies.

open bars	:	undamaged branches
closed bars	:	damaged branches
C	:	control treatment
1	:	low damage treatment
2	:	high damage treatment

in the control and both damage treatments for this parameter. However the growth rate of intact branches on *Pocillopora damicornis* does appear to have been reduced by the damage treatments and appears lower than that for the other two species on damaged colonies. The results of statistical tests (Tables 5.13 and 5.14) support these trends except that the growth rates of intact branches in the high damage treatment did not differ significantly between species. It is also clear that the growth rates of branches on control colonies were the same for the three species (Figure 5.6, Table 5.14).

The trends in the data in Figure 5.6 also suggest that the broken branches on colonies in the two damage treatments grew much more slowly than intact branches on control colonies in the case of *Acropora palifera*, a little more slowly in the case of *Pocillopora damicornis* and at the same rate in the case of *Acropora millepora*. The results of statistical tests (Table 5.13 and 5.14) support this trend.

The growth rate of broken branches of *Acropora palifera* are significantly lower than that of broken branches of *Pocillopora damicornis* and *Acropora millepora* only in the low damage treatment

Table 5.13 Results of Mann-Whitney U-tests used to compare the growth rates of branches between treatments. U is the test statistic, p is the probability that the differences between species were observed by chance

Comparison	*A. palifera*		*A. millepora*		*P. damicornis*	
	U	p	U	p	U	p
Undamaged branches						
: Control vs low damage	9	.543	11	.842	2.5	<.05*
: Control vs high damage	13	1.0	9	.548	9	.548
: low damage vs high damage	6	.222	4	.096	10	.69
Intact branches, control vs broken branches, low damage	0	0.008*	12	1.0	3	.056
Intact branches, control vs broken branches, high damage	0	0.008*	12	1.0	3	.056
Broken branches, low damage vs broken branches, high damage	3.5	.1> <.05	12	1.0	11.5	>.821

* significant at the 5% level;

n1 = n2 = 5. The test is 2-tailed.

Table 5.14 Results of Mann-Whitney U-tests used to compare the growth rates of branches between species. U is the test statistic, p is the probability that the differences between species were observed by chance.

	COMPARISON					
Growth rate	*Acropora palifera* vs *Acropora millepora*		*Acropora palifera* vs *Pocillopora damicornis*		*Acropora millepora* vs *Pocillopora damicornis*	
	U	p	U	p	U	p
branches on undamaged colonies	11	.842	10	.69	10	.69
Intact branches on colonies in						
1. low damage treatment	11	.842	3.5	>.05 <.1	2	.032*
2. high damage treatment	6	.222	11	.222	10	.69
Broken branches on colonies in						
1. low damage treatment	0	.008*	0	.008*	8	.41
2. high damage treatment	3	.056	3.5	>.05 <.1	6	.222

* significant at the 5% level;

n1 = n2 = 5. The test is 2-tailed.

although the results suggest that they are also lower in the high damage treatment (Figure 5.6, Table 5.14). The growth rate of broken branches in both damage treatments did not differ significantly between *Acropora millepora* and *Pocillopora damicornis* colonies (Table 5.14).

Differences in the growth rates of broken branches between damage treatments were not significant for any species (Table 5.12) although the data does suggest that broken branches of *Acropora palifera* in the high damage treatment grew more slowly than those in the low damage treatment (Figure 5.6, Table 5.13).

In summary the growth rate of *Acropora millepora* was not altered by the damage treatments, however the growth rate of both *Pocillopora damicornis* and *Acropora palifera* was decreased. In the case of the latter it was clearly due to a marked decrease in the growth rate of broken branches. As the results in Figure 5.5 show, the repair of broken branches was lowest for this species. In the case of *Pocillopora damicornis* it was due to a decrease in the growth rate of both intact and broken branches.

5.5 SURVIVAL AND GROWTH EXPERIMENT WITH CORAL FRAGMENTS

5.5.1 Aim

This experiment was designed to determine the probability of survival and the growth rate of different sized and differently damaged fragments of three species of coral: *Acropora palifera, Acropora millepora* and *Pocillopora damicornis*.

5.5.2 Methods

The majority of coral fragments produced by trampling in the short-term trampling experiment reported in Chapter 3 fell within a length range of 1cm to 9cm (Figure 3.4). Accordingly we chose the following three size classes, 2cm long, 4cm long and 8cm long for this experiment. Additionally it was observed during trampling that fragments of this size fell into two overlapping groups, those which had most or all of the growing tips of their branches knocked off and those that did not. We therefore selected two damage classes for this experiment, one with growing tips intact and another with all growing tips removed.

These size and damage categories were combined to produce six separate treatments for the experiment as summarized in Table 5.15. For each of the three species there were 20 replicates for each treatment which were divided into five groups of four replicates each. Each of the five groups for every species/treatment combination were allocated to one of five experimental racks which were permanently submerged in shallow outer reef flat pools adjacent to the long term trampling experiment (Figure 1.9).

The racks, 1m x 0.5m, were constructed of stainless steel and were covered with a layer of dead coral skeletons chosen to simulate the physical surroundings of a fragment dislodged by trampling. The four fragments from each group were dropped onto the rack at a randomly chosen position and secured by a piece of fishing line.

The experimental fragments were trimmed to length using a hammer and chisel and at least 16 of the replicates within a treatment each came from separate colonies. All work was done in the field and fragments were not exposed to the air for more than 20 to 30 seconds where it was unavoidable.

The experiment was set up during the last two weeks of August 1982 and the survival of fragments was recorded approximately three months later in November 1982. The growth of these surviving fragments was recorded a year later during the last week of August 1983 and the first week of September 1983.

The data produced by this experiment was not normally distributed and has therefore been analyzed using non-parametric statistics.

Table 5.15 The six experimental treatments in the survival and growth experiment with coral fragments

EXPERIMENTAL TREATMENT	
1.	2cm long fragments with growing tips intact.
2.	4cm long fragments with growing tips intact.
3.	8cm long fragments with growing tips intact.
4.	2cm long fragments with growing tips removed.
5.	4cm long fragments with growing tips removed.
6.	8cm long fragments with growing tips removed.

5.5.3 Results

5.5.3a Survival of fragments

More large fragments survived than small fragments for all species with and without growing tips except for *Pocillopora damicornis* fragments without tips where as many 4cm pieces survived as 8cm pieces (Figure 5.7). This trend was not always statistically significant but the probabilities of the observed differences were mostly consistently low (Table 5.16).

At all sizes with or without growing tips, fragments of *Pocillopora damicornis* had a significantly lower percentage survival than fragments of *Acropora millepora* (Figure 5.7, Table 5.16). Comparison of the percentage survival of fragments between *Pocillopora damicornis* and *Acropora palifera* and between *Acropora palifera* and *Acropora millepora* does not produce such a consistent picture (Figure 5.7, Table 5.17). Nevertheless visual appraisal of Figure 5.7 strongly suggests tha *Acropora palifera* fragments have a survival probability between those of *Acropora millepora* and *Pocillopora damicornis* within the 2cm to 8cm size range and with or without tips.

The probability of survival of *Pocillopora damicornis* and *Acropora millepora* fragments was not significantly altered by the removal of growing tips (Figure 5.7, Table 5.18). However, in the case of

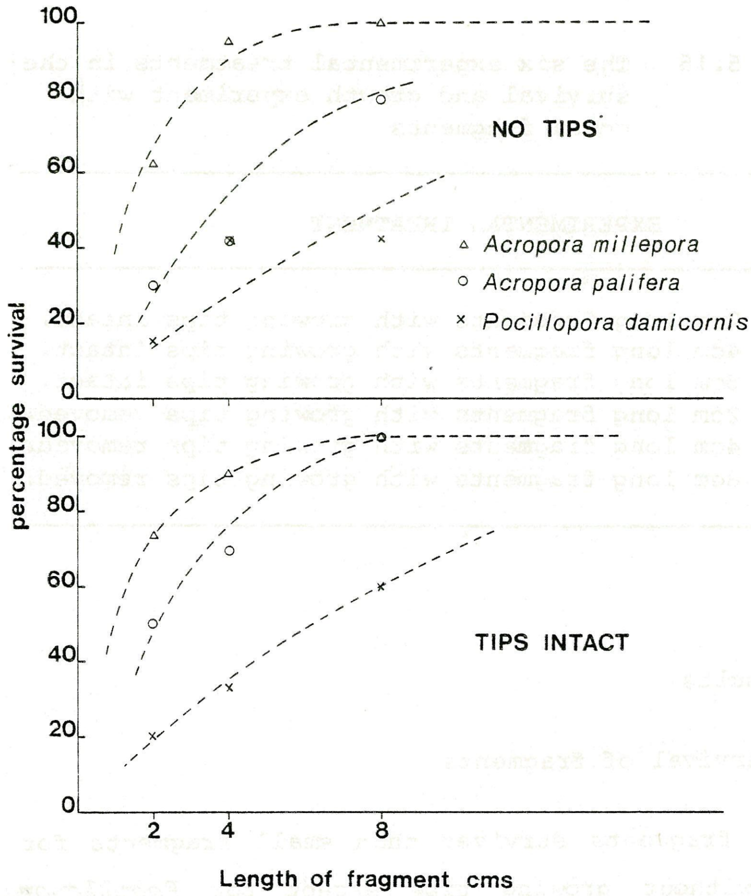


Figure 5.7 The percentage survival of fragments in the survival and growth experiment with coral fragments.

Acropora palifera fragments there was a trend of reduced percentage survival at all fragment sizes when tips were removed (Figure 5.7, Table 5.18).

Finally the survival of fragments did not differ significantly between racks ($X^2_4 = 4.82$, df = 4, p = .3) although the five pools containing the racks are different in position and structure.

To summarize the survival of fragments from the three different species was clearly dependent on size and in the case of *Acropora palifera* on the presence or absence of growing tips. Examination of surviving fragments indicated that nearly all of the *Acropora millepora* fragments and most of the live portions of the *Pocillopora dami-*

Table 5.16 The probabilities calculated using the X^2 test or the Fisher exact probability test (in the cases where the expected frequencies were too small) that the differences in the survival of fragments between the above pairs of treatments were observed by chance.

Species	Size Comparison cm.	Tips	No. Tips
Pocillopora damicornis	2 vs 4	0.19	.2> p> .1
	4 vs 8	.2> p> .1	.8> p> .7
	2 vs 8	.02> p> .01*	.2> p> .1
Acropora palifera	2 vs 4	.5> p> .3	.7> p> .5
	4 vs 8	0.014 *	.05> p> .02*
	2 vs 8	0.0003 *	.01> p> .001*
Acropora millepora	2 vs 4	0.14	0.016*
	4 vs 8	0.24	0.5
	2 vs 8	0.02*	0.003*

The tests are 2-tailed;

*significant at the 5% level.

Table 5.17 The probabilities calculated using the X^2 test or the Fisher exact probability test (in the cases where the expected frequencies were too small) that the differences in the survival of fragments between the above pairs of species were observed by chance.

TREATMENT		COMPARISON		
Damage	Fragment length cm.	*P. damicornis* vs *A. millepora*	*P. damicornis* vs *A. palifera*	*A. millepora* vs *A. palifera*
Tips	2	.001< p< .01*	.05< p< .1	.1< p< .2
	4	.001< p< .01*	.05< p< .1	.08
	8	.00163*	.0025	1.0
No tips	2	.001< p< .01*	.161	.05< p< .1
	4	.001< p< .01*	.7< p< .8	.001< p< .01*
	8	< .001 *	.05< p< .02*	.053

The tests are 2-tailed;

* significant at the 5% level.

Table 5.18 The probabilities calculated using the X^2 test or the Fisher exact probability test (in the cases where the expected frequencies were too small) that the differences between the survival of fragments with or without growing tips were observed by chance.

COMPARISON : TIPS VS NO TIPS

Length of fragment	*P. damicornis*	*A. palifera*	*A. millepora*
2cm	$.98 > p > .95$	$.5 > p > .3$	$.8 > p > .7$
4cm	$.9 > p > .8$	$.2 > p > .1$	0.38
8cm	$.5 > p > .3$	$.2 > p > .1$	1.0

The tests are 2-tailed;

* significant at the 5% level.

cornis fragments had replaced removed growing tips. This was not so for the *Acropora palifera* fragments where many of the removed tips had been replaced by algae encrusted skeleton. The width of a single *Acropora palifera* branch is much wider compared to its length than that of an *Acropora millepora* or *Pocillopora damicornis* branch. Therefore removal of a tip from *Acropora palifera* may have constituted a more severe damage treatment than removal of tips from the other two species as a larger proportion of the living tissue would have been lost.

The survival of fragments was also dependent on species. The survival curves in Figure 5.7 were drawn by eye to aid in visual interpretation of the results however there is insufficient data to complete them at this stage or consider them as more than likely hypotheses for each species. Nevertheless the following characteristics are established.

Firstly all curves will level off at a value very close to 100% survival for the environment we worked in. Independent observations by ourselves and others indicate that large fragments of all species very seldom fail to survive under these conditions. Secondly, the shape and position of the curves on the x-axis will be modified by various environmental conditions although we predict that the curves will be S-shaped. This is suggested by the data here and the casual observation that very small chips of all three species created during the setting up of the experiment did not survive.

5.5.3b Growth of fragments

The presence or absence of intact growing tips did not affect the growth rate of the surviving fragments of any of the three species (Figure 5.8, Tables 5.19 and 5.20). Additionally there was no significant difference in the growth rate of different sized fragments of coral for either *Acropora palifera* or *Pocillopora damicornis* (Table 5.19) despite the trends in the data suggesting that the longest fragments had the lowest growth rate (Figure 5.8). In contrast, size did have a significant affect on the growth rate of *Acropora millepora* fragments (Table 5.20). Trends in the data shown in Figure 5.8

Table 5.19 Results of Kruskal-Wallis one-way ANOVAs comparing the growth rates of surviving fragments between treatments. k = the number of treatments compared (includes only those treatments containing 5 or more surviving fragments) H is the test statistic and p the probability that the differences between treatments were observed by chance.

Species	k	H	p
Acropora millepora	6	14.05	$.02 > p > .01$*
Acropora palifera	5	6.1	$.5 > p > .3$
Pocillopora damicornis	4	3.86	$.5 > p > .3$

* significant at the 5% level

suggest that the larger two fragment sizes had an equal but larger growth rate than that of the smallest fragment size. This is consistent with the statistical results except that the growth rate of 8cm fragments without growing tips was not significantly different from that of the 2cm fragments without growing tips (Table 5.20).

Table 5.20 Results of Mann-Whitney U-tests comparing the growth rates of fragments of *Acropora millepora* between treatments. n1, n2 = number of fragments, U is the test statistic, p is the probability that the differences between treatments were observed by chance.

COMPARISON				n1	n2	U	p
	2cm	vs	4cm	14	16	64	.05*
Tips	2cm	vs	8cm	14	17	82	>.1
	4cm	vs	8cm	16	17	134	>.1
	2cm	vs	4cm	11	18	52	<.05*
No tips	2cm	vs	8cm	11	16	43	<.05*
	4cm	vs	8cm	16	18	138	>.1
2 cm		Tips		11	14	55	>.1
4 cm		vs		16	18	107	>.1
8 cm		No Tips		16	17	107	>.1

* significant at the 5% level;

The test is 2-tailed.

The three species clearly had different growth rates and the general trends in Figure 5.8 suggest that *Acropora millepora* had the highest, followed by *Acropora palifera* and then *Pocillopora damicornis* which had the lowest. The statistical tests support this trend although not all pairwise comparisons are significant (Table 5.21).

The negative growth rates of fragments of *Acropora palifera* and *Pocillopora damicornis* (Figure 5.8) resulted from the death of living tissue which was not completely replaced by new growth. The proportion of surviving fragments which decreased in length differed significantly between species for both damage treatments (tips intact X^2 = 25.6 $p < .001$, tips removed X^2 = 28.05 $p < .001$ df = 2 data from separate size treatments pooled) and as indicated by the data in Figure 5.8 was greatest for *Pocillopora damicornis* and least for *Acropora millepora*.

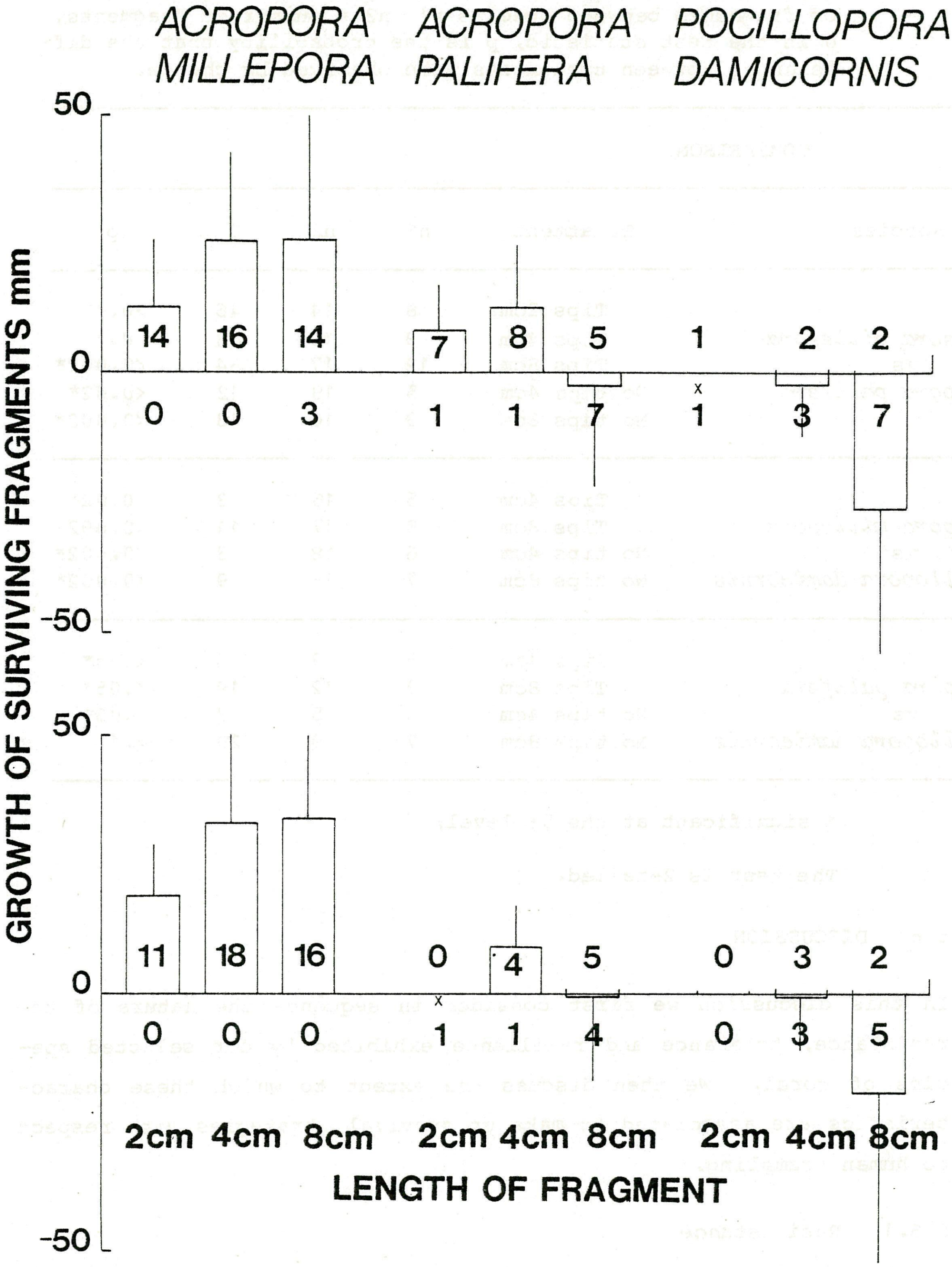


Figure 5.8 The growth of surviving fragments in the survival and growth experiment with coral fragments over a period of 10 months. The numbers of fragments which gained length are given above the X-axis and the numbers of fragments which lost length are given below the X-axis for each treatment.

Table 5.21 Results of Mann-Whitney U-tests comparing the growth rates of fragments between species n1, n2 = number of fragments, U is the test statistic, p is the probability that the differences between treatments were observed by chance.

COMPARISON

Species	Treatment	n1	n2	U	p
Acropora millepora vs *Acropora palifera*	Tips 2cm	8	14	46	>0.1
	Tips 4cm	9	16	43	0.1
	Tips 8cm	12	17	34	<0.002*
	No tips 4cm	5	18	12	<0.02*
	No tips 8cm	9	16	13	<0.002*
Acropora millepora vs *Pocillopora damicornis*	Tips 4cm	5	16	3	0.02*
	Tips 8cm	9	17	11	<0.002*
	No tips 4cm	6	18	3	<0.002*
	No tips 8cm	7	16	9	<0.002*
Acropora palifera vs *Pocillopora damicornis*	Tips 4cm	5	9	6	<.05*
	Tips 8cm	9	12	18	<.05*
	No tips 4cm	6	5	3	.03*
	No tips 8cm	7	9	20	>.1

* significant at the 5% level;

The test is 2-tailed.

5.6 DISCUSSION

In this discussion we first consider in sequence the nature of the resistance, tolerance and resilience exhibited by our selected species of coral. We then discuss the extent to which these characteristics are associated to make up survival strategies with respect to human trampling.

5.6.1 Resi stance

This quality is in some ways the easiest to measure and is perhaps likely to be the most consistent across different environments. This is because only the morphology and the mechanical strength of the coral polyp and skeleton is involved, and we are only recording an immediate response to impact.

The load required to break the branches of the three test species was one order of magnitude greater for *Acropora palifera* than that required to break the branches of *Acropora millepora* with *Pocillopora damicornis* about halfway between them (Fig. 5.1a). However it is apparent when allowance is made for the bending moment and the cross section area at the position of each break, that *Pocillopora damicornis* has the stronger skeleton and the other two species only differ by a factor of two (Fig. 5.3b). This demonstrates that morphological variation is likely to be the most important factor in determining the resistance of corals to mechanical damage; by a factor of 5 within the range of species tested in this experiment. These results agree with the ideas of Chamberlain (1978), Vosburgh (1977) and Bottjer (1980) and indicate that the morphology index developed in Chapter 2 has a sound empirical basis.

The field experiment in which colonies of *Porites lutea* were subject to trampling demonstrates that damage to polyps is a cumulative process, the percentage of damaged surface depending upon the numbers of tramples given to each colony. In comparison the breakage of a branch on a coral colony depends on the force applied to it at one instant rather than the number of footsteps and is, therefore, not cumulative. However if a whole arborescent colony is the object under consideration, then the damage process will have a cumulative aspect as the numbers of broken branches will depend on the numbers of footsteps as well as their force.

From the practical point of view, it is clear that one branch of even the strongest coral (*Acropora palifera*) is unlikely to be able to resist trampling by an adult person, although two or three branches together may well do so. On the other hand, even a small child would considerably damage a large number of branches of *Acropora millepora*. This is especially true if the form of the two species is considered, as it is unlikely that the pressure would be evenly distributed between more than one or two branches of *Acropora millepora*, but quite possible on the more even colony of *Acropora palifera*. *Pocillopora damicornis* would be intermediate between the two *Acropora* species in all cases. In considering these results, it must be borne in mind that the distance from the base at which the force was applied, was a constant 5cm. This would normally be greater in all species, except for very young colonies, and would be especially important in the "thicket" forms of the longer branching species of *Acropora*.

Nevertheless the bending moment required to break the branches calculated as load x distance (Section 5.2.3) gives a reasonable first estimate of the relative vulnerability of coral skeletons to physical damage by human trampling.

From the limited experiment described in this report, it appears that similar considerations of skeleton strength and morphology will determine the resistance of corals to human trampling as those that determine their resistance to hydrodynamic forces. However, since the range of form is so much greater than the range of skeleton strengths, it is likely that form will be much more important in determining resistance to trampling. In these experiments, the range of form (cross section area) is five times that of the range of skeleton strength, as can be seen by a comparison of Fig. 5.1b and Fig. 5.3b. This generalisation is supported by the fact that the reef crest, consisting mainly of encrusting forms, was 16 times more resistant than the reef flat, as shown in Chapter 2.

5.6.2 Tolerance

The tolerance of a living organisms or its ability to survive after being damaged, is primarily dependant upon its physiology and the subsequent interactions with the environment.

The fixed colonies of *Porites lutea* and of the other three species had a 100% tolerance rate over the periods of the experiments, 3 and 10 months respectively. The damaged polyps of *Porites lutea* all appeared to recover but the technique of breaking branches off the other colonies did not create great visible polyp damage that we could record although mucous was produced by the newly damaged colonies. It is uncertain however just how long should be allowed after damage for a useful measurement of tolerance to be made. It would be useful to know if the total life expectancy of these individuals has been altered by the experimental treatments. We could find no comparable experiments on fixed colonies reported in the literature so we are unable to make other comparisons.

The detached fragments showed clear patterns of tolerance associated with size and species (Fig. 5.7). The size effect may be either a question of the ratio of living polyps to the area of damage (Cf Connell 1973) or just the absolute minimum area that can survive the physical and physiological shock of detachment. The greater tolerance of the fragments of *Acropora* species, particularly *A. millepora* must be due to some physiological feature but the mechanism is unknown. Differences would also be expected in relation to the environment in which the fragments come to rest (Maragos 1974, Highsmith et al 1980).

As pointed out in Section 5.5.3a the effect of the removal of the tips of *A. palifera* may have been a surface area effect.

In summary the main differences between species only appeared in the smaller detached fragments and in all other conditions it was at or near 100% tolerance for the relatively short time period of these experiments.

5.6.3 Resilience

The regrowth of a damaged organism is again a physiological process and would depend upon the species and the environment in which it is growing. For this reason it is important to measure regrowth of damaged coral and, where possible, to compare this with normal growth rates of undamaged colonies.

The resilience of the polyps of *Porites lutea* appears to be quite low as the dead area was only reduced by 33% in 3 months after the highest level of impact (Fig. 5.4) although their tolerance was almost 100%. The resilience of the fixed colonies of *Acropora millepora* was high with over 88% of the damaged area in the most highly damaged colony being covered (Fig. 5.5) after two months. The resilience of *Acropora palifera* was of a similar order to *Porites lutea* and *Pocillopora damicornis* was intermediate. One interesting point about our observations is that the growth rates of the undamaged branches on damaged colonies appeared to be affected (Fig. 5.6). Regrowth in length of damaged branches is in the same order between species as the spread of polyps over damaged areas (Fig. 5.5 and 5.6 respectively). The resilience of the detached fragments which survived (Fig. 5.8) had a similar species pattern to that of the attached colonies.

Resilience appears to differ between species at all sizes and this is obviously very important in the recovery of trampled colonies and incidentally may have implications for the experimental techniques which utilise detached portions of live coral.

5.6.4 Strategy

The resistance, tolerance and resilience characteristics displayed by each of the four species in our experiments fall into three distinct groups. We suggest that those represent three survival strategies which may have evolved as a consequence of mechanical damage.

1. Resistant

High resistance, low tolerance and low resilience. *Porites lutea* and *Acropora palifera* appear to fit this format. The large size and the great ages of some colonies of *Porites lutea* support this finding (Edmondson 1929).

2. Resilient

Low resistance, high tolerance and high resilience. This summarises the behaviour of *Acropora millepora* in our experiments. It is essentially a resilient or fragmentation strategy in which damage may easily occur but survival and recovery readily follow. The large number of broken and rejoined anastomising branches in the colonies of this species testify to its success.

3. Recruitment

The intermediate resistance, tolerance and resilience of *Pocillopora damicornis* constitute a third strategy when coupled with its high rate of colonisation from planktonic spat.

At this stage our knowledge is not adequate to forecast the relative success of these strategies in trampled areas but the results of the 18 month experiment (Chapter 2) do suggest that corals which strategy 2 are most likely to survive in heavily trampled areas.

It would be interesting to discover if other coral species all tend to fall into one of these three strategy groups. With greater knowledge it might be possible to scale communities according to their strategic composition as we can at present (in general terms) on the basis of their morphology.

CHAPTER 6 SUMMARY OF RESULTS

CHAPTER 6 SUMMARY OF RESULTS

The work presented in this report was carried out in two habitats, the outer reef flat and reef crest. They represented two extremes in a spectrum of community types ranging from upright and open coral colonies on undulating, broken and often friable substrata to low and compact on hard level substrata. Our experiments indicated that the community on the crest was at least 16 times less vulnerable to trampling than that on the reef flat and that the structural disturbances occuring in each zone due to the physical impact of trampling were different in kind and quantity.

Trampling had no effect on the consolidated dead substrata of the reef crest and even after a total of 480 passages on a narrow path over 18 months the composition of the coral community was not significantly altered. Most of the corals in this habitat had digitate to low corymbose or caespitose morphologies where the short branches on the colonies rarely extended outside of the encrusting colony bases. Although trampling broke off many of the branches of these colonies (0.7kg m^{-2} coral was detached by 20 passages) the colonies survived and their surface area remained unchanged. The broken off fragments were mostly washed away in the relatively turbulent conditions of the crest zone, no rubble accumulated along the trampled pathways and the visible effects of trampling were confined to the breaks in live coral after each trampling treatment.

In contrast trampling broke up much of the unconsolidated dead substrata on the reef flat and the structure of the habitat and the composition of the coral community was altered after only 30 passages along a path after 18 months. This community was made up of corals of a wide variety of morphologies but those with open arborescent, high corymbose to caespitose and wedge or blade-like branched colonies dominated. The first two types were easily damaged by reef walking and many of their fragmented branches contributed to the rubble which was produced by the destruction of unconsolidated dead coral. Twenty passages detached 5.7kg m^{-2} of live coral on the outer reef flat which is over eight times as much as they did on the reef crest where 0.7kg m-2 was detached. Trampling also would this "rubble" form a satisfactory, stable "path"?

formed "ditches" in this area which has implications for local drainage patterns and geomorphological processes. Furthermore rubble accumulated in these ditches and was not washed away as it was on the reef crest.

The recovery experiment designed to determine the impact of the guided reef walks from the Heron Island tourist resort has not yet produced conclusive results. However, other evidence suggests that the area in which the reef walks are conducted would not easily be damaged by human trampling.

This evidence was derived mainly from a model, based on subjective reasoning and the evidence from the trampling experiments in the reef flat and crest zones, which describes the relationship between trampling intensity, reduction in percentage cover and coral morphology or substrate type. In its present form it can be used to arrange inter-tidal coral communities on a scale of vulnerability to trampling but requires further development to improve the precision of its predictions about changes in percentage cover.

The final part of the work involved a series of small scale experiments with individual coral species to determine the mechanical strength of their skeletons (or the resistance of their polyps to damage) and the probability of survival and the growth rate of their colonies and colony fragments when damaged. These three characteristics, resistance, tolerance and resilience respectively, differed between the four corals which were examined suggesting that three distinct strategies exist in relation to physical disturbances at the species level. These have been nominated here as resistant, resilient and recruitment strategies.

CHAPTER 7 MANAGEMENT IMPLICATIONS

7.1 INTRODUCTION

7.2 ZONATION

7.2.1 between reefs

7.2.2 within reefs

7.3 WIDESPREAD OR SPATIALLY LIMITED REEF WALKING

7.4 PATH LOCATION ON REEF FLAT

7.5 ROTATIONAL USE?

7.6 ASSESSMENT OF ENVIRONMENTAL QUALITY FOR VISITORS

7.7 SITE MONITORING

7.8 EDUCATION OF VISITORS

CHAPTER 7 MANAGEMENT IMPLICATIONS

7.1 INTRODUCTION

The major objective of this project was to provide information that can be used as a general basis for management decisions about reef walking in the Great Barrier Reef. The purpose of this chapter is to describe more precisely how our results can be used in the implementation of different techniques in the management of reef walking. As far as possible we have avoided repeating the details of our findings but in each section we indicate where the relevant data may be found within this report.

The primary aim of these management techniques is to provide a high quality environment, in the sense that it is as natural and unspoilt as possible, for the reef walking tourist or, in some cases, for scientific research. Accordingly these techniques are based on the idea of controlling the intensity of use at a level where there is little or no long-term degradation of the habitat or at a level which will not cause permanent damage and where recovery during a closed period occurs within a reasonable time.

At the present time the location and nature of many recreational and commercial activities in the Great Barrier Reef Province are the result of the past history of use rather than management decisions. This is particularly true where an infrastructure of tourist or other facilities is in existence; for example the area used for reef walking on Heron Island reef is largely determined by the convenient proximity of the resort and research station. In the future the existence of such facilities and history factors will define a general pattern of reef usage which can be influenced by the following techniques but could not often be completely changed.

7.2 ZONATION PLANS

Zonation plans drawn up for the purposes of managing reef walking will involve the classification of different reefs or reef zones on a scale of vulnerability to trampling damage and a knowledge of the changes that will occur in such areas under different trampling regimes. The results of the long-term experiment, the coral morphology/substrate type scheme and the resistance, tolerance and resilience (RTR) model all provide data for this procedure as described in the following subsections.

7.2.1 Zonation between reefs

On this scale an assessment of the areas and positions of the various habitats within a reef can give a broad guide to its suitability for reef walking. The morphology scheme combined with RTR data can be used as a basis for determining the vulnerability of various areas of the reef flat (Sections 2.4.2, 5.6). The presence of a consolidated reef crest ~~which could be~~ is clearly an advantage and where feasible it should be used as a landing at low tide on those reef used for walking which do not have islands.

7.2.2 Zonation within reefs

This essentially requires the use of the morphology and RTR information at a more local scale. The differentiation in vulnerability between habitats is clear but in view of the conflicting requirements of presentation and provisions of a good experience management will have to be sensitive to local variation within the reef flat habitat. (Sections 2.4.2, 5.6).

7.3 WIDESPREAD OR SPATIALLY LIMITED REEF WALKING

The experiments have demonstrated that as few as 5 passages in one place on the reef flat can detach a large amount of coral. This suggests that widespread walking can only take place without changing the reef flat if people do not repeatedly walk on the same place in vulnerable areas, at least within periods of one or two years.

In contrast, the changes to the corals on the reef crest were minimal and large numbers of people could walk repeatedly on the crest and cause little deterioration. (Section 2.4.1).

7.4 PATH LOCATION ON THE REEF FLAT

Given that the corals on the reef flat are generally vulnerable and that the arborescent and, plate-like forms are the most unusually spectacular there is a clear conflict between use by, and presentation for, the reef walkers. The first suggestion to minimise damage is to locate routes through the sandy pools, leading eventually to the crest. These routes could be located and used by reef walk guides or they could be marked in some way to guide independent walkers. The provision of a self-guided 'nature trail' leaflet might help to direct people in certain circumstances.

The paths could be chosen so that they passed through sandy pools which are wide enough to allow walkers to pass through without damaging corals. The pools could be connected either by breaking passages between pools or by locating routes passing over consolidated substrate or rubble. Reinforcing mobile rubble and possibly seeding with corals with high tolerance and resilience characteristics may be needed. Raised walkways have been used in extreme conditions ie. high vulnerability and high use ratios.

The morphology and RTR models developed in this report should be used as a basis for the initial surveys when the routes are first laid out and these need development to the stage where they can readily be used by people who do not have skills in the complex art of coral taxonomy.

7.5 ROTATIONAL USE

The period needed for a reef flat community to recover after it has been damaged by trampling will depend on the nature of the community and the degree of damage. Consequently the details of a rotational use or closed season management plan will depend on predictions of damage occuring at different trampling levels and estimates of the time it takes to repair this damage. The morphology scheme (Section 2.4.2) and the results of the trampling experiments in Chapters 2 and 3 provide a rough estimate of potential damage but until the tolerance and resilience (Chapter 5) of more corals are measured we cannot make estimates about the survival and recovery. The short time for which the exclosure experiment has been in existence has not allowed us to detect any significant trends in coral recovery.

However it is clear from other studies (Yamaguchi 1975, Loya 1976) that rotational use would have to allow 5 to 10 years for full recovery from a heavily damaged condition. The possibility of accelerated recovery by 'seeding' with corals of high tolerance and resilience (Section 5.5.3) in locally important areas should (is) being investigated.

7.6 ASSESSMENT OF ENVIRONMENTAL QUALITY FOR VISITORS

The expectation of tourists using the reefs does not appear to have been investigated but it seems reasonable to assume that they want to see a wide range of organisms and fully grown, preferably to brightly coloured, coral colonies. The morphology scheme (Section 2.4.2) would include the best requirement if colour is added to the records and the scheme could be extended to rank the quality of the inert substrate as a habitat for other organisms. It may also be possible to utilise broken end counts to monitor the recent effect of visitors to particular areas.

Seeding with live coral fragments or colonies may be an appropriate technique to enhance the visitors' experience.

7.7 SITE MONITORING

The quality of an area used for reef walking needs to be checked at intervals to ensure that it is not being degraded by excessive or badly controlled use. The morphology index (Section 2.4.2) coupled with broken end counts (Sections 2.3.7 and 3.4) in selected areas or on particular colonies could form a sound basis for a monitoring scheme that is relevant to the visitors experience. The recording systems used in our experiments could be used as a basis for the development of a monitoring scheme.

7.8 EDUCATION OF VISITORS

While our research did not touch on this problem directly, it is an essential part of management of wildlife areas. The morphology scheme is readily understood and could easily be used to inform people as to the vulnerability of corals so that they avoided excessive damage by trampling, poking with sticks and similar activities. A static display of skeletons of representative coral colonies giving their vulnerability could be readily prepared and placed at reef access points. An alternative way of influencing people could be the setting up of target markers on the reef crest so that walkers can see them from a distance and will tend to follow a predetermined route towards them. The provision of information relevant to that site, might ensure that visitors would walk directly to the marker and thus along chosen walking routes.

Further knowledge of visitors behaviour is clearly required for the development of these techniques.

CHAPTER 8 THE FUTURE

CHAPTER 8 THE FUTURE

8.1 INTRODUCTION

Figure 8.1 summarizes the various components of the management process and how they interrelate with one another on a first order basis. The experimental work described in this report provides information for components 2 and 3 and the introductory review in Chapter 1 considers the philosophy behind components 4.5 and 7. In the context of this scheme and our current results we have devoted this concluding chapter to outlining the additional research work which needs to be done for the management of reef walking and discussing the experiments presently in progress that should be continued.

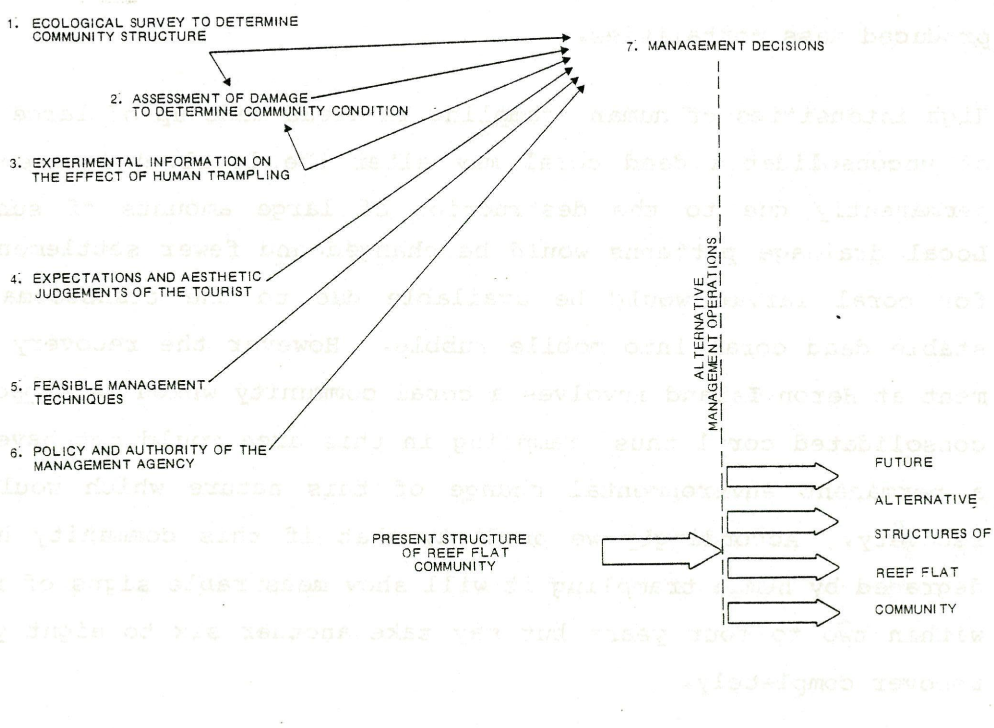


Figure 8.1 The components of the management process. Thin black arrows indicate information flow and the thick open arrows indicate ecological processes.

8.2 CONTINUATION OF EXPERIMENTS

8.2.1 The recovery experiment at Heron Island

The recovery of permanently submerged coral communities on reef slopes may take two or more decades following heavy damage caused by catastrophic events such as hurricanes or plagues of the crown of thorns starfish *Acanthaster planci* (Endean, 1977). However studies on reef flats suggest that the recovery of coral communities take much less time (in this zone) providing no permanent changes in the environment have occurred and that conditions prior to the disturbance were favourable for coral growth (Pearson, 1981). For example Loya (1976) observed that the recovery of an unpolluted reef flat community in the Northern Gulf of Eilat in the Red Sea was well advanced three years after the coral had been severely decimated by an extreme low tide, and was likely to be complete in five or six years. Similarly Yamaguchi (1975) recorded the partial recovery of reef flat communities in Gaum three years after an unusually low tide produced mass mortalities.

High intensities of human trampling in areas made up of large amounts of unconsolidated dead coral may alter the local environment semi-permanently due to the destruction of large amounts of substrata. Local drainage patterns would be changed and fewer settlement sites for coral larvae would be available due to the transformation of stable dead coral into mobile rubble. However the recovery experiment at Heron Island involves a coral community which is supported by consolidated coral thus trampling in this area would not have caused a permanent environmental change of this nature which would delay recovery. Accordingly we predict, that if this community has been degraded by human trampling it will show measurable signs of recovery within two to four years but may take another six to eight years to recover completely.

The results of the recovery experiment reported in Chapter 4 only cover one year of trampling exclusion. We cannot, therefore, make any final conclusions about the impact of trampling in this zone until the experiment has continued for another two or three years despite the other evidence suggesting that it has had little impact in this area (see section 4.4). This experiment began in May 1982, thus we propose that it should continue up until May 1986 at least. If evidence of recovery is detected by this time we recommend that the exclusion plots remain in place until the recovery growth has stabilized so the relative condition of the surrounding trampled community can be assessed.

8.2.2 Recovery of the long-term trampling transects

The rate of site recovery is an important factor in the implementation of closed seasons and rotational use management techniques. In this respect the outer reef flat transects of the long-term trampling experiment reported in Chapter 2 provide an excellent opportunity to monitor the recovery of a vulnerable site which has been damaged by known levels of trampling and which had been surveyed prior to the trampling impact.

The transects were last trampled in October 1983 and we propose to record their recovery at six monthly or yearly intervals for at least 1984 and 1985.

8.3 FUTURE WORK

8.3.1 Green Island: survey and damage assessment

Green Island, a coral cay which is situated in the central region of the Great Barrier Reef 27km northeast of Cairns, is surrounded by reef flats which are likely to be the most intensively trampled in the entire Great Barrier Reef Province. The cay supports several tourist attractions, including a resort, and two or more Green Island cruises operate daily from Cairns. These features encourage and facilitate high numbers of visitors each day.

To our knowledge no descriptions of the areas regularly used by walkers on this reef are available and no quantitative or experimental measurements have been made to assess the damage these visitors may be causing despite the general rumour amongst coral reef scientists that this reef has been ruined by excessive trampling. As indicated in Figure 8.1 both these pieces of information are needed for the formulation of future management decisions.

Accordingly we propose that a survey be made of areas on Green Island which are accessible to reef walkers and that a recovery experiment be commenced there in a heavily trampled area. We also envisage that the information from the survey would be used to predict the vulnerability of these areas to trampling damage using a refined version of the coral morphology/substrate type model presented in Chapter 2.

8.3.2 Other site surveys

Over 16 island tourist resorts exist in the Great Barrier Reef province and about three quarters of these offer reef walking as one of the possible holiday activities. In addition, numerous cruises operate from Mackay, Shute Harbour, Townsville and Cairns, many of which enable people to visit and walk over coral reefs exposed at low tide.

At the time of writing the locations of these reef walking areas have not been recorded and listed in any scientific study, the intensity of use is unknown and information describing the composition, condition and vulnerability of the coral communities concerned has not been gathered. A project designed to provide all of the above information would be essential, if future management of these areas is desirable. However this extensive survey is beyond the capacity of a small research team represented by the authors. Accordingly we propose a survey project on a much smaller scale with the aim of producing this type of baseline data for five of the most frequently used reef walking sites, besides Heron Island and Green Island. Firstly this survey will provide information for those areas which are most likely to require future management and secondly it will test and establish field techniques which could be used by personel directly concerned with management.

8.3.3 Development of predictive models

8.3.3a Aim

The degree of confidence with which a management decision can be made will depend largely on the accuracy of quantitative predictions about the impact of trampling on coral communities of different composition. We have presented the basic elements of two models in this report, the coral morphology/substrate type model in Chapter 2 and the resistance, tolerance and resilience model in Chapter 5 which are designed to make such predictions.

The following two sections outline the work that is needed to develop both these models and establish their predictive power.

8.3.3b Coral morphology and substrate type

In its present form this model can be used to arrange sites on a scale of vulnerability to trampling and is therefore a useful management tool. However as pointed out in Section 2.4.2 predictions about reductions in percentage cover of a given morphological or substrate type could not be precise because they were estimated subjectively drawing on the experimental results of the long-term trampling experiment and some simple arguments about the structural strength of different shaped coral colonies.

Future work for this model, therefore, would involve a more thorough analysis of the relationship between coral form and mechanical strength and the incorporation of experimental information on the survival of damaged coral immediately after trampling. The experiments described in Chapter 5 which record the probability of survival of damaged colonies and fragments provide this type of information.

After the relationship between trampling intensity and the amount of reduction in percentage cover was quantified and the accuracy of the predictions tested in the field the effect of trampling duration could be examine. This would require information on the ability of different coral morphologies to replace material that was destroyed by trampling. Such data could be provided by experiments the same as, or similar to, those in Chapter 5 which record the growth rates of coral fragments and damaged colonies. Prediction testing would also follow this part of the work.

In conclusion it is clear that future work for this model will draw on past and future work for the resistance, tolerance and resilience model and that there is an obvious potential for the amalgamation of the two into one predictive scheme.

8.3.3c Resistance, Tolerance and Resilience

As explained in Section 5.6.4 the different resistance, tolerance and resilience of the four common reef flat corals used in our smaller scale experiments were consistent with three distinct strategy types. This indicated that the scheme has good potential as a conceptual model for catagorizing species responses to physical disturbances however the potential of the resistance, tolerance and resilience model for making precise predictions about changes in percentage cover due to trampling has not been tested. This is, therefore, the next phase of the work that needs to be undertaken for the development of this model.

Firstly, it will involve transforming the present data we have for the four coral species into a form which can be used to make predictions. Secondly these predictions will be compared with the results of the long term trampling experiment and other field trials in order to assess their accuracy and the predictive power of the model.

Subsequent work would entail measuring the resistance, tolerance and resilience of other common species, preferably in more than one location, using similar techniques to those described in Chapter 5. The model could then be used to make predictions for a greater range of species in more than just one habitat and management decisions could be made with greater understanding.

This work would also increase our understanding of the consequences of other man induced physical disturbances on reef flats such as shipwrecks and the movement of amphibious vehicles as well as natural mechanical disturbances such as boulder movement in storms and cyclones. In the future, therefore, it may also be possible to broaden the application of the resistance, tolerance and resilience model so that the damage caused by such agents could be predicted.

8.3.4 Tourist behaviour on reef flats

The information provided in this report describes the response of reef flat communities to trampling but it does not show how people behave in the reef flat environment and what they expect to see. This type of information is also important for the management process (Figure 8.1) and is unavailable at present. For example, do people aggregate or spread out on the reef flat in this environment? Do they tend to follow in single file and do they quickly understand the vulnerability of coral? How can their behaviour be influenced by prior information, marked routes or reef walk guides? How do people differ in behaviour between different ages and social groups? The answers to these kinds of questions would be of help to management and we propose a project starting with observations and questioning questions to the reef flat at Heron Island.

ACKNOWLEDGEMENTS

We are grateful to many people for assistance with field work, in particular Mike Coates, Kerry-Ann Collins, Ross Mather and Peter McRae. Also we would like to thank Richard Kenchington, Anne Bothwell, Mike Coates and Anne Berlow-Olsen for other general help and advice before and during the project. Peter McRae prepared the material for the laboratory resistance experiment and Judith Archer, with the help of Heather Chapman and Michael Jozefowicz, did the preliminary processing of the raw transect data from the long-term trampling experiment. Our thanks also go to Richard Blundell and Susan Rea for the preparation of the figures in this report and to Lacey Shaw for typing the manuscript.

REFERENCES

Bak, R.P.M. (1976) The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Netherlands Journal of Sea Research. 10, 285-337.

Bayfield, N.G. (1971) Some effects of walking and skiing on vegetation at Cairngorm. In "The Scientific Management of Animal and Plant Communities for Conservation". E. Duffey and A.S. Watt (Eds.). Oxford, Blackwell, 469-485.

Bell, K.L. and Bliss, L.C. (1973) Alpine disturbance studies: Olympic National Park, U.S.A. Biological Conservation. 5(1), 25-32.

Bottjer, D.J. (1980) Branching morphology of the reef coral Acropora cervicornis in different hydraulic regimes. Journal of Paleobiology. 54, 1102-1107.

Bowles, J.M. and Maun, M.A. (1982) A study of the effects of trampling on the vegetation of Lake Muron sand dunes at Pinery Provincial Park. Biological Conservation. 24, 273-283.

Chamberlain, J.A. Jr. (1978) Mechanical properties of coral skeleton: compressive strength and its adaptive significance. Paleobiology. 4, 419-435.

Chamberlain, J.A. and Graus, R.R. (1975) Water flow and hydromechanical adaptation of branched reef corals. Bulletin of Marine Science. 25, 112-125.

Clark, R.N. and Stanky, G.H. (1979) The Recreational Opportunity Spectrum: A Framework for Planning, Management and Research. U.S.D.A. Forest Service, General Technical Report PNW-98, Portland Oregon.

Connell, J.H. (1973) Population ecology of reef building corals. In "Biology and Geology of Coral Reefs". O.A. Jones and R. Endean (Eds.), Vol 11, Biology 1, Academic Press, 205-245.

Connell, J.H. (1983) Disturbance and patch dynamics of reef corals. In "Proceedings: Inaugural Great Barrier Reef Conference", J.T. Baker, R.M. Carter, P.W. Sammarco and K.P. Stark (Eds.). Townsville, Aug. 28-Sept 2, 1983. JCU Press, 179-190.

Crawford, A.K. and Liddle, M.J. (1977) The effect of trampling on neutral grassland. Biological Conservation. 12, 135-142.

Davies, G.E. (1977) Anchor damage to coral reef on the coast of Florida. Biological Conservation. 11, 29-34.

Dollar, S. (1975) Zonation of reef corals off the Kona coast of Hawaii, M.S. thesis, University of Hawaii, Honolulu.

Edington, J.M. and Edington, M.A. (1977) Ecology and Environmental Planning. Chapman and Hall, London.

Endean, R. (1977) Acanthaster planci infestations of reefs of the Great Barrier Reef. In Proceedings of the Third International Coral Reef Symposium. University of Miami, Miami 1: 186-191.

Falinski, J.B. (1975) Reaction of forest soil vegetation to trampling in the light of experimental research. Die Reaklion der Waldboden vegetation auf Trittwirkung im Luchte experimenteller Forschiengen. Phytocoenolegia. 2, 451-465.

Folk, R.L. and Robles, R. (1964) Carbonate sands of Isla Perez, Alacran Reef comlex, Yucatan. Journal of Geology. 72, 255-292.

Force, L.M. (1969) Calcium carbonate size distribution on the west Florida shelf and experimental studies on the micro architectural control of skeletal breakdown. Journal of Sedimentology and Petrology. 39, 902-934.

Gladfelter, E.H., Monahan, R.K. and Gladfelter, W.B. (1978) Growth rates of 5 reef building corals in the northeastern Caribbean. Bulletin of Marine Science. 28(4), 728-734.

Goldsmith, F.B. (1974) Ecological effects of visitors in the countryside. In "Conservation in Practice". A. Warren and F.B. Goldsmith, Wiley, London, 217-231.

Graus, R.R., Chamberlain, J.A. and Boker, A.M. (1977) Structural modification of corals in relation to waves and currents. In "Reefs and Related Carbonates - Ecology and Sedimentology". S.H. Frost, M.P. Weiss and J.B. Saunders (Eds.). American Association of Petrology and Geology. Studies in Geology. 4, 135-153.

Grime, J.P. (1979) Plant strategies and vegetation processes. Chichester: John Wiley and Sons. 222.

Harper, F.C., Warlow, W.J. and Clarke, B.L. (1961) The Forces Applied to the Floor by the Foot in Walking. 1. Walking on a Level Surface. Research Paper 32. National Building Studies. H.M.S.O., London.

Harrison, C. (1981) Recovery of lowland grassland and heathland in southern England from disturbance by seasonal trampling. Biological Conservation. 19, 119-130.

Highsmith, R.C., Riggs, A.C. and D'Antonio, M.D. (1980) Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. Oecologia (Berl.). 46, 322-329.

Highsmith, R.C. (1982) Reproduction by fragmentation in corals. Marine Ecology-Progress Series. 7: 207-226.

Holmes, D.O. and Dobson, H.E.M. (1976) The effects of human trampling and urine on subalpine vegetation, a survey of post and present backcountry use and the ecological carrying capacity of wilderness, Yosomite National Park, Sierra Nevada, U.S.A. Report of the College of Natural Resources, University of California, Berkley.

Hutchings, P. (1983) Bioerosion of coral substrates. In "Proceedings: Inaugural Great Barrier Reef Conference", J.T. Baker, R.M. Carter, P.W. Sammarco and K.P. Stark (Eds.). Townsville, Aug. 28-Sept. 2, 1983. J.C.U. Press, 113-120.

Hylgaard, T. and Liddle, M.J. (1980) The effect of human trampling on a sand dune ecosystem dominated by Empetrum nigrum. Journal of Applied Ecology. 18, 559-569.

Jackson, J.B.C. (1979) Morphological strategies of sessile animals. In "Biology and Systematics of Colonial Organisms". G. Larwood and B.R. Rosen (Eds.). Academic Press, London and New York, 499-555.

Kaiser, C. and Helber, L. (1978) Tourism Planning and Development, CBI, Publishing Company, Boston.

Kay, A.M. and Keough, M.J. (1981) Occupation of patches in the epifaunal communities on pier pilings and the bivalve Pinna bicolor at Edithburgh, South Australia. Oecologia (Berl). 48, 123-130.

Kay, A.M. and Liddle, M.J. (1983) The effect of human trampling on coral reefs. In "Proceedings: Inaugural Great Barrier Reef Conference", J.T. Baker, R.M. Carter, P.W. Sammarco and K.P. Stark (Eds.). Townsville, Aug. 28-Sept. 2, 1983. JCU Press, 517-524.

Kellomaki, S. (1973) Ground cover response to trampling in a spruce stand of Myrtillus type. Silva Fennica. 7, 96-113.

Kendal, P.C. McM. (1982) The effect of season and/or duration of trampling on vegetation in an open forest of South East Queensland. Master of Science thesis, Griffith University, Brisbane.

Knowlton, N., Lang, J.C. Rooney, M.C. and Clifford, P. (1981) Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. Nature (Lond.). 294 (5838), 251-252.

Leney, F.M. (1974) The ecological effects of public pressure on picnic sites. PhD thesis, University of Aberdeen.

Liddle, M.J. (1973) The effects of trampling and vehicles on natural vegetaton. PhD thesis, University College of North Wales, Bangor.

Liddle, M.J. (1975) A selective review of the ecological effects of human trampling on the natural ecosystems. Biological Conservation. 7, 17-36.

Liddle In press. A classification of the interactions between animals and plants with particular reference to human trampling. In "The Ecological basis of interactions between organisms". M.J. Liddle and J. Tothill (Eds.). AES, Griffith University Monograph.

Liddle, M.J. and Greig-Smith, P. (1975a) A survey of tracks and paths in a sand dune ecosystem I. Soils. Journal of Applied Ecology, 12, 893-908.

Liddle, M.J. and Greig-Smith, P. (1975b) A survey of tracks and paths in a sand dune ecosystem II. Vegetation. Journal of Applied Ecology. 12, 909-930.

Little, A.D. (1974) An investigation on trampling in a dune valley, effects on mesofauna and vegetation. Publication No. 215, Institute for Environmental Studies, Free University, Amsterdam.

Loya, Y. (1976) Recolonisation of Red Sea corals affected by natural catastrophes and man-made perturbations. Ecology. 57, 278-289.

Loya, Y. (1978) Plotless and transect methods. In Coral reefs: research methods. D.R. Stoddart and R.E. Johannes (Eds.). 197-218, UNESCO. Paris.

Maragos, J.E. (1974) Coral communities on a seaward reef slope, Fanning Island. Pacific Science. 28, 257-278.

Maragos, J.E. (1972) A study of the ecology of Hawaiian reef corals. PhD thesis, University of Hawaii.

Mercer, D. (1981) Trends in recreational participation. In "Outdoor Recreation: Australian Perspectives" Mercer, D. (Ed.). 24-44. Sorrett, Malvern.

Orme, G.R. (1977) Aspects of sedimentation in the coral reef environment. In "Biology and Geology of Coral Reefs". O.A. Jones and R. Endean (Eds.), Vol IV, Geology 2, Academic Press, 129-176.

Paine, R.T. (1977) Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Reprinted from "The changing scenes in natural sciences, 1776-1976" Academy of Natural Sciences, Special Publication. 12, 245-270.

Pearson, R.G. (1981) Recovery and recolonization of coral reefs. Marine Ecology - Progress, Series 4, 105-122.

Pigram, J. (1983) Outdoor Recreation and Resource Management, Croom Helm, London.

Ploeg, S. (1972) Why Destination Areas Rise and Fall in Popularity. Unpublished paper, Travel Research Association, Los Angelos. [Cited in Kaiser and Melber, 1978].

Ploeg, S.W.F. vander and Wingerden, W.K.R.E. van (1974) The influence of trampling on spiders. Proceedings of the 6th Arachnological Congress. 167-172.

Rogova, T.V. (1976) Influence of trampling on vegetation of forest meadow and whortleberry-moss Pine forest Cenosis. Soviet Journal of Ecology. 7, 356.

Siegel, S. (1956) Non-parametric statistics for the behavioural sciences. Tokyo. McGraw-Hill, Kogakusha.

Speight, M.C.D. (1973) Outdoor recreation and its ecological effects. Discussion papers in Conservation No. 4. University College, London.

Stoddart, D.R. (1969) The ecology and morphology of recent coral reefs. Biological Review. 44, 433-498.

Studler, S.M. (1980) Trampling effects on bryophytes. Trail surveys and experiments. The Bryologist. 83, 301-313.

Thyer, N. and Liddle, M.J. (in press). The effects of trampling and live in a subtropical Schlerophyll forest. Biological Conservation.

Vosburgh, F. (1982) Acropora reticulata: structure, mechanics and ecology of a reef coral. Proceedings of the Royal Society, London. B214, 481-499.

Vosburgh, F. (1977) The response to drag of the reef coral *Acropora reticulata*. In "Proceedings of the Third International Coral Reef Symposium", Vol. 1. University of Miami, 477-482.

Wall, G. and Wright, C. (1977) The environmental impact of outdoor recreation. Waterloo, Ontario, University of Waterloo. (Department of Geography Publication, Series No. 11).

Wallace, C.C. (1978) The coral genus *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) in the central and southern Great Barrier Reef Province. Memoirs of the Queensland Museum. 18(2), 273-319.

Watt, A.S. (1957) The effect of excluding rabbits from grassland B (Mesobrometrum) in Breckland. *Journal of Ecology*, 45, 861-78.

Weaver, T. and Dale, D. (1978) Trampling effects of hikers, motorcycles and horses in meadows and forests. *Journal of Applied Ecology*. 15, 451-457.

Westman, W.R. (1978) Measuring the inertia and resilience of ecosystems. *Bioscience*. 28, 705-710.

Winer, B.J. (1971) Statistical principles in experimental design. New York: McGraw-Hill.

Woodland, D.J. and Hooper, J.N.A. (1977) The effect of human trampling on coral reefs. *Biological Conservation*. 11, 1-4.

Yamaguchi, M. (1975) Sea level fluctuations and mass mortalities of reef animals in Guam, Mariana Islands. *Micronesica*. 11, 227-243.

APPENDICES

Appendix 4.1 Results of Mann-Whitney U-tests comparing the percentage cover of coral genera, and various other community components between open and exclosure plots. U is the test statistic and p is the probability that the differences were observed by chance. The test is 2-tailed.

Appendix 4.1

	0 months		12 months	
	Open/Closed		Open/Closed	
	U	P	U	P
				.886
Acropora	8	1.0	7.5	<1.0
Montipora	8	1.0	3	.2
Pavona	7	.886		
Cyphastrea	7	.886	6	.686
Favia	7	.886	7	.886
Favites	5	.486	7	.886
		> .886		
Goniastrea	7.5	<1.0	4	.342
Hydnophora	2	.114	7	.886
		> .886		> .886
Leptoria	7.5	<1.0	7.5	<1.0
		> .886		> .886
Platygyra	7.5	<1.0	7.5	<1.0
Plesiastrea	6	.686		
Fungia	6	.686	6	.686
Lobophyllia	6	.686	6	.686
		> .2		
Pocillopora	3.5	< .342	6	.686
Stylophora	6	.686	6	.686
				> .886
Goniopora	5	.486	7.5	<1.0
				> .486
Porites	8	1.0	5.5	< .686
Galaxea	8	1.0		
				> .886
Palythoa	6	.686	7.5	<1.0
		> .886		
Lobophyton	<7.5	<1.0	7	.886
Sinularia	6	.686		
		> .886		
Tridacna	7.5	<1.0	4	.342
Dead Coral	8	1.0	8	1.0
Live Coral	7	.886	7	.886
Chlorodesmis	6	.686	6	.686
				> .686
Caulerpa	3	.2	6.5	< .886
green brown tufts	7	.886	8	1.0
unidentified algae	7	.886	6	.686
unidentified coral	7	.886	6	.686
Dead Coral	8	1.0	8	1.0
Live Coral	7	.886	7	.886
(Sessile invertebrates		> .486		
- coral)	5.5	< .686	6	.686
total algae	6	.686	7	.886

Appendix 4.2 The percentage cover of coral genera and other community components in the eight plots of the recovery experiment.

0 months: percentage cover

Appendix 4.2

	open plots						exclosure plots					
	1	2	3	4	$\bar{X}$	(S.D.)	1	2	3	4	$\bar{X}$	(S.D.)
Acropora	20.1	9.6	6.1	9.9	11.4	(6.0)	17.7	6.4	11.5	7.6	10.8	(5.1)
Montipora	4.5	0.8	0.1	0.3	1.4	(2.1)	0.5	4.4	0.5	0.2	1.4	(2.0)
Pavona									0.3		0.1	(0.2)
Cyphastrea				0.6	0.2	(0.3)						
Favia		0.3	0.1	1.7	0.5	(0.8)		0.2	0.2	1.9	0.6	(0.9)
Favites	0.6	0.1	0.2	4.9	1.5	(2.3)	2.4	0.9	0.4	2.0	1.4	(0.9)
Goniastrea	1.2	0.5	0.2	0.5	0.6	(0.4)	0.5	0.1	0.1	1.3	0.5	(0.5)
Hydnophora		0.1	0.1	0.1	0.1	(0.1)						
Leptoria				0.5	0.1	(0.3)				0.3	0.1	(0.2)
Platygyra				0.3	0.1	(0.2)				1.1	0.3	(0.6)
Plesiastrea			0.1	0.1	0.1	(0.1)			1.1	0.2	0.3	(0.5)
Fungia		0.1			0.0	(0.1)						
Lobophyllia		0.1			0.0	(0.1)						
Pocillopora		1.2	1.1	1.5	1.0	(0.7)	0.2	0.3	1.0	1.4	0.7	(0.6)
Stylophora								0.1			0.0	(0.1)
Goniopora	0.5	0.3			0.2	(0.2)	0.1		0.6		0.2	(0.3)
Porites	1.0	2.7	1.2	0.4	1.3	(1.0)	1.9	2.8			1.2	(1.4)
Galaxea				0.1	0.0	(0.1)			0.1		0.0	(0.1)
Palythoa				0.4	0.1	(0.2)						
Lobophyton	0.7				0.2	(0.4)				0.3	0.1	(0.2)
Sinularia		1.5			0.4	(0.8)						
Tridacna	0.3		0.1		0.1	(0.1)	0.1			0.2	0.1	(0.1)
Chlorodesmis	1.9	2.6	3.3	6.9	3.7	(2.2)	3.8	0.1	6.4	6.9	4.3	(3.1)
Caulerpa				0.1	0.0	(0.1)	0.2	0.3		0.1	0.2	(0.1)
Drift algae	4.5	3.3	0.1		2.0	(2.3)		8.5			2.1	(4.3)
unidentified algae			0.5	1.1	0.4	(0.5)	0.2		0.7	0.8	0.4	(0.4)
unidentified coral	.2	1.0	1.0	3.5	1.4	(1.4)	0.4	0.3	1.0	2.1	1.0	(0.8)
Dead Coral	64.5	76.7	85.8	68.9	74.0	(9.4)	65.1	75.1	77.1	73.3	72.6	(5.3)
Live Coral	28.1	16.3	10.2	22.2	19.2	(7.7)	24.1	15.8	15.7	18.3	18.5	(3.9)
(Sessile invertibrates - coral)	1.0	1.5	0.1	0.4	0.8	(0.6)	0.1			0.5	0.2	(0.2)
total algae	6.4	5.9	3.8	8.0	6.0	(1.7)	10.9	9.0	7.1	7.8	8.7	(1.7)

12 months: percentage cover

Appendix 4.2

	open plots						exclosure plots					
	1	2	3	4	$\bar{X}$	(S.D.)	1	2	3	4	$\bar{X}$	(S.D.)
Acropora	9.8	7.3	6.3	11.3	8.7	(2.3)	10.7	7.3	9.4	8.9	9.1	(1.4)
Montipora	0.2	1.0	0.8	3.3	1.3	(1.4)	5.1	0.9	1.3	4.5	3.0	(2.2)
Pavona												
Cyphastrea				0.1	0.0	(0.1)						
Favia	0.9		0.1	0.5	0.4	(0.4)			0.3	1.1	0.4	(0.5)
Favites	3.7	0.4		3.8	2.0	(2.1)	1.9		1.8	3.3	1.8	(1.4)
Goniastrea	0.1	0.1		0.5	0.2	(0.2)	0.6	0.3	0.2	0.6	0.4	(0.4)
Hydnophora			0.1		0.0	(0.1)				0.3	0.1	(0.2)
Leptoria			0.1	0.5	0.2	(0.2)		0.1		0.6	0.2	(0.3)
Platygyra				0.1	0.0	(0.1)				0.4	0.1	(0.2)
Plesiastrea												
Fungia		0.1			0.0	(0.1)						
Lobophyllia		0.1			0.0	(0.1)						
Pocillopora	0.7	0.3	1.7	1.6	1.1	(0.7)		0.1	1.4	2.1	0.9	(1.0)
Stylophora				0.3	0.1	(0.2)						
Goniopora	0.1				0.0	(0.1)		0.3			0.1	(0.2)
Porites	1.4	3.0	1.1	1.7	1.8	(0.8)	0.8	3.9	1.1	0.8	1.7	(1.5)
(Galaxea) Palythoa				0.7	0.2	(0.4)			0.1		0.0	(0.1)
Lobophyton				0.1	0.0	(0.1)	0.2			1.4	0.4	(0.7)
Sinularia								0.9			0.2	(0.5)
Tridacna	0.4	0.2	0.2		0.2	(0.2)	0.1			0.2	0.1	(0.1)
Chlorodesmis	3.0		1.3	3.8	2.0	(1.7)	1.6	4.6	2.5	2.8	2.9	(1.3)
Caulerpa		0.1	0.4		0.1	(0.2)	0.4				0.1	(0.2)
Drift algae	10.7	0.8			2.9	(5.2)	4.1	2.2			1.6	(2.0)
Halimeda	0.1				0.0	(0.1)		0.1			0.0	(0.1)
unidentified algae										0.1	0.0	(0.1)
unidentified coral	0.8	0.2	0.5	0.5	0.5	(0.2)		0.1	1.2	0.5	0.5	(0.5)
Dead Coral	69.8	85.4	87.1	71.1	78.35	(9.2)	74.9	79.5	82.1	73.2	77.4	(4.1)
Live Coral	16.0	13.5	10.9	24.3	16.18	(5.8)	19.0	13.0	15.3	22.1	17.4	(4.0)
(Sessile invertebrates - coral)	0.4	0.2	0.2	0.8	0.4	(0.3)	0.3	0.9	0.1	1.6	0.7	(0.7)
total algae	13.7	0.9	1.7	3.8	5.0	(5.9)	5.8	6.8	2.5	2.9	4.5	(2.1)

Appendix 4.3

	0 months		12 months	
	Open/Closed		Open/Closed	
	U	P	U	P
massive	2	.114	7	.886
encrusting	8	1.0	8	1.0
wedge or blade like	7.5	> .886 <1.0	6	.686
digitate or low corymbose	8	1.0	7	.886
solitary	6	.686	3.5	>.2 <.342
clustered branchlets	7	.886	6	.686
open arborescent	7.5	> .886 <1.0	7	.886
soft corals	4	.342	4	.342

Appendix 4.3 Results of Mann-Whitney U-tests comparing the percentage cover of different morphological categories of coral between the open and closed plots of the recovery experiment. U is the test statistic and p is the probability that the differences were observed by chance. The test is 2-tailed.

Appendix 4.4 The percentage cover of the different morphological categories of coral in the eight plots of the recovery experiment.

Appendix 4.4

0 months: percentage cover

Morphology	open plots 1	2	3	4	$\overline{X}$	S.D.	exclosure plots 1	2	3	4	$\overline{X}$	S.D.
massive	4.2	4.4	1.9	7.1	4.4	(2.1)	4.9	4.9	1.3	6.9	4.5	(2.3)
encrusting	4.7	1.4	1.2	3.9	2.8	(1.8)	0.9	4.8	1.6	2.4	2.4	(1.7)
wedge or blade like	1.3	2.8	0.3	1.0	1.3	(1.1)	2.4	0.9	0.3	1.8	1.4	(0.9)
dignitate or low corymbose	18.8	6.8	5.8	8.4	10.0	(6.0)	15.5	5.6	9.9	5.8	9.2	(4.6)
solitary	2.3	0.1	0.1	0.0	0.6	(1.1)	0.1	0.0	0.0	0.2	0.1	(0.1)
clustered branchlets	0.0	0.4	1.1	1.5	0.7	(0.7)	0.2	0.4	1.0	1.4	0.8	(0.6)
open arborescent	0.0	0.0	0.0	0.5	0.1	(0.3)	0.0	0.0	1.3	0.0	0.3	(0.7)
soft corals	0.7	0.0	0.0	0.4	0.3	(0.3)	0.0	0.0	0.0	0.3	0.1	(0.1)

12 months: percentage cover

Morphology	open plots 1	2	3	4	$\overline{X}$	(S.D.)	exclosure plots 1	2	3	4	$\overline{X}$	(S.D.)
massive	5.0	3.6	1.7	7.2	4.4	(2.3)	6.2	4.6	2.0	7.1	5.0	(2.2)
encrusting	2.9	1.2	1.3	3.8	2.3	(1.3)	2.1	1.0	2.5	5.0	2.7	(1.7)
wedge or blade like	3.2	1.3	0.1	1.7	1.6	(1.3)	1.2	2.5	0.5	1.1	1.3	(0.8)
dignitate or low corymbose	6.6	6.0	6.2	9.6	7.1	(1.7)	9.4	4.8	8.9	7.8	7.7	(2.1)
solitary	0.4	0.3	0.2	0.0	0.2	(0.2)	0.1	0.0	0.0	0.2	0.1	(0.1)
clustered branchlets	0.7	0.3	1.7	1.9	1.2	(0.8)	0.0	0.1	1.4	2.1	0.9	(1.0)
open arborescent	0.0	0.0	0.0	0.1	0.0	(0.1)	0.0	0.0	0.0	0.0	0.0	(0.0)
soft corals	0.0	0.0	0.0	0.8	0.2	(0.4)	0.2	0.6	0.1	0.6	0.4	(0.3)

Appendix 5.1 Breaking experiment 1 - basic data

	Load at time of break g (L)	Distance to break mm (D)	Cross-section area at break - bivalve hole mm^2 (C)	Total cross-section area mm^2 (C)	Bending moment LXD	$\frac{WXD}{C}$
Acropora millepora	2720	47	77		127840	1660
	2120	52	70	-	110240	1575
	1890	26	63	-	49140	780
	2110	40	49	-	84400	1723
	1910	40	59	-	76400	1295
	2450	50	72	-	122500	1701
	2250	36	57	-	81000	1421
	1980	19	38	-	37620	990
	2500	50	80	-	125000	1563
	2070	45	65	-	93150	1433
Mean	2200	40.5	63	-	90729	1414
Standard deviation	276	10.9	12.9	-	31337	313
Pocillopora damicornis	9330	20	129	142	186600	1447
	7240	23	44	81	166520	3785
	13300	34	114	154	452200	3967
	18320	45	231	252	824400	3569
	11930	48	134	-	572640	4273
	12350	50	227	-	617500	2720
	9300	60	139	-	465000	3345
	7240	27	90	-	195480	2172
	11120	45	145	174	500400	3451
	15790	43	174	-	678970	3902
Mean	11590	38.5	156.7	142.7	465971	3263
Standard deviation	3574	11.5	53.6	57.3	223716	889
Acropora palifera	38040	50	881	-	1902000	2159
	9390	28	266	-	262920	988
	25800	20	414	-	516000	1246
	9170	17	158	-	155890	987
	21530	50	223	-	1076500	4827
	9960	46	224	241	458160	2045
	30500	50	279	-	1525000	5466
	26830	25	265	-	670750	2531
	40270	35	447	-	1409450	3153
	29890	25	203	-	747250	3681
Mean	24140	34.6	337.7	336	872392	2708
Standard deviation	11480	13.3	210.8	221.7	582698	1566

Tourist impact on reef corals : 1984 report to Great Barrier Reef Marine Park Authority / A.M. Kay and M.J. Liddle

D. Wachenfeld	29/6/99	