THE EFFECT OF SEDIMENTS ON AUSTRALIAN SCLERACTINIAN CORALS

by

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ABSTRACT

Effects of calcareous sediments on the behaviour, morphology and physiology of hermatypic corals from Lizard Island, northern Great Barrier Reef, Australia, are described.

Principal sediment rejection mechanisms of 42 species from 31 genera involve tissue expansion, ciliary currents, tentacles, mesenteries, mucus secretion, and pulsed contractions of tissues. Sediment responses are normally size-specific: cilia and mucus are employed for silts and fine sediments (<250um), mainly tissue expansion for larger sediment sizes; silts can be manipulated by all corals, but the number of species capable of moving larger sizes with ease decreases as particle size increases; coarse sediments (500um-1mm) are cleared more slowly than fine (63-250um), but fine sed' ent may be more dangerous to corals. Intensity of the sediment influx can affect the sediment response: silts arriving at tissue surfaces *en masse* are agglutinated in mucus and can sometimes flow off the surface whereas silts arriving singly or in small clusters must often be removed actively even from inclined surfaces. Interspecific rejection capability and efficiency are correlated with calice size. Some corals adapt to persistent sediment influxes by increasing rejection efficiency.

Sediment rejection efficiency is not directly related to sediment tolerance: some species are poor sediment rejectors but have high sediment tolerance. Persistent sediment influxes of $50mg.cm^{-2}.day^{-1}$ for <4 days *in situ* can be lethal to susceptible tissues of intolerant species. Mortality of *Leptoria phrygia* in the laboratory occurs at $25mg.cm^{-2}.day^{-1}$ over 23 days and may underestimate field mortality. Morphology, from macro to very fine scales, is a crucial control on tissue damage from sediments, both between and within species. Turbulence influences differ between species.

Modified techniques are developed for tissue recovery and total lipids in *Leptoria phrygia*. 24-hour photosynthesis to respiration ratios are used to show that calcareous sediment layers of substantially less than 1mm can cause energetic imbalance due to light attenuation.

Interspecific differences in sediment responses can explain several natural species distributions: for example, *Leptoria phrygia* and *Favia stelligera*, excluded from high sediment areas, are very intolerant of overlying sediment; *Porites lobata*, *P. lutea* and *Montipora aequituberculata*, common in high sediment areas, show very high tolerance to sediment accumulations; *Echinopora lamellosa*, also common, shows direct growth responses to sediment. Return times of turbulence and sediment 'events' can also explain morphology and species differences between habitats. Particle size will be very important in predictions of community responses to increased sediment loads.

CHAPTER 1

GENERAL INTRODUCTION

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INTRODUCTION

Background

Coral reefs are complex ecosystems which have major scientific, economic and aesthetic importance. Their productivity is high and supports a diversity of organisms that is probably without equal in the marine world. Reef-dependent fish, molluscs, crustaceans, echinoderms, macroalgae and many other organisms, provide a major source of protein and vitamins for the human inhabitants of many of the world's archipelagos. Many reef organisms exist in symbiotic associations and most have intricate predator-prey relationships, where survival depends upon complex recognition, including a wide diversity of defensive and offensive chemicals. These chemicals make reefs one of the richest sources of medically active compounds for the treatment of human disease. Income from reef tourism has become very important to the economies of many countries and its importance continues to increase as populations multiply and as other resources dwindle. Reefs also play an often undervalued role in protecting coastal zones from erosion by dissipating wave energy.

High impact events of climatic and biological origin such as cyclones (e.g. Endean, 1976; Williams, 1984), and population explosions of 'pest' species such as *Acanthaster* (Moran, 1986), can have dramatic effects on coral reefs. However, in the past few decades, coastal zone ecosystems have been subject to increasing degradation from human activities, with enormous loss of major ecosystems and vital natural resources. Such degradation results from direct loss of habitat through coastal construction and indirect loss from changes to coastal water quality and dynamics. The latter include major changes in ambient sediment loads, and many forms of chemical, thermal and biological pollution.

The prevention or control of human activities causing this damage is far from simple as developments are often of major commercial importance. In many cases, too little is known about the tolerance

limits of reef organisms to environmental degradation to offer clear guidelines for effective management and sustainable conservation practices.

Of the variety of impacts causing reef degradation, the effect of increased sediment loads in waters surrounding reefs is one of the most widespread and severe. Deterioration of coral reefs as a result of sedimentation and turbidity has been reported from all biogeographic regions of the world (*Caribbean*: Rodriguez, 1981; Rogers, 1985; *Indian Ocean*: Salm, 1983; IUCN/UNEP, 1985; *West-Pacific*: Gomez, 1980; Dahl, 1984, 1985; Lal, 1984; Musik, 1985) and the incidence of such reports is increasing. Johannes (1977) considered sedimentation and turbidity resulting from human activities to be a greater problem in the marine environment than "all other forms of human insult combined". Although this may underestimate the importance of other forms of degradation, evidence from the recently compiled Coral Reefs of the World (UNEP/IUCN, 1988a-c) is clear. These volumes give detailed accounts of important reef areas worldwide and their status in relation to present or impending impact. Sedimentation problems are severe in all regions: in the Caribbean, for example, almost half of the 37 countries discussed report widespread damage from increased sediment loads.

Sedimentary regimes of coral reefs

The range of natural sedimentary regimes generally associated with Indo-Pacific coral reefs is, in many ways, comparable with the range of reef types themselves. Within constraints of bathymetry and sea temperature, substrate characteristics of the sea floor are the primary control of the types of benthos that can occur. If hard substrate is prevalent and permits the development of a coral reef, the structure and morphology of that reef, together with the range of ecosystems occurring with it, will largely reflect past and present sedimentary regimes which themselves reflect the proximity of major land masses and associated river outlets.

Indo-Pacific reefs can be classified in a spectrum ranging from open-ocean atolls remote from any land mass, to fringing reefs growing

in close association with continents and large islands[1].

Atolls and other isolated types of reef, are entirely biological in origin and exist as 'oases' in nutrient-poor regions of the deep open oceans. All surface structures are almost exclusively composed of calcium carbonate: hard substrates being the product of calcifying organisms and the cementing action of coralline algae, and soft substrates being composed almost entirely of carbonate debris. On these reefs, clear ocean water allows penetration of an abundance .of light resulting in high productivity of organic carbon, principally by symbiotic algae in calcareous organisms. Other nutrients, notably nitrate and phosphate, a, 'ery limiting and are strongly conserved through internal recycling.

In great contrast, reefs subject to major terrigenous influence, are relatively poorly consolidated. Fringing reefs exposed to strong wave action may are often devoid of limestone, consisting of isolated corals growing directly onto exposed rock surfaces, while those adjacent to protected shorelines are often little more than accumulation of terrigenous debris, sand and mud, held in place by a veneer of actively growing coral. Where terrigenous influences are greatest, organic carbonate production is greatly reduced by sedimentation and turbidity, but other nutrients, so conspicuously lacking in the open ocean, generally abound. Coral communities associated with major land masses are restricted by turbidity to shallower depths. They are less *Acropora*-dominated than open-ocean reefs and are generally more diverse, both in species composition and community types.

There are no atolls associated with the Great Barrier Reef (other than shelf atolls), but most general aspects of the ecological variation found in the Indo-Pacific is expressed between the outer barrier reefs, which are entirely carbonate and border clear deep oceanic water, and onshore fringing reefs which are overwhelmingly dominated by turbid

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1. For reviews of reef types and origins see Stoddart (1969), Sheppard (1982), and Scoffin and Dixon (1983). For specific discussion of the Great Barrier Reef Province see Fairbridge (1950), Hopley (1982), Scoffin and Dixon (1983), Veron (1986), and in particular, Maxwell (1968, 1973) who also provides a comprehensive examination of sediment distributions.

water and terrigenous sediments. Lizard Island, where the studies described in this thesis have been undertaken, is situated approximately mid-shelf, and has a range of marine environments well within these extremes, with resulting ecosystems expressing some of the characteristics of both. Offshore waters are moderately clear, sediments are dominated by carbonates, but have a (local) terrigenous component; turbulence is moderate on exposed reef slopes to low in the lagoon. The resulting coral communities are heterogeneous compared to the uniformity of the barrier reefs, but lack the variation found among the many types of onshore fringing reefs occurring along the adjacent coastline. The major habitats of Lizard Island are introduced in the final section of this Chapter.

Principal influences on sedimentary regimes. The prevailing sediment regime surrounding a reef is inextricably interwoven with that of water movement[1]. The direction, persistence and energy of waves are all substantially influenced by wind speeds, fetch and local topography. Waves, in turn, create water movement which suspends and resuspends bottom sediments and determines the extent and size of particles persistently in suspension. In general, the size distributions of sediments reflect the energy of the surrounding water environment: coarser sediments are found in high energy environments and finer sediments in low energy environments. In most circumstances, this is modified by the availability, density and composition of sediments and can also be substantially altered by imports from foreign environments via currents or river outflows. There is a decline of wave energy with depth which generally causes a reduction in the size of particles that are resuspended, although larger sediments resuspended at shallower depth as a result of high wave energy may ultimately be transported to depths where they would not normally be resuspended. Local topography can also have a significant effect on the local sediment environment of a coral by creating eddies and surge channels.

Effects on local turbidity, sedimentation and abrasion characteristics caused by increased ambient sediment loads are

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1. Mechanics of water movement and sediment transport are discussed in texts by Tritton (1977), Reineck and Singh (1980) and Leeder (1982).

complex and difficult to predict without detailed knowledge of prevailing currents, wind speeds (direction and periodicity), and topography. Understanding the biological effect of increased sedimentation on corals is even more difficult. Increased sediment loads resulting from human activities are rarely isolated, but generally occur in synergism with other factors. For example, river outflows may be sites of periodically reduced salinity, or may contain increased nutrients, organic content, or levels of pathogens. Artificial structures such as breakwaters, may change circulation patterns and modify the effects of increased sediment loads from terrestrial sources.

Sedimentation rates and their influence on coral communities. It is widely recognised that naturally high sediment loads in waters surrounding reefs can strongly affect the ecology and composition of coral communities (Roy & Smith, 1971; Loya, 1976; Randall & Birkeland, 1978; Acevedo & Morelock, 1988) and be determinants of the morphology of component species (Marshall & Orr, 1931; Maragos *et al*, 1970; Chappell, 1980; Veron, 1981). Changes in species composition or abundance have also been attributed to increases in sedimentation loads due to human activities (Brock *et al*, 1966; Marsh & Gordon, 1974; Dodge & Vaisnys, 1977; Cortes & Risk, 1985).

Measurements of sedimentation rates are not always inter-comparable because collecting traps are of different types, or placed at different depths and heights above the substrate (all of which can affect the sediment collected). However, reported average sedimentation rates surrounding naturally occurring reefs range from less than $1mg.cm^{-2}.day^{-1}$ to more than $200mg.cm^{-2}.day^{-1}$ (e.g. Dodge *et al*, 1974; Loya, 1976; Randall & Birkeland, 1978; Marszalek, 1981; Rogers, 1983; Kojis & Quinn, 1984; Tomascik & Sander, 1985), with levels from human impact of $>150mg.cm^{-2}.day^{-1}$ (e.g. Marszalek, 1981; Sakai *et al*, 1989[1]) and reaching well over $>1000mg.cm^{-2}.day^{-1}$ (Maragos, 1972). These studies suggest that rich coral growth and diversity are normally limited to areas where mean yearly

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1. Calculated from their Table 1, allowing for trap area of approximately $20cm^2$ and a 30-day collecting period.

sedimentation rates are less than about $20mg.cm^{-2}.day^{-1}$. In assessing the available information, Pastorok and Bilyard (1985) develop a classification of degree of impact which argues that rates as low as $1-10mg.cm^{-2}.day^{-1}$ may cause impacts on coral communities and that $50mg.cm^{-2}.day^{-1}$ can cause "severe to catastrophic" effects. However, greater understanding of the relationship between sedimentation and turbidity, and coral cover, species diversity, and relative dominance, is clearly needed. Fringing reef communities of the Great Barrier Reef are very diverse, often with high coral cover (Ayling & Ayling, 1987; Veron, 1987; Veron, *pers.comm.*) despite the fact that sediment traps have recorded sedimentation rates of $>250mg.cm^{-2}.day^{-1}$ for periods of up to two months, with rates of $50-100mg.cm^{-2}.day^{-1}$ being very common (Marshall & Orr, 1931; Willis, 1987; Mapstone *et al*, 1989), and giving mean yearly rates of $>80mg.cm^{-2}.day^{-1}$ (Willis, 1987)[1].

These two, apparently conflicting, perspectives may not be as incompatible as first appears. Firstly, although those communities which are adapted to very low sedimentation rates may be impacted and show reduced cover when regimes change abruptly, there may be another stable state at higher sedimentation rates which has a different composition and species dominance, but which shows a similar diversity. But, at present, probably a more important point relates to the methods of sedimentation rate measurement mentioned above, and the implications of temporal differences in sedimentation rates to communities (i.e. the absolute number of days that extreme rates persist, in contrast to measurements of mean rates over days, months or years). Some of the studies cited by Pastorok and Bilyard (1985) referred to above showed very high variance around the mean indicating that over some periods, the sedimentation rates can also be extreme. As will become apparent during the course of this thesis, the variability and the persistence of high levels of sedimentation or long periods of calm, may explain some anomalies in species distributions. It will therefore be very important to standardise depths and sampling periods for sedimentation rate data to improve the inter-comparability of studies.

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1. Calculated from Figure 14, p.41 in Willis (1987), corrected for 56-day period and trap aperture of $7.07cm^2$.

Potential effects of sediments on corals

There is an increasing body of information relating to the effects
of sediments on corals, but as yet, it is still very difficult to
predict changes occurring from variations in ambient sediment loads.
The principal reason is that the sediment problem is very complex,
involving a multiplicity of interactions between the huge range of
potential sediment influence and a similarly huge range of potential
responses shown by corals.

Most corals cannot withstand total burial or heavy coatings of
sediment for more than a few hours (Mayer, 1918; Edmondson, 1928;
Marshall & Orr, 1931; Roy & Smith, 1971; Thompson, 1979; Rogers, 1983),
and thus, where increased sedimentation levels are extreme, reef species
may simply become buried and die. Where sediment increases are less
extreme, one of the most important effects is the disruption of a
coral's energy budget. Corals can use a wide variety of food sources to
fulfil their energy requirements: they can feed heterotrophically, using
tentacles, cilia and/or mucus nets to capture passing planktonic
organisms (Yonge, 1930; Abe, 1938; Lewis & Price, 1975, 1976); they can
also feed on suspended particulates (Lewis, 1976), and are able to
absorb dissolved organic matter (Sorokin, 1973); and, most
significantly, they are able to utilise solar energy through the
translocation of photosynthetic products from symbiotic zooxanthellae
(e.g. Muscatine & Cernichiari, 1969). All of these feeding mechanisms
can be affected by variations in sedimentation.

Because of their dependence on photosynthesis, the local
distribution and abundance of corals is strongly controlled by factors
that affect the level of incident light, such as shading and depth (e.g.
Sheppard, 1982). Light is also attenuated by sediments in suspension
(Jerlov, 1970; Kirk, 1983), and thus turbidity may place similar
constraints on coral distributions and abundance. However, the effects
of turbidity may not be identical to those of depth or shading because
of differences in the spectral quality of light reaching the coral.
Such parameters vary with the properties of suspended sediment such as
its size, reflectivity, and organic content (Jerlov, 1970; Kirk, 1983).
Reductions in photosynthesis and calcification rates resulting from

turbidity have been demonstrated experimentally (Dallmeyer *et al*, 1982).
In this case the effect of suspended peat caused very significant
spectral changes at critical wavelengths.

Settling and suspended sediments may interfere with normal
heterotrophic feeding by clogging up feeding tentacles and cilia
(Szmant-Froelich *et al*, 1981). Most corals attempt to dislodge
overlying sediments using mucus secretions to consolidate the particles,
and then removing them from the surface with tentacle movements, ciliary
currents, and tissue expansion (Hubbard & Pocock, 1972; Bak &
Elgershuizen, 1976). Mucus secretion may constitute a significant
energy loss to a colony (Benson & Muscatine, 1974; Daumas & Thomassin,
1977; Ducklow & Mitchell, 1979a; Crossland *et al*, 1980; but see Krupp,
1984). Behavioural sediment rejection activities also constitute a
drain on energy reserves (Aller & Dodge, 1974; Dallmeyer *et al*, 1982).

Sediments overlying the substrate may inhibit the settlement of
coral larvae (Edmondson, 1928; Harrigan, 1972; Maragos, 1972; Dodge &
Vaisnys, 1977; Babcock & Davies, *in press*), and this may be a
significant cause of longterm changes in community composition where
layers of sediments form on the substrates as a result of changing
sediment regimes.

Several authors have alluded to the potential importance of abrasion
in local distribution of corals (Johannes, 1975; Loya, 1976; Rogers,
1983), but the importance of this factor is unknown as there have been
no studies on the direct effect of abrasion on coral tissues.

Turbidity and sedimentation can clearly affect both autotrophic and
heterotrophic feeding mechanisms, while at the same time increase energy
expenditure on sediment removal and tissue repair. At high levels these
may lead directly to exhaustion and death. But in more chronic
situations there may be significant decreases in energy available for
growth and reproduction. Correlative studies have indicated links
between high sedimentation or turbidity and lowered reproduction in
Acropora palifera (Kojis & Quinn, 1984), and calcification and growth
(Aller & Dodge, 1974; Dodge *et al*, 1974; Dodge & Vaisnys, 1977; Bak,
1978; Rogers, 1979; Hudson & Robbin, 1980; Dodge, 1981; Hudson *et al*,
1982).

Where morphology allows, sediment accumulations may cause increases in diffusion barriers, increases in tissue abrasion, and increases in the risk of disease. Hodgson (1990) has recently provided evidence of a potentially significant role of bacteria in tissue mortality. He tested corals under sedimentation regimes with and without the addition of an antibiotic and found a very significant decrease in tissue death in the presence of sediment and antibiotic combined, compared to sediment alone. Bacteria have been found to be present in high concentration in coral mucus and surface tissues (Ducklow & Mitchell, 1979b; Paul *et al*, 1986; Coffroth, 1988) and may be an important supplementary cause of tissue necrosis even under conditions of naturally high sedimentation or turbidity where bacterial numbers are not enhanced from terrestrial sources.

All of the factors described above may reduce the relative or absolute abundance of a species by decreasing its ability to compete successfully for resources such as substrate or light, by reducing growth rates and reproductive output, or by directly reducing living surface area through tissue death. Restrictions on larval settlement will also have consequences for species composition and abundance which will inevitably be influenced by inter-species variations in larval tolerance.

Biological indicators of change

Of fundamental importance to reef management is the ability to reduce the scale of impact occurring on reefs and to recognise degrading influences in time to take some effective action. Both physiological criteria and selected species survival have been used successfully in terrestrial and marine environments as *indicators* of environmental conditions (Gilfillan *et al*, 1984; Bock & Webb, 1984; Geller, 1984). To be useful, an environmental indicator must show a detectable response to levels of a stress which have not yet caused widespread mortality in the general community. Ideally, the *type* and *intensity* of the stress should be predictable from the response of the indicator, but in reality these are not often well defined. Grizzle (1984) argues that indicator species should not only be intolerant of changes in the environment but should also be abundant. This view is supported by Mergner (1977),

who highlights the advantages of sessile or homing organisms over mobile species. In his own studies, he used hydroids as indicators of water movement and illumination in the Caribbean and Red Sea, which fitted both of these additional criteria. Reese (1981) argued that obligate coral-feeders such as chaetodonts (butterflyfish) should provide useful indications of overall coral cover and substrate. But, although these fish may be useful in long-term studies, the theory assumes that corals have already undergone mortality, often on a major scale, and as indicators these species are therefore too far temporally removed from the impact event.

In the marine environment, it is particularly important that indicator species be conspicuous and readily identifiable, as underwater time is always a significant restriction. Corals are known to have narrow tolerance limits to a variety of environmental parameters and there is a real danger that levels of stress will exceed these limits before they are detected, even in responsive species. There should, however, be considerable scope for the use of indicator species in the detection of chronic (as opposed to acute) sediment influences. Community composition studies show that the relative abundance and distribution of species varies with sediment regimes, some species being entirely excluded from turbid environments or environments with high sedimentation rates. At least some of these species should have *potential as environmental indicators.*

THESIS STRATEGY, AIMS AND OBJECTIVES

The purpose of this study is to investigate the effect of settling inorganic sediment on a selection of corals occurring on a midshelf reef of the central Great Barrier Reef. The principal aim is to examine the range of sediment responses adopted by Australian corals in order to (a) provide insight into the extent to which sediment acts as a control on natural distributions of corals, and (b) to highlight, where possible, those species or species-characteristics which could serve as indicators of sediment stress on the wider community. The study specifically excludes the effects of turbidity and organic sediments (with the

exception of a few small exploratory tests) and thus minimises synergistic effects associated with pollutants.

As far as possible, all species used in experiments were chosen on the basis that they are widespread throughout the Indo-Pacific, and are relatively common and easy to identify in the field. The results therefore, should be readily applicable to other regions of the Great Barrier Reef and elsewhere. Where species did not fulfil these criteria (e.g. identification of *Porites* to species was not easy either in the field or the laboratory), they were included for important ecological reasons.

Although laboratory work has formed an important part of this study, corals did not always respond the same way in the laboratory and in the field. Experiments were therefore concentrated in the field, laboratory experiments playing a major part only when field conditions did not allow adequate environmental control, or where field experimentation was logistically impractical. As far as possible, this laboratory work has been backed up by substantial fieldwork to validate (or otherwise) the laboratory findings.

The thesis is organised into two principal Sections. The first concerns responses of many species to sediments and the second concerns physiological responses of *Leptoria phrygia*. As background to these Sections, the Introduction concludes with a general description of Lizard Island, where all field and aquarium experiments were undertaken.

The aim of the first Section (Section I: Chapters 2-5) is to characterise interspecies variations in sediment response and to identify sediment-sensitive and sediment-tolerant species. It examines the general strategies that Indo-Pacific corals use to overcome problems of sedimentation, the interspecific differences in sediment rejection efficiency and sediment tolerance, the effects of sediment size, and the importance of morphology and water turbulence.

Chapter 2 examines behavioural responses of a total of 41 species, highlighting those which are especially active or inactive in their responses. Chapter 3 investigates the rejection efficiencies of 22

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species in calm sea conditions followed by an evaluation of the effects of increasing turbulence on a subset of these species. Chapter 4 examines the sediment tolerance of 10 species subjected to daily sediment influxes over a period of eight days, and highlights the influence of minor variations in colony morphology. Chapter 5 describes the physical attributes of habitats at Lizard Island, and relates the distribution of experimental species and the morphological attributes of *Leptoria phrygia* to these habitats.

The aim of the second section (Section II: Chapters 6-8) is to relate specific physiological responses of the meandroid faviid *Leptoria phrygia* to sediment influx.

Using modified methods for tissue recovery and lipid analysis which are described in Chapter 6, Chapter 7 examines lethal and sub-lethal effects of sediment loads to assess threshold tolerance levels. (This study was designed to incorporate measures of total lipid, but frozen samples were destroyed during storage.) To conclude this Section, Chapter 8 models the effect of light attenuation due to sediment accumulations on the 24-hour photosynthesis to respiration (P/R) ratio of this coral, and discusses the implications in relation to autotrophy and energy budgets.

The Discussion, Chapter 9, integrates the results of both Sections in the light of existing knowledge, and discusses sedimentation in relation to other effects of sediments on corals and their distributions.

All information about individual species examined during the course of these studies is summarised on a species by species basis in Appendix A. Most of the experimental corals are illustrated either within the main body of the thesis, or in two Plates bound with this Appendix. If an illustration exists, its Plate reference and location can be obtained either from the Table of Plates, or from the relevant species summary in Appendix A.

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LIZARD ISLAND

All experimental work in the field and in laboratory aquaria was undertaken at Lizard Island, Great Barrier Reef (Figure 1.1, Plate 1.1).

Lizard Island is a midshelf, granitic, continental island (maximum height 360m) of the northern Great Barrier Reef (14°41'S, 145°24'E), 36km from the Queensland coast and 16km from the outer barrier reef. The island has permanent fresh water with most of the rainfall (1.5-2.0m annually) falling between December to April. Surface seawater temperatures ;e from 23-30°C. Maximum spring tidal range ir ? metres, but normally tides are <1m (neaps) to 2.5m (springs). During the months of March to September prevailing winds are from the south-east and consistently reach 15-25 knots. From October to March the region experiences lighter and more variable winds, with long periods of calm weather or light north-westerlies. At Lizard Island, wave action closely reflects wind conditions, the force of open ocean swells having been completely broken by the outer barrier reefs situated at the continental shelf edge.

Three principal regions of Lizard Island were defined by visual inspection, corresponding broadly to exposure categories. The first, or 'Exposed' region, stretches from the southern tip of South Island, around the south-east and north-east sides of Lizard Island via Pidgin Point, to North Point (Figure 1.1). This region is exposed to the force of the prevailing and consistently strong south-easterly winds throughout the winter. The second, 'Moderately-exposed' region, stretches from Granite Head across the north-west side of the island to Vicky's Reef and is exposed to the somewhat milder summer north-westerlies but sheltered in winter from the strong south-easterlies. The third, 'Sheltered' region, includes the lagoon and adjacent reefs which are protected by islands and reefs at all times.

Exposed region (Coconut Bay via Pidgin Point to North Point)[1]. The intertidal and immediate subtidal of Coconut Bay comprises a wide

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1. The southeast-facing reef between South and Bird Islands also falls within this region but was not examined in detail.

Map labels: North Point, Mermaid Cove, Granite Head, Turtle Beach, Watsons Bay, Osprey Is, Crystal Beach, Cook's Look, Pidgin Point, Coconut Bay, Lizard Head, Lagoon, Bird Is, PALFREY ISLAND, SOUTH ISLAND, Research Station

LIZARD ISLAND

0   0.5   1   1.5
KILOMETRES

N
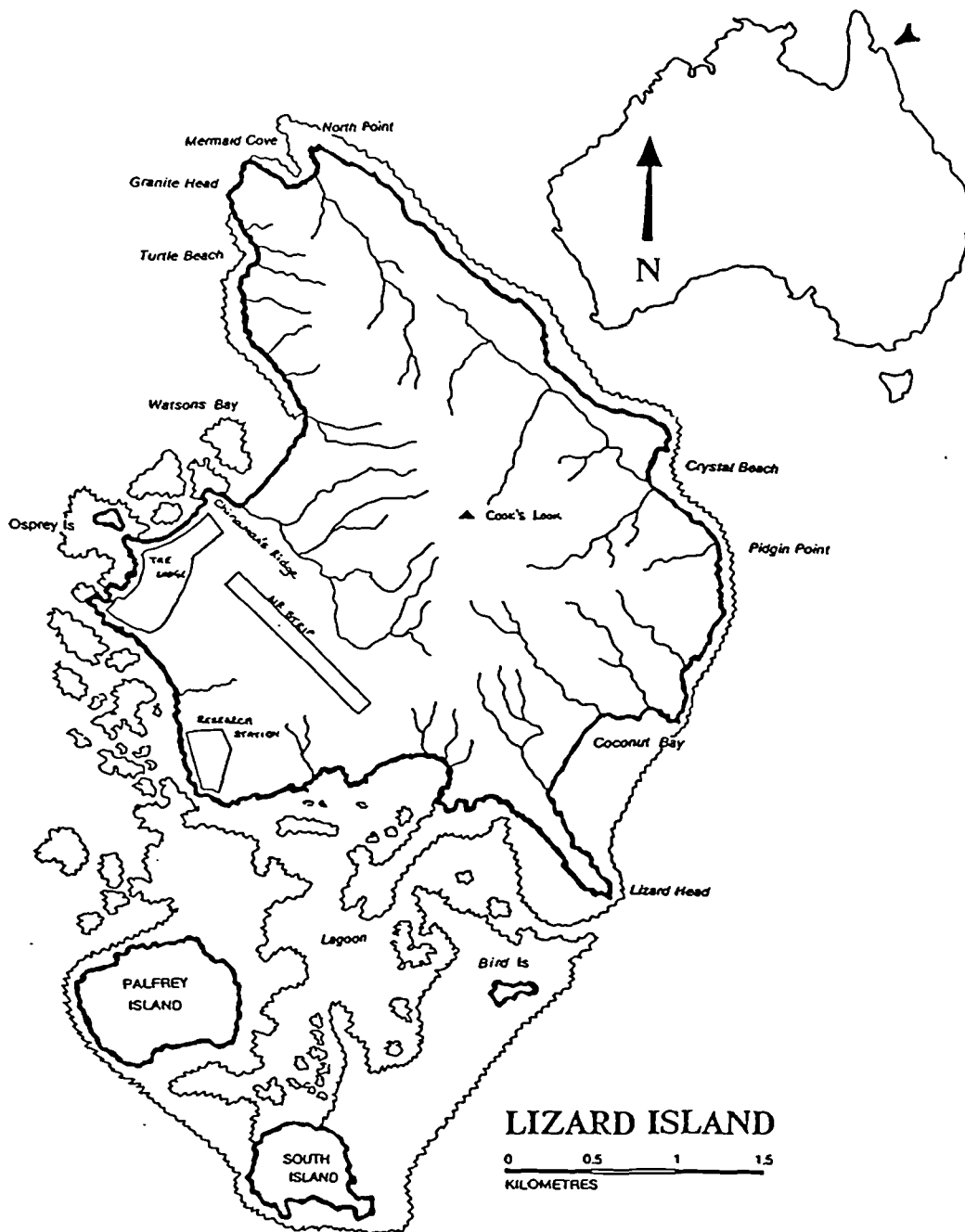
Figure 1.1. Lizard Island and its location.

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reef flat of several hundred metres which is exposed at low tide and
gives way to a short (generally 2-3m) but abrupt dropoff for most of
its length. At the base of the dropoff is a shelving reef-rock
and/or sand substrate which in many areas has a rich and diverse
coral and fish fauna. Intermittently along the length of the bay,
the drop-off is broken by surge channels or sections of smoothly
shelving reef-rock with a lower and less diverse coral cover. At
variable depth but generally around 8-12m, the hard reef substrate
gives way to a shelving soft-bottomed substrate.

The reef topography from the northern end o. Coconut Bay around
Pidgin Point, Crystal to North Point is fairly uniform. With the
exception of the shelving substrates scattered with rocky outcrops
which front the various beaches along this section of coast, the
fringing reef is more or less continuous. In general there is a
narrow to moderately wide reef flat (approximately 20-100m) which
falls in an abrupt vertical drop-off to a depth varying from 2-3m
(rare) to 6-10m (common). The base is generally soft sediment of
varying thickness overlying rock interspersed with coral outcrops.
This substrate slopes more gently to greater depth. In several
regions the drop-off is cut by narrow surge-channels and caves.
Coral growth in the first two metres of the drop-off is rich and
diverse but declines abruptly thereafter. There is a distinct
difference in the general morphology of the corals which is strongly
three-dimensional at the shallow depths but becomes less so with
encrusting forms more obvious on the often somewhat shaded vertical
walls. Along the north-east face (Pidgin to North Point) there is a
consistent current (<0.5 knot) from south-east to north-west. In
certain areas such as the current-facing edges of promontories, the
predictable flow of water is exploited by a profusion of gorgonians,
crinoids, and other filter-feeding organisms.

Moderately exposed region (Granite Head to the north of Palfrey Island).
Reef fringes the coast to the south-east of Granite Head along to
the base of Cook's Look at the northern end of Watson's Bay. Within
the bay itself are a number of widespread patches of reef which rise
from 6-8m to mean low water levels. Clams, extensive soft corals,
large *Porites* bommies and faviids are all dominant features in this

Plate 1.1.   Lizard Island. View southwards from
                    Cook's Look to the lagoon showing
                    Bird Islets, South and Palfrey
                    Islands.

region. Most of the central and offshore areas of the bay are soft-bottomed with many typical soft-bottom communities including seagrasses, algae and free-living hard corals such as *Heteropsammia*, *Cycloseris* and *Trachyphyllia* (see also Fisk, 1981). The entire area is relatively shallow with depths still only reaching about 20m across the line from Osprey Island to Granite Head. *The subtidal* region between Osprey and Palfrey Islands is again relatively shallow and punctuated with wide patches of shallow reef dominated in some cases by banks of *Pocillopora damicornis*, in others by soft corals, along with faviids, encrusting *Montipora* spp., and acroporids.

The reefs in this moderately exposed region appear to be variable in both topographic complexity and coral cover and diversity. The region is fully exposed to the summer north-west storms but these are generally less persistent than the prevailing winter south-easterlies.

Sheltered region, including the Lagoon. The shallow patch reefs located between Palfrey and Research Point are locally rich and varied but much of this region is exposed at low water spring tides and thus represents a stressful intertidal region which probably limits the range of species present. Again soft corals are present in abundance and faviids, pocilloporids and acroporids are common with a range of other species in the deeper pools. *Acropora palifera* is found in what is, for Lizard Island, unique abundance in the reef area fringing the north of South Island. This section of reef was not examined in any detail during the present work but appeared to be fairly heavily scoured with much larger coarse grain sediments than any other section of the lagoon region. It may experience stronger water movement than would be expected from its relatively sheltered position from both south-east and north-west winds.

The central lagoon represents a different habitat. It is dominated by huge stands of only a few species which include enormous outcrops of branching *Porites*, both *P. nigrescens* and *P. cylindrica*; similarly huge stands of branching *Pachyseris rugosa* and *Echinopora mammiformis* and of foliose *Echinopora gemmacea*; somewhat smaller outcrops of *Pavona cactus* and fine branching *Millepora* sp.

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Comparable outcrops were never seen at any location in Exposed or Moderately-exposed regions with the exception of the south-east end of the patch reef to the north of Chinaman's ridge where small stands of *Porites rus* and both *P. cylindrica* and *P. nigrescens* were observed.

A range of massive corals such as *Diploastrea heliopora*, two *Platygyra* species, massive *Porites*, *Favia laxa*, etc., are present at Bird Island although their abundance is well short of that in Exposed locations. *Acropora* species are not abundant in any of these lagoon sites.

SECTION I

CHAPTER 2

SEDIMENT REJECTION MECHANISMS OF AUSTRALIAN

SCLERACTINIAN CORALS

SEDIMENT REJECTION MECHANISMS OF AUSTRALIAN SCLERACTINIAN CORALS

SUMMARY

The active sediment rejection mechanisms of 42 species from 31 genera of Australian mid-shelf scleractinian corals were investigated *in situ* and under the microscope in the laboratory. Influxes of four sediment sizes (silt: <63um; fine: 63-250um: coarse: 500um-1mm: and granule: 1-3mm) were simulated onto flat areas of tissue at doses of 50mg.cm^{-2} or 200mg.cm^{-2}.

Ciliary currents, tissue expansion and mucus entanglement were the most universal mechanisms for sediment rejection and were observed for all corals studied. Other mechanisms included direct tentacle manipulations and pulsed contraction/expansion of the polyp or tissues.

There was an overall decline in the ease of sediment movement as particle size increased.

The significance of ciliary mechanisms declined, and that of tissue expansion increased, as sediment particle size or sediment density increased. All corals were able to manipulate both silt and fine sediment with their cilia, and mucus entanglement was a very common ancillary mechanism for these sizes. Tissue expansion was rarely necessary for silt or fine sediment influxes of less than 50mg.cm^{-2} but became increasingly common if accumulations occurred or higher input loads were experienced. Mobilisation of coarse and granule sized sediments was principally through tissue expansion and contraction. Ciliary currents were sometimes important for coarse sediments but were rarely effective for granules.

Dense influxes of silts were usually trapped in mucus and could flow off the surface. Silt particles and neutrally buoyant particles of larger sizes meeting the surface singly or in small clusters, often required active rejection even from almost vertical surfaces. Sedimentation due to suspensions of these particles will tend to affect more of the tissue surface than larger, denser particles whose active rejection is more morphology specific. The energetic consequences may be important in limiting species distributions.

On the whole, congeneric species showed similar active rejection mechanisms. At the family level, the type of mechanism and balance between active and passive influences was diverse.

Active rejection capability was related to calice diameter. All large-polyped species were capable of rejecting all sediment sizes with comparative ease. Species with very small calices (*Porites* spp, *Montipora* spp.) were very poor active sediment rejectors. Those medium-polyped species which were relatively active normally had strong ciliary mechanisms.

The species examined are grouped into categories according to the degree of active rejection observed.

INTRODUCTION

Changing agricultural practices, widespread deforestation, and expanding coastal and offshore construction have caused major increases in ambient sediment loads in waters surrounding coral reefs. Increased sedimentation and turbidity have been implicated in the deterioration of
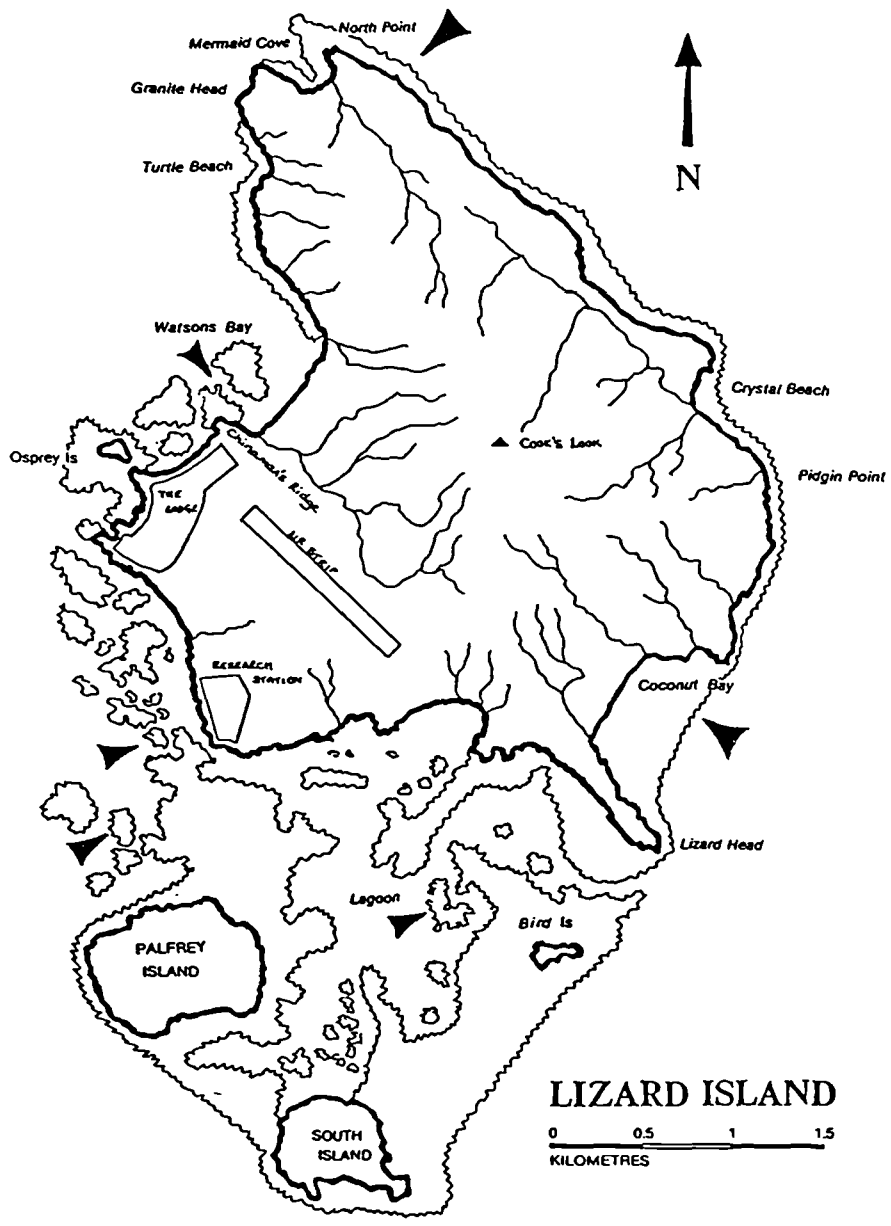
Figure 2.1. Lizard Island: arrows indicate the locations of field sites for behavioural observations.

coral reefs in all tropical oceans (UNEP/IUCN, 1988a-c), and a fuller understanding of comparative species responses to sediment is urgently required as a basis for informed management action.

As a precursor to a series of more detailed experiments examining sediment rejection efficiency and tolerance, a general survey of sediment rejection mechanisms was made of a representative range of Australian mid-shelf corals.

Sediment rejection mechanisms of Caribbean coral species have been studied in some detail (Hubbard & Pocock, 1972; Hubbard, 1973; Bak & Elgershuizen, 1976; Rogers, 1979, 1983; Lasker, 1980). A number of early studies were carried out on Indo-West Pacific species in the first half of this century (Mayer, 1918; Mayor, 1924; Marshall & Orr, 1931), but more recent work has been confined to certain species groups (Fungiids: Schuhmacher, 1977, 1979; Fisk, 1981), to a small number of species (Chansang, *pers. comm.*), or has been incidental to ecological studies.

During the present study, species were examined *in situ* to record their sediment-related behaviours, as well as environmental, morphological, and other incidental characteristics which could have a bearing on sediment tolerance. Individuals of each target species were then collected and their sediment rejection mechanisms were studied under the microscope in laboratory aquaria.

METHODS

All investigations were carried out at Lizard Island, northern Great Barrier Reef, Australia[1].

Field observations. Active sediment rejection mechanisms were examined *in situ* for a wide range of species at Coconut Bay, North Point, reefs fronting the research station, and sites within the lagoon

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1. For further descriptions of Lizard Island see the General Introduction and Chapter 5.

Plate 2.1.   Range of sediment grain sizes used
for experiments described in this
thesis (x 10).

Coarse	Fine
Granule	Silt

Plate 2.2.   Ingestion of fine sediment by
Acanthastrea echinata (x 5).

(Figure 2.1). Sediments were applied evenly to an area of the colony delimited by a 5cm x 5cm quadrat. The standard dose was 1.25g (50mg.cm^{-2}), although 5g (200mg.cm^{-2}) and extremes of 25g (1000mg.cm^{-2}) were used to investigate particular aspects of interest[1]. Mechanisms by which colonies rid themselves of sediment, as well as the apparent importance of morphology, water movement and commensals, were recorded. For most species, observations were made in daylight, at dusk, and in the dark.

General observations discussed in this Chapter, and summarised in species by species accounts in Appendix A, come from two sources: (a) from transects laid across community or depth zones to encompass range of reel ᵤₚ⁻⁻⁻phy, turbulence and microhabitats. For each target colony crossed by the transect line, observations were made of gross morphology and orientation, sediment-trapping or avoiding characteristics, distance from the nearest sediment pocket, presence of sediment on tissues, presence of mucus sheets or mesenteries, and any other characteristics of apparent significance; and (b) from incidental observations made during the course of other field studies.

Laboratory observations. Replicate colonies of each species (generally three) were collected from different field sites and maintained in flow-through aquaria at Lizard Island Research Station. Sediment rejection mechanisms of these colonies were examined under a binocular microscope.

The rejection of four sediment sizes was investigated: 'silt' (<63um), 'fine' (63-250um), 'coarse' (500um-1mm) and 'granule' (1-3mm) (Plate 2.1). The sediment was a quartz/calcareous sand (approximately 30%/70%) characteristic of the local region, which had been washed, oven-dried for 4-8 hours, and sieved through a series of stainless steel Endicott sieves. In the laboratory, carborundum powder was also used to examine rejection of silt-sized particles, as the darker colour allowed ciliary currents to be seen more readily.

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1. See the General Introduction for a review of normal sedimentation rates on Australian coral reefs.

Species	n (S F C G)	nf	D/N Exp	Cilia (S F C G)	Mucus (S F C G)	Tissue expn General (S F C G)	Plp (D N)	Tentacles General (S F C G)	Spec (D N)	Mesents (S F C G)	Ingestn (S F C G)	Ps	Sed expn (mm)	Calice diam (mm)
Pocillopora damicornis	3 3 3 3	4*	D/N									■	<1	1.1
Montipora danae	3 3 3 3	4	D/N										<1	0.65
Montipora foliosa	3 3 3 3	3	D/N										<1	0.7
Montipora aequituberculata	3 3 3 3	4*	D/N										<1	0.6
Acropora hyacinthus	3 3 3 3	3*	D/N									■	<1	0.85
Acropora florida	1 3 3 2	3	D/N										<1	1.1
Astreopora myriophthalma	3 3 3 3	3*	N										≈1	2.3
Porites lobata	3 3 3 3	3*	D/N										<1	1.5
Porites lutea	1 1 1 1	3*	D/N										<1	1.25
Goniopora lobata	1 1 1 1	3	D/N										≈4	4
Gardineroseris planulata	4 4 4 4	3*											≈2	7
Coeloseris mayeri	3 3 3 3	3*	N										≈3	6
Pachyseris speciosa	3 3 3 3	3	---										<1	5
Fungia repanda	3 3 3 3	3*	N										≈5	200
Sandolitha robusta	3 3 3 3	3*	N										≈1	2.75
Galaxea fascicularis	3 3 3 3	3*	D/N										≈3	7
Mycedium elephantotus	3 3 3 3	3*	N										≈5	14
Pectinia lactuca	3 3 3 3	3*	N										≈45	40
Pectinia paeonia	3 3 3 3	3	N										≈50	50
Acanthastrea echinata	3 3 3 3	3*	N										≈8	19
Lobophyllia hemprichii	3 4 4 3	3	N										≈15	40
Lobophyllia corymbosa	0 3 3 0	3	N	NT	NT	NT NT NT	NT	NT NT	NT	NT NT	NT NT	NT	≈8	35
Symphyllia recta	3 3 3 3	3	N										≈10	16
Symphyllia radians	3 3 3 3	3*	N										≈12	22
Hydnophora microconos	3 3 3 3	3*	N										≈2	2.5
Merulina scabricula	3 3 3 3	3*	N										≈1	4
Favia stelligera	3 3 3 3	3*	N										≈1	3
Favia pallida	4 4 4 4	3*	N										≈4	8
Favites abdita	3 3 3 3	3	N										≈2	9.5
Goniastrea retiformis	1 1 1 1	3	N										≈1	4
Platygyra lamellina	1 3 3 1	3	N										≈6	4
Leptoria phrygia	4 4 4 4	3*	N										≈4	4.1
Oulophyllia crispa	3 3 3 3	3*	N										≈15	14.5
Montastrea curta	3 3 3 3	3	N										≈4	5
Plesiastrea versipora	3 3 3 3	3*	N										≈4	2.5
Diploastrea heliopora	3 3 3 3	3*	N										≈3	7
Cyphastrea serailia	3 3 3 3	3*											≈1	2.15
Cyphastrea chalcidicum	3 3 3 3	3											≈1	2
Echinopora lamellosa	3 3 3 3	3*	N										≈2	4
Echinopora mammiformis	3 3 3 3	3*	N										≈1	3.5
Turbinaria peltata	3 3 3 3	3	D/N										≈2	4
Turbinaria mesenterina	3 3 3 3	3											≈1	3

Table 2.1. A summary of the significance of active behavioural responses to sediment influxes on a species-by-species basis.

Explanation of headings.

'n' replication used in laboratory observations
'S': Silt; 'F': Fine sediment; 'C': Coarse sediment; 'G': Granules
'nf' field replication; '*' indicates that further field work was carried out at a later date, increasing field replication
'D/N Expn' refers to normal expansion period of coral. 'D': principally daytime; 'D/N': full or partial expansion day and night; 'N': principally at night
'Cilia' strength of ciliary activity
'Mucus' presence of mucus causing agglutination of sediment
'Tissue expn: general' refers to presence and intensity of tissue expansion of coenosarc, wall tissues and parts of the oral disc during *daytime* influxes that could be attributed unequivocally to a *direct* sediment response
'Tissue expn: plp: D' importance of partial or full polyp expansion in dislodging sediment during the day, whether or not in direct response to sediment influx
'Tissue expn: plp: N' importance of partial or full polyp expansion in dislodging sediment at night, whether or not in direct response to sediment influx
'Tentacles: general' importance of tentacle movements in dislodging and/or moving sediments
'Tentacles: spec: D' sediment-specific tentacle manipulations observed during the day
'Tentacles: spec: N' sediment-specific tentacle manipulations observed at night
'Mesents' presence of mesenteries as an immediate response to sediment (mesenterial response to tissue damage not included, see text)
'Ingestn' ingestion of sediments following influx
'Ps' pulsing of tissues causing mobilisation of sediments
'Sed expn (mm)' maximum expansion of tissues (mm) observed during the day as a *direct* response to sediment influx. Polyp expansion at night not included.
'Calice diam (mm)' calice diameter (mm) (or meander width where applicable) either by direct measurement, or obtained from Scleractinia of Eastern Australia (see text).

NT	Not tested
□	Present/of minor importance/only under specific conditions/not intense
▨	Moderately important/moderately intense
◩	Important/intense
■	Extremely strong

To examine the influence of calice dimension on sediment rejection capability, and on tissue expansion specifically in response to sediment influxes, an approximate mean calice diameter for each species examined during this study was obtained from the monograph series Scleractinia of Eastern Australia (Veron & Pichon, 1976, 1980, 1982; Veron et al, 1977; Veron & Wallace, 1984). For meandroid species the meander width was used as the equivalent diameter. In the course of field and laboratory studies, the maximum tissue expansion observed in response to sediment influx was recorded. Full polyp expansion was very rare during the day as a direct response to sediment and night-time polyp expansion occurred whether or not sediment was present. For this reason, only expansion that could be attributed unequivocally to sediment rejection has been indicated and the expansion figure is generally less than the expansion capacity of the polyp.

RESULTS

The sediment rejection capability of a species was influenced by both 'passive' and 'active' components. Nevertheless, without exception, all species under investigation were found to show at least some active rejection of sediments. Mechanisms involved ciliary movements, localised tissue expansion, partial (or, rarely, whole) polyp expansion or retraction, mucus secretion, tentacle activities, mesenteries, and pulses of contraction/expansion of polyp or tissues. Ciliary activity, expansion of coral tissues (coenosarc and/or polyp), and the presence of mucus were observed for all of the species investigated. However, the relative importance or usefulness of these and other behaviours in the physical rejection of sediment varied substantially both between species and for different sediment sizes.

Active sediment rejection

Active rejection mechanisms were investigated for a total of 42 species from 31 genera. The principal mechanisms employed by each species for each of the four sediment sizes are summarised in Table 2.1. For the majority of species, at least four field and three laboratory
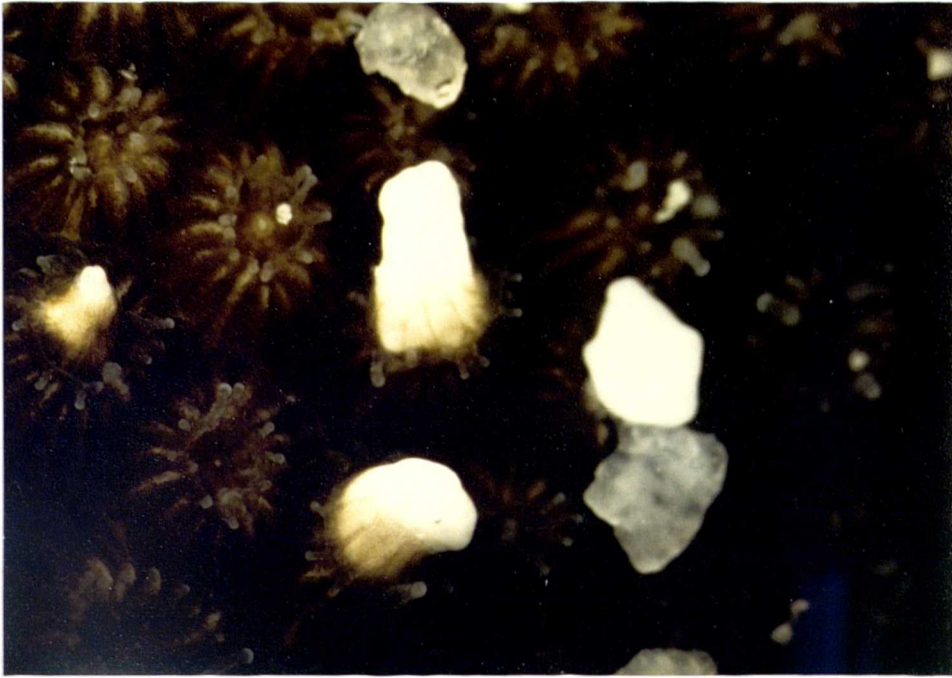
Plate <u>2.3</u>.   Substantial eversion of mouth and
                     oral disc tissues by *Favia
                     stelligera* to allow partial
                     ingestion of individual granules
                     (*x 3.5*).

Plate <u>2.4</u>.   Typical response of coral species to
                     fish homogenate, showing expanded
                     and open mouth (*Oulophyllia
                     crispa*, *x 5*).

replicates were examined (exceptions were *Porites lutea*, *Goniopora lobata* and *Goniastrea retiformis*), but in many cases later field investigations increased field replication substantially. These species have been highlighted (**) in Table 2.1. Incidental observations were made on an additional 45 species encompassing a further 15 genera, some of which are referred to briefly in the following text.

The investigations described in this Chapter focussed on a survey of the *mechanisms* and rejection *capability* of a wide range of species with respect to different sediment sizes. Rejection *efficiency* (i.e. the rate of sediment rejection) and sediment *tolerance* for a number of species are examined in greater depth in Chapters 3, 4 and 7. To avoid repetition, rejection mechanisms on a species by species basis are described in Appendix A which provides a summary and discussion of all information for each species resulting from studies described in this thesis.

Initial tissue retraction. As a sediment influx reached the surface, the initial reaction of polyps and tissues was normally to retract. Variations between species appeared to relate to polyp size and/or tissue fleshiness: *Symphyllia* species, *Lobophyllia* species and other large-polyped corals rarely showed this response to fine sediment or silt and only occasionally to coarse sediment, whereas small-polyped species such as *Porites lobata*, *P. lutea*, *Montipora* spp. and *Astreopora myriophthalma* gave this response for all sediments but silt. Several species showed a response in regions unaffected by the influx. For example, all the polyps of a branch of *Acropora hyacinthus* retracted when sediment fell on any part of the branch but adjacent branches were not affected; the entire club-shaped head of *Goniopora lobata* retracted if sediment fell on any of the polyps, although polyps of adjacent heads usually did not.

Ingestion. During day or night, many species were observed to ingest sediment particles prior to the onset of rejection behaviour (Plates 2.2 and 2.3). A number of plocoid species with medium-small to large polyps (such as *Diploastrea heliopora*, *Echinopora mammiformis* and *Favia pallida*) showed strong ciliary movement from the coenosarc to the top of the polyp wall. At the top, sediments were moved down

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the interior wall towards the mouth of the retracted polyp. The
mouth then opened just wide enough to allow ingestion of particles.
Clean sediment was retained for only a few to 30 or 40 minutes
before being rejected from the mouth and carried away by ciliary
currents. Although the cycle of ingestion to rejection for any one
polyp was often less than 10 minutes for clean sediment, other
polyps were observed to begin ingestion 30 minutes after the initial
sediment influx. Generally, beyond this time, no polyp would ingest
particles already resting on its tissues or the nearby coenosarc,
and all sediment movement was in a direction away from the mouth.

Sediments coated with homogenised fish tissue were ingested in a
similar way but were held in the mouth for longer periods (often 1-2
hours or more). Ingestion was also more widespread, with a larger
proportion of polyps ingesting nearby particles. Alone, the fish
homogenate caused similar ciliary currents towards the mouth but the
mouth expanded more widely (Plate 2.4) to engulf the material and no
rejection was noted during the following 2-3 hours.

When a *Favia stelligera* individual had previously been offered
clean sediment, its response to fish homogenate was noticeably
slower than the response from individuals with no prior sediment
experience. When experienced individuals finally began to transport
fish to their mouths, this activity was again extended to the
sediment grains still remaining on the coenosarc.

Cilia. The presence and direction of ciliary transport on a coral
tissue were readily detectable with silt particles, but the
significance was less easily quantified with larger sediment sizes.
Ciliary activity was assumed only when particles were moved in the
absence of any other reaction such as tissue expansion or tentacle
movement, and particularly where such movement was against gravity
(Table 2.1).

There was a general decline in the ability of corals to
manipulate sediment with cilia as the particle size increased. All
42 species examined in detail were able to manipulate both silt and
fine sediment, but in some species cilia appeared to be relatively
unimportant because of the dominance of other factors such as colony

morphology (e.g. *Pocillopora damicornis* and *Acropora hyacinthus*). In other species, only weak ciliary currents were observed in response to sediment (*Porites lobata, P. lutea* and *Montipora* spp.). Many species were able to move coarse sediment, but often only slowly, and the range of species with ability to manipulate granules easily using cilia alone was limited. Nevertheless, certain species were substantially more able to move all sediment sizes than others. In particular, this group included *Gardineroseris planulata, Fungia repanda* (and *F. concinna*), *Pectinia lactuca* and *P. paeonia*, and *Echinopora mammiformis*, as well as *Favia pallida, Favites abdita, Oulophyllia crispa, Diploastrea heliopora, Turbinaria peltata* and *T. mesenterina.*

Ciliary movement of sediment, even when it eventually became strong, did not always begin immediately. For example, about two minutes usually elapsed before strong ciliary movement in *Turbinaria peltata* was observed. Delays may allow secretion of mucus to take place before attempts are made at rejection.

Mucus. The presence of mucus was inferred whenever sediment particles became agglutinated and sticky (Plates 2.5 and 2.6, and Appendix Plate 2.*j*). Mucus played a role in the rejection of silt and fine sediments for all species under investigation, but was nevertheless of much greater significance for some species than others, a significance that could be readily underestimated in laboratory conditions in the absence of natural water movement. Agglutination of silts and fine sediments usually occurred quickly (30 seconds to a few minutes). An exception was *Gardineroseris planulata* where mucus only became obvious after sediment had been static for many minutes. Even with silt and fine sediment this species usually manipulated individual particles separately with its strong ciliary currents.

In field situations, the presence of mucus in conjunction with wave action was extremely effective at cleaning silt and fine sediment from individuals. A number of *Acropora* species including *Acropora hyacinthus, A. florida* and *A. gemmifera*, were observed to secrete mucus strands along which a few to several tens of fine or

Plate 2.5.   Mucus entrapment of fine sediment on the surface of *Pachyseris speciosa* (*x 5*).

Plate 2.6.   Mucus strands on *Sandolitha robusta* (*x 5*).

silt-sized sediment grains became attached. The strands usually became detached at one end, were caught by wave action, and eventually washed away. Wave action was very significant for these species, particularly for the thick branched *A. florida*. Wave action in combination with mucus was also important for *Diploastrea heliopora*. This coral formed mucus sheets, trapping fine sediments and silt in a sheet about 1-3 sediment particles thick. *D. heliopora* also showed strong ciliary activity, capable of rejecting heavy loads of sediment through active mechanisms alone. However, on many occasions, quite minor turbulence was seen to create lift underneath the mucus sheet and to remove large sections without further active participation from the colony. Sheet formation was also important for *Pacnyseris speciosa*, *Mycedium elephantotus*, *Pectinia lactuca* and *P. paeonia*, *Turbinaria peltata* and *T. mesenterina*.

Mucus entrapment was not always advantageous to the individual. In still water and where slight dips occurred in colony microtopography, agglutination of fine sediments resulted in an accumulation which could not then be rejected by ciliary currents. Strong tissue expansion capability was necessary to reject these accumulations. Tissues with weak expansion capability were vulnerable. In particular, this appeared to be a serious causal factor in the field mortality of *Merulina scabricula* (see Chapter 4), but contributed to the persistence of sediment accumulations for several other species. *Coeloseris mayeri* may not commonly suffer from this problem, but small areas of two colonies died under still conditions *in situ* when fine sediments in slight dips became matted. In each case the underlying tissues distended dramatically (approximately 3-4mm above the calice walls) but were unable to dislodge the sediments, and the tissues eventually died. Similar effects did not normally occur with silt unless fine sediments were also present.

All or part of undisturbed *Porites* colonies *in situ* were commonly covered in a mucus sheet. The form of this sheet was very different from those observed in any other genus, being apparently less fluid and more continuous over the colony, even where sediment was not visibly present. Furthermore, sheets of the type observed

on undisturbed colonies were never produced as an immediate response to artificial sediment influx.

Tissue expansion. Tissue expansion, either of the coenosarc, corallite wall tissues or polyp, was a principal rejection mechanism for most species examined and was observed (though sometimes rarely) for all species in response to large sediment particles. However, as with ciliary mechanisms, the scale of expansion, and its importance relative to other rejection mechanisms, varied substantially from species to species and with sediment particle size. In contrast to ciliary activities and mucus, the importance of tissue expansion increased as sediment particle size increased.

Both *Pectinia lactuca* and *P. paeonia* showed very strong ciliary responses to sediment influx. However, on many occasions, the tissues surrounding the oral disc were observed to expand many centimetres (often 3-4cm and occasionally up to 5-6cm with fine sediment or silt) away from the underlying skeleton as a direct response to accumulating sediment. The tissue expansion capacity of these species was the most impressive of all sediment rejection behaviour studied. A similar response, though on a lesser scale (up to about 15mm), was shown by *Oulophyllia crispa*.

In the four large-polyped mussids, *Lobophyllia hemprichii*, *L. corymbosa*, *Symphyllia recta* and *S. radians*, the globular roughness of the tissue encouraged sediment to collect in tissue folds as a result of gravity. This sediment could be removed by tissue expansion, but small accumulations of sediments were often not removed for considerable time, and surrounding tissues simply expanded and obscured them from view. Presumably sediments caused less irritation to these species. Direct shading effects on photosynthesis would be negligible due to local expansion around sediment accumulations.

Tissue expansion of the corallite walls and coenosarc was of relatively high significance for many species with small and medium-small polyps, despite the restricted scale of expansion. These species, apparently unable to move the larger sediments (coarse and granule) with their cilia, often relied on slow, small-scale changes

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in local tissue expansion to overcome static friction. Corals falling into this category included *Astreopora myriophthalma*, *Coeloseris mayeri*, *Hydnophora microconos*, *Merulina scabricula*, *Goniastrea retiformis*, *Cyphastrea serailia* and *C. chalcidicum*. Tissue expansion and contraction was rarely as important for fine sediments and silt sized particles because most species were able to manipulate these particle sizes adequately with cilia. Nevertheless, the general trend of increasing tissue expansion activity for increasing sediment particle size prevailed throughout most corals, whatever the polyp size.

General movements of the polyps during periods of expansion helped to mobilise sediments but full expansion of the polyp as a direct response to sediment was very rare (see also observations made at night, discussed below). Partial expansion of polyps of *Lobophyllia* spp., *Symphyllia* spp., *Favia stelligera*, *Favia pallida*, *Plesiastrea versipora* and *Mycedium elephantotus* was observed, but this response was sporadic and minor. The diurnally expanded polyps of *Montipora danae*, *M. foliosa*, *M. aequituberculata*, *Acropora hyacinthus* and *A. florida* all retracted when sediment fell on the tissues but expanded through the sediment where possible shortly afterwards to re-establish their former expanded condition. The long fleshy polyps of *Goniopora lobata* are normally extended over 20mm during the day and are usually in a continual state of motion. This movement has, perhaps inadvertently, a major clearing role although ciliary activity and mucus secretion were also well developed. However, polyps retracted if sediments fell in quantity on any tissue and, at the same time, tissues at the sides of the calice expanded, cleaning the polyp stalk as it retracted into the skeleton.

An unusual response was observed in *Turbinaria peltata* when fine sediment in an agglutinated mucus mass became stuck against the side of a single polyp. After some while the polyp retracted deep into the skeleton allowing the entire sediment/mucus bundle to be swept overhead by cilia and gravity in one sheet. No other polyp retracted, there was no other visible stimulus, and following the passage of the mucus-sediment bundle, the polyp re-expanded.

Plate **2.7.**   Manipulation   of   granules   by
                        individual tentacles of *Galaxea*
                        fascicularis (*x 5*).
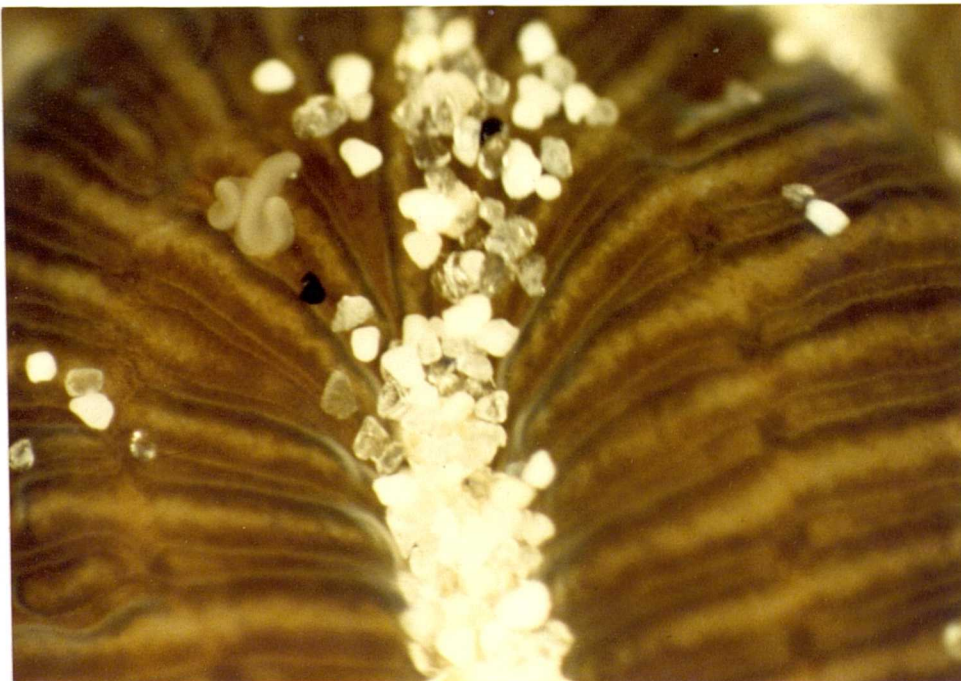
Plate **2.8.**   Mesentery (top left) extruded from
                        the wall of a meander in response
                        to   fine sediment on *Leptoria*
                        phrygia (*x 20*).

Pulsing of tissues. Very short-lived pulses of expansion or contraction (less than a second) of polyp, tentacles, or tissues were observed in eleven of the species examined (Table 2.1). In all species, pulsing had a strong influence on the mobilisation of sediments, but particularly for *Pocillopora damicornis*, *Acropora hyacinthus*, *Porites lobata*, *P. lutea* and *Coeloseris mayeri*.

Tentacles. Tentacles were involved in sediment rejection in two ways. The first occurred in conjunction with a general increase in polyp movement. Both *Pocillopora damicornis* and *Acropora hyacinthus* showed increases in the intensity of general tentacle and polyp movements in response to sediment influxes. The movements did not appear to be well coordinated with actual presence of sediment particles but were dispersed throughout the polyps in the general region of influx. The increased activity was nevertheless effective at mobilising sediment.

The second involved more coordinated tentacle movement. *Coeloseris mayeri* snowed increased tentacular activity in the vicinity of sediments but not elsewhere on the colony. Each tentacle manipulated sediment particles using cilia for silt and, more slowly, for coarser sediment. A number of species demonstrated an additional coordinated strategy: in the vicinity of a sediment influx, the tips of one or two tentacles of a *Favia stelligera* polyp expanded to form a club-shape. The tentacle curved inwards to the oral disc where a sediment particle became attached to the expanded tip. The particle was then transported over the corallite wall as the tentacle extended upwards and outwards and was deposited on the coenosarc. In general, tentacles of this species were able to move silt and fine sediment very readily and coarse grains were transported occasionally; however, movement of granules by this method was not observed. *Galaxea fascicularis* (Plate 2.7), *G. astreata* and *Favia pallida* were also commonly observed using tentacles in this way but could manipulate all sediment sizes.

As might be expected, tentacle participation was observed more commonly during night-time when the polyps were expanded, and tentacles of a number of other species were observed to manipulate

sediment particles (*Acanthastrea echinata, Favites abdita/halicora.
Montastrea curta, Plesiastrea versipora, Diploastrea heliopora*).
Most species were actively feeding: capturing passing plankton with
their tentacles and passing them to the mouth. Sediments 'captured'
by tentacles at night also commonly moved to the mouth and ingested,
rather than removed from the oral disc to the coenosarc (as observed
during the day).

Mesenteries. Although it was clear that mesenteries were extruded by
several species in response to sediment, they were often unobtrusive
and difficult to see *in situ*. In *Leptoria phrygia* (Plate 2.8) and
Platygyra lamellina, short filaments protruded from the walls and
valleys of the meanders, through the epithelium. Mesenteries more
commonly originated from the mouth in other species. Those from a
number of species were observed to surround individual granules or
grains of coarse sediment. This reaction generally occurred in
small to medium-polyped species (*Montipora aequituberculata,
Pachyseris speciosa, Hydnophora microconos, Favia stelligera* and
Plesiastrea versipora) that were actively ingesting smaller
particles. *F. stelligera*, for example, ingested silt, fine
sediment and the smaller coarse grains. Particles of about 1mm were
taken singly into polyp mouths with considerable expansion of
tissues outwards over the grain but commonly leaving half of the
particle protruding (Plate 2.3). No attempt was made to ingest the
larger granule-sized grains, but mesenteries engulfed them on the
nearby coenosarc. At approximately the same time as the polyps
began to eject particles from their mouths, mesenterial filaments
were withdrawn from larger particles and rejection began. For these
species, observations suggest that mesenteries were extruded for the
purpose of feeding, not as a stress or sediment rejection response.

in situ, two or five plate-like colonies of *Echinopora
mammiformis* extruded very long (2-3cm) mesenteries as a direct
response to sediment. These were occasionally seen to wrap around
sediment particles, apparently actively moving them across the
coenosarc. The mesenteries or one colony of *Hydnopnora microconos*
in an aquarium, moved very slowly away from the polyp dragging
granules with them. Similarly, mesenteries had a direct effect on
sediment movement in *Favia stelligera, Leptoria phrygia* and

Platygyra lamellina. Although, in all of these species, sediment was moved by mesenteries, it is possible that this movement was simply a by-product of mesenterial feeding.

In a few colonies of *Coeloseris mayeri, Leptoria phrygia, Echinopora lamellosa,* on which sediments had been static for more than 48 hours, and which were later found to have suffered tissue damage or death, mesenteries were observed within the sediment mass or at its periphery. Again, these mesenteries were not easy to see *in situ.* In contrast, mesenteries were often clearly visible without magnification on individuals from the same and other species that had been ᴵaged as a result of cuts or lesions. or which had been exposed to low salinities or substantial temperature changes. The reason for this difference was almost certainly the camouflaging effect of the cream-coloured sands, obscuring the mesenteries from view.

In summary, these observations indicate that mesenteries are extruded under at least two quite distinct conditions in relation to sediments. The first is in response to occasional, light, clean sediment which cause no physical damage. This is likely to be a feeding rather than a stress response. The second is a response to tissue damage caused by sediment accumulations. In addition, fully extended mesenteries of a few species may assist in sediment rejection, but probably more by chance than design as they appear to have low mechanical strength.

Dusk and nighttime observations. Tentacles of most Lizard Island corals are fully extended by the onset of night. This occurs in synchrony with the appearance of clouds of demersal plankton, on which the corals begin to feed. Gross polyp movements were of greater significance to sediment mobilisation and rejection during these periods of polyp expansion. Instead of minor tissue retraction when sediment fell on the surface tissues, the fully expanded polyps generally responded by total or partial contraction. With later re-expansion, sediment was relatively easily dislodged. This may be particularly important for a few massive, plocoid species with relatively small polyps and an even surface such as *Astreopora myriophthalma.* Nevertheless, the majority of gross expansion

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behaviour could be attributed to re-establishing a feeding position rather than to sediment rejection. It was noticeable that maximum mobilisation or disturbance to sediment accumulations occurred either when corals initially expanded at dusk or, if sediment influxes began while fully expanded, when they first re-expanded after contraction. Once full or partial re-expansion had taken place, further polyp movements caused less significant sediment movement and were generally related to feeding activities rather than to sediment rejection. Possible advantages of increased polyp movements after expansion were partially offset by other factors, notably obstruction (by the expanded polyps) of the passage of sediments on the coenosarc and reduction of the advantageous effects of water movement. In many species (*Favia stelligera, Diploastrea heliopora, Acanthastrea echinata, Montastrea curta*), mucus/sediment accumulations built up between polyps, slowing down the rejection process .

The ability of a coral to re-expand in the presence of sediment on its tissues was examined. Although not always immediate, sediment accumulations of 50 or 200mg.cm^{-2} only partially hindered re-expansion of most of the large mussids (*Symphyllia* spp., *Lobophyllia* spp., *Acanthastrea echinata*), the larger faviids (*Diploastrea heliopora, Oulophyllia crispa, Favites abdita, Favia pallida, Plesiastrea versipora, Echinopora* spp., *Platygyra lamellina*), and a number of other species (*Goniopora lobata, Mycedium elephantotus, Pectinia* spp.). Heavier loadings (more than 400mg.cm^{-2}), resulted in increasingly longer periods prior to tissue re-expansion while sediments were removed from peripheral areas by other rejection mechanisms. Re-expansion in species with small polyps (*Montipora danae, M. foliosa, M. aequituberculata, Porites lobata, P. lutea, Porites* spp., *Cyphastrea* spp.) could be severely hindered by 50mg.cm^{-2}. Some of these species (*Montipora* spp. and *Porites* spp.) remain partially or wholly expanded day and night and this inhibition was similar in either case.

Some corals that had been inundated with sediment during the day did not completely cleanse themselves until nightfall, despite a obvious ability to do so. *Favia pallida*, for example, was a very active sediment rejector during the day but rejection was rarely

complete. Under natural conditions, sediment was regularly observed in the calices of this species and this was generally rejected only at dusk as the polyps expanded. Other species that showed similar behaviours include *Favia lizardensis, F. matthaii* and *Favites abdita/halicora.* Large mussids (*Lobophyllia* spp. and *Symphyllia* spp) often refrained from rejecting substantial accumulations from their tissues (50-100mg.cm^{-2}) until dusk.

Modification of active rejection by passive influences

Observations so far described have concentrated on active sediment rejection, and the mechanisms used to manipulate sediments in the laboratory and *in situ in* the absence of water movement. The actual energy required to remove sediments is modified by the influence of passive mechanisms. The extent of passive rejection was principally affected by tissue and skeletal morphology, colony orientation, and water movement. On the whole, observations at Lizard Island confirmed patterns discussed by previous workers (Marshall & Orr, 1931; Bak & Elgershuizen, 1976; Dryer & Logan, 1978; Lasker, 1980; Rogers, 1983). A general summary and points of particular interest are outlined as follows:

Gross morphology and wave action. Gross skeletal morphology was of great significance to sediment removal, gravitational loss being very dominant in finely branching species (*Pocillopora damicornis, Seriatopora hystrix, Porites cylindrica, P. nigrescens, Psammocora contigua,* and many others) to the extent that active mechanisms were mostly redundant. Similar advantages were observed for many plate-like individuals of *Pachyseris speciosa, Mycedium elephantotus* and, occasionally, for *Merulina scabricula* colonies having predominantly upright plates. Even massive species were often able to take advantage of a high degree of passive sediment loss by morphology: some individuals of *Favia stelligera* displayed a semi-columnar morphology with slightly or strongly convex tops up to 10cm diameter (Appendix Plate 1.*l*).
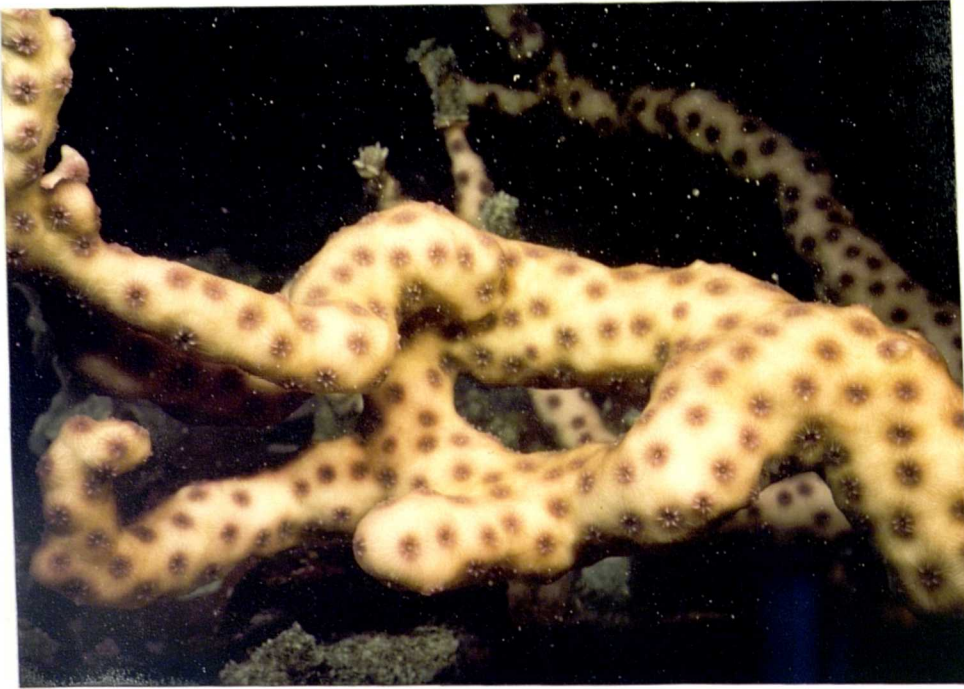
Plate 2.9 (x 1)

Ramose (Plate 2.9) and encrusting to
laminar (Plate 2.10) growth forms
of *Echinopora mammiformis*

Plate 2.10 (x 1.5)
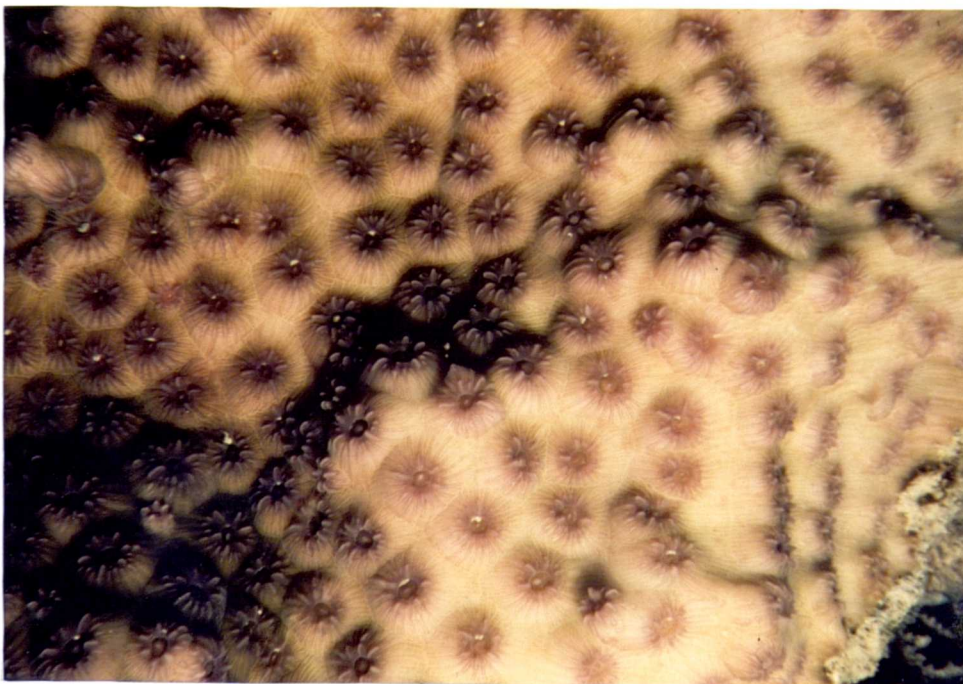
The importance of active rejection mechanisms for *Echinopora mammiformis* was greatly influenced by habitat and growth form. This species displayed two distinct morphologies: a highly ramose form (Plate 2.9) in the lagoon in contrast to a plating form (Plate 2.10) in the more exposed North Point and Crystal sites (Chapter 5).

Pectinia colonies have complex morphologies combining horizontal and vertical plates. When sediments were introduced many individuals were observed to have channels along which the sediment moved. When examined in detail, sediments were seen to follow very shallow downward paths, often in long circuitous routes, before finally falling off the colony perimeter. Thus this genus, whilst having the most dramatic active mechanisms of any species examined, often had additional assistance from passive gravitational forces. In a somewhat similar way, individuals of a number of other species showed what can be described as 'drains'. Several foliose *Montipora* spp., some colonies of *Echinopora lamellosa* and *E. gemmacea*, and *Oxypora lacera*, formed spiral plates which focussed at the base in a dead patch with a drain hole nearby through which sediment could fall away. These drains probably develop as the coral grows, by marginal death of tissues where sediment build-up becomes lethal rather than by deterministic growth. Whatever its origins, the resulting morphology reduces the active rejection costs to the coral.

Turbinaria peltata as described above, showed strong active rejection abilities with particular emphasis on ciliary mechanisms. At sites between North Point and Crystal, colonies were sporadically found at the base of a 6-8m dropoff, close to sandy bottoms. Many formed vase-shaped colonies at an angle such that one side was angled approximately 10° upwards from the horizontal and the other was vertical. Thus sediment could collect at the base and would only be removed by strong wave action or sustained active effort. Sediment was almost always found at the base of these vases, but underlying tissue was not normally dead (two colonies had small dead areas at the apex). Instead, the number of polyps per area was reduced in comparison to the rest of the colony and tissues were bleached. Bleached tissue of eight individuals were periodically observed for 12 months but did not die during this time.

Surface detail of *Montastrea aequituberculata* showing the significance of surface projections or tubercles to rejection of larger-sized particles (Plate 2.11) in comparison to silt-sized particles (Plate 2.12) which can be moved by cilia between the projections.

Plate 2.12 (*x* 5)

Goniopora lobata had well-developed active rejection mechanisms but passive rejection in this species was also considerable. Colonies had long fleshy polyps and were often columnar (see also Veron, 1986) resulting in a relatively convex tissue surface which strongly encouraged passive loss.

Several species usually or exclusively occurred in areas of high wave action (*Favia stelligera, Montastrea curta, Hydnophora microconos* and *Acropora hyacinthus*) and sediments landing on their tissues would normally be removed quickly by water movement.

Microtopography. The scale of sediment particles in relation to topographical features of the skeleton was observed to have a significant bearing on the ease of sediment rejection for a number of species. For example, granules (1-3mm) became jammed between the hydnophores of *Hydnophora microconos* and were twice seen to cause minor tissue lesions. Substantial turbulence was required to dislodge these particles. The complex skeletal projections of *Montipora* spp. (e.g. *Montipora danae, M. foliosa, M. aequituberculata*) were also seen to trap sediment particles (Plates 2.11 and 2.12). However, polyp expansion was not always seriously hindered by the presence of occasional large particles as gaps between the particles and tissues often allowed polyps to expand to one side. Dense accumulations of finer sediments on these colonies were a more serious hindrance to polyp expansion. In *Echinopora lamellosa* and *Cyphastrea* spp., the granular nature of the coenosteum appeared to hinder sediment rejection.

Commensals. A number of commensal organisms were observed to have an incidental or, in some cases, active effect on sediment rejection. Commensal crabs on *Pocillopora damicornis, Acropora hyacinthus*, and *Galaxea fascicularis* became more active as sediment settled, thus creating local currents or directly dislodging particles from the coral tissues. Tube-dwelling microcrustacea on the surface of *Cyphastrea chalcidicum* collected silt and fine particles in a constant stream via their extended appendages. On the same species, the movement of polychaetes across the tissue surface helped to

overcome the static friction of fine sediments in mucus bundles. Tube worms collected sediment particles from the surface of *Montipora aequituberculata*. Crinoids were observed to play a direct role in sediment removal from *Montipora foliosa*, *Porites* spp. and *Gardineroseris planulata*. In one *M. foliosa* colony during the day, a crinoid was observed wrapped around the skeletal tubercles, sweeping sediment away by movements of its arms. Crinoids carrying out similar activities on *Porites* spp. and *G. planulata* lived in crevices in the skeleton and were active only at night.

Local turbulence resulting from the activities of fish were observed both to cause sediment influxes and to clear tissues of sediments.

General trends

Active rejection mechanisms were very consistent between replicates of the same species. However, morphological variation and *in situ* location considerably modified the extent of intra-species passive rejection.

On the whole, congeneric species showed similar, though not always identical, active rejection mechanisms (e.g. *Montipora danae*, *M. foliosa* and *M. aequituberculata*; *Porites lobata* and *P. lutea*; *Pectinia lactuca* and *P. paeonia*; *Lobophyllia hemprichii* and *L. corymbosa*; *Symphyllia recta* and *S. radians*; *Cyphastrea serailia* and *C. chalcidicum*; *Turbinaria peltata* and *T. mesenterina*). There were exceptions (*Favia stelligera* and *F. pallida*; and *Echinopora lamellosa* and *E. mammiformis*) and further work will probably highlight others. At the family level, the type of mechanism and the balance between active and passive influences was very diverse.

In general. species showed sediment size-specific rejection. For most species dense influxes of silts were trapped in mucus and moved off the colony on ciliary currents. The mucus/sediment mass could show almost fluid properties and may require relatively little active ciliary intervention on species with smooth, angled surfaces. However, when silt particles met the surface singly or in small clusters, mucus

secretion was either less common, or less effective in creating this response even on almost vertical surfaces, with the result that cilia were usually seen to continue active transport even on strongly angled surfaces. Particle density is an additional factor in this response, as neutrally buoyant particles of sizes up to about 500um were also observed to be actively manipulated on strongly angled tissues. Nevertheless, all species examined were capable of manipulating silts. As particle size increased there was an overall decline in the ease of sediment movement. Ciliary transport and mucus secretion was also the principal rejection mechanism for fine sediments, but tissue expansion was the most important mechanism for larger sizes.

On the basis of observations described here, in Table 2.1, and at greater length in Appendix A, the 42 species of coral examined can be divided into groups, according to the ease with which they were able to actively reject sediment (Table 2.2). This categorisation summarises active rejection *capability* – that is, the observed ability of a coral to move different particle sizes and the observed physical intensity of the active rejection response. Passive loss of sediment is not considered except where it appeared to dominate over active mechanisms (*Pocillopora damicornis* and *Acropora hyacinthus*). An understanding of the basis of this summary is essential because further work makes clear that active rejection capability, though usually reflecting potential rejection efficiency (Chapter 3), is not always correlated with sediment tolerance (Chapters 3 & 4).

Calice dimension. The influence of calice size is considered in two ways: (a) in relation to the maximum tissue expansion observed during sediment rejection (Table 2.1); and (b) in relation to the active rejection categories defined in Table 2.2.

There was a strong positive correlation between maximum tissue expansion in response to sediment and mean calice diameter for each species ($r=0.8649$, $n=42$, $p<0.001$, Spearman's rank correlation coefficient), demonstrating that species with large polyps showed significantly greater expansion of tissues in response to sediments than species with smaller polyps.

<u>Group 1A</u>

EASILY MANIPULATES ALL SEDIMENT SIZES
USUALLY VERY ACTIVE

Goniopora lobata (*)
Gardineroseris planulata
Fungia repanda
Pectinia lactuca
Pectinia paeonia
Favia pallida
Oulophyllia crispa
Diploastrea heliopora
Echinopora mammiformis
Turbinaria peltata

<u>Group 1B</u>

EASILY MANIPULATES ALL SEDIMENT SIZES
NOT ALWAYS ACTIVE

Lobophyllia hemprichii
Lobophyllia corymbosa
Symphyllia recta
Symphyllia radians

<u>Group 2</u>

EASILY MANIPULATES SILT, FINE AND COARSE SEDIMENT, USUALLY VERY ACTIVE
MOVEMENT OF GRANULES SLOW

Pachyseris speciosa
Galaxea fascicularis
Mycedium elephantotus
Acanthastrea echinata
Favites abdita
Platygyra lamellina
Leptoria phrygia
Plesiastrea versipora
Turbinaria mesenterina

<u>Group 3</u>

EASILY MANIPULATES SILT AND FINE SEDIMENT, USUALLY ACTIVE
MOVEMENT OF LARGER SIZES LABOURED

Coeloseris mayeri
Sandolitha robusta
Merulina scabricula
Favia stelligera
Goniastrea retiformis
Montastrea curta

<u>Group 4</u>

MANIPULATES SILT AND FINE SEDIMENTS, SOMETIMES SLOW, USUALLY ACTIVE
LARGER SIZES OFTEN VERY LABOURED

Acropora florida
Astreopora myriophthalma
Hydnophora microconos
Cyphastrea serailia
Cyphastrea chalcidicum
Echinopora lamellosa

<u>Group 5</u>

MANIPULATES SILT, MOVEMENT OF FINE SEDIMENT SLOW, OFTEN INACTIVE
VERY LITTLE REJECTION OF LARGER SIZES

Montipora danae
Montipora foliosa
Montipora aequituberculata
Porites lobata
Porites lutea

<u>Group 6</u>

PASSIVE MECHANISMS SO DOMINANT THAT
ACTIVE REJECTION MOSTLY REDUNDANT

Pocillopora damicornis (*)
Acropora hyacinthus (*)

<u>Table 2.2</u>. Categorisation of test corals according to their active rejection capability, based on behavioural observations. (*) *Goniopora lobata* was a very active sediment rejector but passive influences were normally dominant *in situ*. In contrast. *Pocillopora damicornis* and *Acropora hyacinthus* were less active sediment rejectors and relied more heavily on passive mechanisms.

NB: This categorisation is based on the *capability* of species to move sediments of different sizes and the apparent ease with which this movement is carried out. In general, this ability does seem to correlate with rejection efficiency (though not necessarily with sediment tolerance. see Chapters 3 & 4). However. there are exceptions: *Gardineroseris planulata*. which is very capable of moving all grain sizes and is placed in Group 1A above, is shown in Chapter 3 to reject sediments efficiently in the first 2 hours but then to cease rejection altogether.

Figure 2.2 shows a plot of calice diameter against active rejection category as defined in Table 2.2. All species with large calices were capable of very active rejection for all sediment sizes and all of those species with mean calice diameters of <1mm were either almost inactive for all sediment sizes or principally relied on passive rejection. Species with mean calice sizes of 2-8mm varied from very active (*Echinopora mammiformis*) to relatively inactive (*Cyphastrea* spp. and *Astreopora myriophthalma*).

DISCUSSION

Behavioural responses to sediment

Behaviours associated with feeding and waste or silt removal have been described in the course of feeding studies (Indo-West Pacific: Yonge, 1930; Abe, 1938; Caribbean: Yonge, 1930; Lewis & Price, 1975, 1976). Most Indo-West Pacific species examined by Yonge (1930) were from the northern Great Barrier Reef and Torres Strait (a few from Lizard Island itself). Detailed description of ciliary currents was not a principal aim of the present study, but where present observations conflict or augment previous work, they are highlighted in the relevant species description (Appendix A).

A number of early studies provide background information on sediment rejection by Indo-Pacific species (Mayer, 1918; Mayor, 1924; Marshall & Orr, 1931), followed by detailed studies of the fungiids (Schuhmacher, 1977, 1979; Fisk, 1981). However, more comprehensive studies have been restricted to Atlantic species. Hubbard and Pocock (1972) examined sediment rejection mechanisms for a total of 26 Caribbean species to establish a link between skeletal morphology and function. Bak and Elgershuizen (1976) focussed on 19 Caribbean species in a comparative study of clean and oil-contaminated sediments. Both studies concluded that rejection was carried out by four mechanisms: ciliary activities, mucus entanglement, tissue expansion and tentacular action. The first three activities were similarly dominant in the course of the present study, but tentacle movements were apparently of less universal importance in sediment *rejection* activities than implied by Hubbard and

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RELATIONSHIP BETWEEN CALICE DIAMETER AND ACTIVE REJECTION CATEGORY
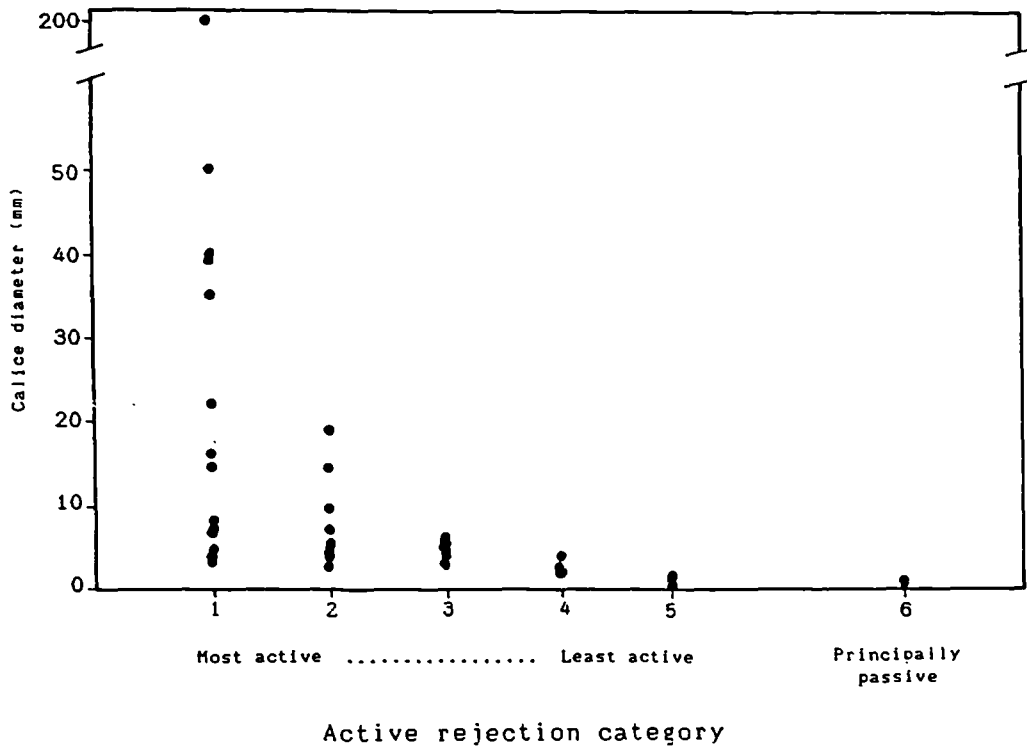
Figure 2.2. The relationship between calice diameter (mm) (or meander width for meandroid species) and active rejection category (as defined in Table 2.2). All species in Category 1 with small calices (<10mm) are strong ciliary rejectors (Gardineroseris planulata, Favia pallida, Diploastrea heliopora, Echinopora mammiformis, Turbinaria peltata).

Pocock (1972) or Bak and Elgershuizen (1976). It is possible that this is due to a difference in definition: in the present study, tentacles were often observed to mobilise sediments at night, but their activities were commonly indistinguishable from control polyps and could not be directly related to sediment. Such movements are listed in Table 2.1 as 'general tentacle movements' and applied to most corals. Nevertheless, it is known from feeding studies (Yonge, 1930; Abe, 1938; Lewis & Price, 1975, 1976) that tentacles have considerable capacity to manipulate prey, and thus it seems probable that tentacular sediment rejection may be an option for many species, even though it was not commonly observed.

All of the corals tested in the feeding studies reported by Yonge (1930), Abe (1938) and Lewis and Price (1976) had cilia and could move silts on ciliary currents. However, observations made here and elsewhere (Marshall & Orr, 1931; Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976) show that the capacity of cilia to move sediments depends upon particle size. The mechanical strength of cilia also varies between species, although this does not seem to be directly related to fleshiness or polyp size, as several species with medium-sized polyps such as *Gardineroseris planulata* and *Turbinaria mesenterina* were strong ciliary rejectors.

Mucus is produced by corals as a feeding aid (Yonge, 1930; Abe, 1938; Lewis & Price, 1976; Lewis, 1977) as well as in response to a variety of stresses such as desiccation (Krupp, 1984; *pers. obs.*), oil and various other chemicals (Jaap & Wheaton, 1975; Mitchell & Chet, 1975), changes in temperature (Neudecker, 1981), physical damage (*pers. obs.*), and sediment (Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976; this study). However, the form the mucus takes can vary greatly. For example, in response to desiccation, intertidal species produce thick and relatively solid mucus mats over coral tissues; in response to sudden temperature changes of many degrees, copious secretion can occur, although mucus does not form such a solid layer (*pers. obs.*). Mucus secretion involved in sediment rejection described above is always much less than this. Substantial mucus secretion in response to sediment was only observed once, in a small-scale test of the effect of sudden influxes of high *turbidity* (simulated in the laboratory) when sedimentation was low but suspended sediments just above the tissue surface were very dense. Silts and clays may cause more substantial

mucus secretion under these extreme conditions. This contention is supported by the work of Thompson *et al* (1980) who studied the effects of drilling muds on seven Caribbean corals and found that all species increased their mucus production substantially.

Mucus sheets observed naturally on *Porites* species in the field were clearly different from either sediment-induced secretions of *Porites*, or those of other species. Mucus sheet formation has been described for many poritid species both in the Caribbean (Lewis, 1973; Bak & Elgershuizen, 1976; Ducklow & Mitchell, 1979; Coffroth, 1984, 1985, 1988b; Edmunds & Davies, 1986), and in the Indo-Pacific (Kato, 1987). During the present study, although *Porites* did produce mucus to assist in the ciliary rejection of silt and fine sediment, the type of sheet naturally present on colonies could not be directly attributed to sediment influxes. This observation is in contrast to that of Bak and Elgershuizen (1976), who imply that sheet formation could be induced by sediments. However, *P. astreoides* and *P. furcata* both form mucus sheets on a lunar cycle which is not correlated to fluctuations in salinity, temperature, particulate matter or sedimentation (Coffroth, 1988a), although colonies experimentally exposed to sedimentation for 24 hours were subsequently covered by a mucus sheet for longer periods than the controls (Coffroth, 1988b). Sheet formation may therefore serve a protective function. It is unlikely that the minor sediment-related mucus secretions observed during this study were precursors to full mucus sheets, because sheet formation appeared to be independent of the region of sediment influx. But the possibility that sheets are responses to fine sediments in suspension close to the tissue surface cannot be ruled out.

The synergistic effects of mucus and water movement have been discussed by other authors (e.g. Marshall & Orr, 1931; Bak & Elgershuizen, 1976; Rogers, 1983). In agreement with the present study, Bak and Elgershuizen (1976) also found that mucus was not always an advantage to corals and argued that mucus build-up in sediment accumulations on the Caribbean corals *Porites astreoides* and *Agaricia agaricites* was an additional causative factor in mortality.

All investigators of sediment rejection have stressed the importance of tissue expansion and stomodaeal water uptake in cleansing of coral

tissues (e.g. Marshall & Orr, 1931; Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976). In their study of the effects of drilling muds, Thompson *et al* (1980) observed tissue expansion for *Montastrea annularis* but not for a range of other species. Some influence of sediment size on the extent to which tissue expansion predominated over ciliary activity is implied in all investigations.

Short-lived, pulsed contractions of the polyps and tissues occur in a number of Australian species and can be instrumental in mobilising sediments on the tissue surface. Although such pulsing has not been discussed by earlier workers (Marshall & Orr, 1931; Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976), it may not have been distinguished from other polyp and tissues expansion or contraction activities.

Tissue retraction appears to be a very universal response to sediment influxes (Marshall & Orr, 1931; Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976). It is also commonly observed as a feeding response (Yonge, 1930; Abe, 1938; Lewis & Price, 1976; *pers. obs.*) once tentacles have captured plankton. The Caribbean species studied by Bak and Elgershuizen (1976) retracted their tentacles with polyp mouths closed in response to non-food particles, in contrast to open mouths for food. The closed-mouth retraction response to sediments was also observed during the present study but later ingestion was very common. Ingestion of silt-sized particles (carborundum or carmine powders) was also observed by Yonge (1930) and Abe (1938). On the other hand, species tested by Bak and Elgershuizen (1976) did not ingest very small oil particles.

Bak and Elgershuizen (1976) found that for some species rejection behaviour varied with the degree of expansion of the tissues. There is some evidence that the solitary Caribbean coral *Scolymia cubensis* may show enhanced rejection during the night (Logan, 1988). The present work shows that mobilisation of sediment is particularly enhanced during dusk and that this period may be important for species such as *Astreopora myriophthalma*.

Several early studies indicated that mesenteries play a role in extra-coelenteric digestion for corals (e.g. Matthai, 1918; Yonge, 1930; Abe, 1938). On the other hand, mesenterial extrusion of this nature was

not observed by Lewis and Price (1976) and was principally attributed to the fact that mesenterial digestion tends to be connected to the presence of food particles on the tissue surface, whereas their studies involved mobile plankton. However, other workers have observed mesenterial extrusion in response to amino acids which would not require a tactile stimulus (e.g. Goreau et al. 1971). In the present study, a tactile stimulus may have been necessary: mesenteries were frequently extruded when sediments landed on the tissue surface but were never observed in response to fish homogenate which did not normally come to rest on the surface. Mesenteries are known to be extruded as a result of stress (oil: Lewis, 1971; starvation: Goreau et al. 1971; detergent: Yamasu & Mizofuchi, 1989; drilling muds: Thompson et al. 1980) and it was clear from current observations that mesenteries were frequently exposed when tissue lesions had been caused by mechanical damage. Following the initial mesenterial response to sediments (which stopped when ingestion of other sediment particles ceased), mesenteries were only observed once sediment accumulations had resulted in observable tissue damage. This provides a further demonstration of mesenterial extrusion in response to stress.

Corallite morphology

There has been considerable debate over the role of calice dimension and corallite form on a coral's ability to reject sediment. Hubbard and Pocock (1972) and Hubbard (1973) suggested that calice size and internal angle may affect the capacity of that species to expand, and that efficiency increases in the order cerioid to plocoid to meandroid. Bak and Elgershuizen (1976) did not find a strong relationship between calice size and speed of rejection, and found no evidence for the suggested corallite influence from cerioid to meandroid.

In the present study, there was a significant correlation between calice dimension and observed tissue expansion in response to sediment. There was also a relationship between active rejection (as defined in Table 2.2) and calice diameter. All large-polyped species were capable or very capable of rejecting all sediment sizes, and all non-ramose species with the smallest polyps (Porites spp. and Montipora spp.) were poor active sediment rejectors. However, in the mid-range, some species

were relatively inactive, and some were very active. Interestingly, all of the active mid-range species were strong ciliary rejectors.

Observations on the meandroid corals *Leptoria phrygia*, *Platygyra lamellina* and *Oulophyllia crispa* show that the ends of meanders are significant hurdles to be overcome in sediment rejection. Furthermore, sediment almost exclusively travels along meanders to a 'dead-end', and is rarely lifted over the walls except at this point. This would argue that individuals with relatively straight meanders (resulting in less distance for the sediment to be moved to the edge of the colony) *or* fewer dead-ends might be at an advantage over conspecific colonies with more sinuous meanders with shorter valleys, the most favour morphology being straight meanders with no dead-ends.

Johnson (1988) has shown that meander complexity in the Caribbean coral *Manicina areolata* shows significant variation in different environments. Complexity increased with colony size and the rate of increase tended to be greater in inshore habitats associated with finer sediments (and perhaps higher sedimentation rates) but, notably, complexity relative to sedimentation apparently *increased* rather than decreased. This finding is in conflict with predictions based on observations on meandroid Australian corals, so presumably other factors may be involved.

No such morphological trends are apparent between species. Many plocoid species are highly active sediment rejectors because of the arrays of cilia on their coenosarc tissues. *Gardineroseris planulata* and *Favites abdita*, both cerioid species, are very active rejectors because of the strength of their ciliary mechanisms.

There is evidence from other studies that polyp or calice size may be correlated with function. Porter (1974) and Lewis and Price (1976) found that polyp diameter of Caribbean corals was positively correlated with zooplankton capture (measured by amount of zooplankton in gut contents). Porter (1976) went further to suggest that small-polyped species may be more dependent upon autotrophy than larger species.

Significance of sediment ingestion

Although observations were not made on capture of living plankton, the present study made clear that many species will ingest sediments with virtually no nutritive value which had fallen on their tissues. Lewis (1976, 1977) has shown that corals are able to act as suspension feeders and Sorokin (1973) provides evidence that bacteria and organic matter can also be exploited. In fact Goreau *et al* (1971) suggest that some species will accept practically any type of particulate food. Provided that sedimentation rates are not in excess of a species' active rejection capability, it is likely that detritus or bacterial films coating settling sediments could be important food sources to some of these species, especially under conditions where planktonic organisms are less abundant. It is also probable that some species may be specifically adapted to exploit this food source. Such exploitation has been suggested by Foster (1980) for the Caribbean coral *Siderastrea siderea* based on her finding that its growth rate was positively correlated with sedimentation rates.

Sediment movement: random or directional

Dodge and Vaisnys (1977) used video recordings made by Hubbard and Pocock (1972) to argue that rejection of sediment showed no directional routing and could be approximated by a 'random walk'. They further argue that for .large corals this form of sediment rejection would require disproportionately more energy and that large corals would therefore have a lower chance of survival under increasing ambient sedimentation than smaller ones. In the present survey, sediment rejection was often not random. For many species, and particularly foliose, encrusting or laminar colonies, sediment followed gravitational paths dictated by colony morphology. Movement of sediment in mucus sheets on *Diploastrea heliopora*, where specific gravitational channels were rare, principally occurred in a direct line. Less directional movement was most common in massive species which had relatively rounded surfaces but showed poor mucus sheet production such as *Astreopora* species.

Sediment size

The sediment size-specific nature of species responses may be very important in modelling the energetic costs of different sediment sizes. The responses to silts, in particular, may be illuminating. Dense masses of silts reaching the surface were sometimes observed to flow off smooth, angled surfaces of a colony in a way that may require little energy. But corals did not show this response to individual particles, (or to neutrally buoyant particles of larger sizes) which often continued to require ciliary activity even on strongly angled surfaces. In many field situations where turbidity is high, suspensions of very fine particles may be suspended and resuspended c.ose to the tissue surface. Particles hitting the surface can adhere to surface mucus and require active removal. Irritation from a light silt rain of this nature could constitute a very significant energy drain because it would tend to affect the whole colony rather than be morphology-specific. Such an energy drain may be an important factor in limiting coral distributions in turbid areas with high levels of suspended particulates close to the tissue surfaces.

CHAPTER 3

SEDIMENT REJECTION EFFICIENCY OF AUSTRALIAN

SCLERACTINIAN CORALS

SEDIMENT REJECTION EFFICIENCY OF AUSTRALIAN SCLERACTINIAN CORALS

SUMMARY

Coarse (500um-1mm) and fine (63-250um) sediment rejection rates of a range of Australian mid-shelf corals were examined *in situ*. Rejection was measured as the percentage of a 25cm^2 area of flat tissue cleared after 1, 2, 4 and 24 hours. The input sediment dose was 200mg.cm^{-2} comprising locally collected, clean, calcareous/quartz sands, and was applied between 0930 and 1200 hours. In principal experiments, ten colonies were tested per treatment per species. Additional species were tested at lower replication (n=4 to 6 per treatment): these are indicated (*).

Under main conditions, very significant differences between clearance rates of non-branching species were found, which were correlated with calice dimension. *Fungia repanda* was the most effective sediment rejector, and *Oulophyllia crispa** was very competent. *Diploastrea heliopora*, *Galaxea fascicularis*, and *Symphyllia radians* also rejected sediment relatively fast. *Porites lobata*, *P. lutea** and *Montipora aequituberculata** were significantly slower than other species. Overall tissue clearance was significantly faster for fine sediment than for coarse.

With the exception of *Porites lobata*, *P. lutea**, *Montipora aequituberculata** and *Gardineroseris planulata**, on average all species had cleared about 90% or more of their tissues after 24 hours. However, intraspecific variation was high and only for *Fungia repanda* and *Diploastrea heliopora* had all replicates cleared >90% of their tissues.

Four branching species (*Porites cylindrica*, *Pachyseris rugosa*, *Psammocora contigua* and *Echinopora mammiformis*) were similarly tested and showed significantly faster sediment rejection than any non-branching species. There were significant differences in clearance rates between branching species.

The effect of increasing turbulence was investigated for six species. Sediment clearance rates were not significantly increased during periods of moderate wind (approximately 15 knots) and moderate local turbulence (measured by timed sediment loss from flat control surfaces *in situ*). However, during strong winds (approximately 20-25 knots) and substantial local turbulence, significantly increased clearance rates were shown by *Leptoria phrygia* and *Porites lobata* (p<0.01), *Astreopora myriophthalma* (p<0.05), and *Coeloseris mayeri* (p<0.10). No differences were detected for *Fungia repanda* or *Diploastrea heliopora*. In rough conditions, no statistically significant differences could be detected between the clearance rates of coarse and fine sediment (p>0.10).

As a result of one influx of 200mg.cm^{-2}, some tissue death occurred in three *Leptoria phrygia* and four *Favia stelligera* colonies in 24-48 hours. Four colonies of *Gardineroseris planulata* bleached and parts of 2 died over several days. Parts of 14 colonies of *Porites lobata* (n=20), 9 colonies of *P. lutea* (n=10) and 11 colonies of *Montipora aequituberculata* (n=12) bleached but subsequently recovered.

These experiments highlight major differences in rejection efficiency and tolerance of a total of 22 Australian hermatypic species and show that sediment rejection efficiency is not directly related to sediment tolerance. These findings are discussed in the light of other sediment rejection characteristics and the known distributions of species.

INTRODUCTION

It is widely recognised that high sediment loads in waters surrounding coral reefs strongly affect the ecology and composition of resulting coral communities (Roy & Smith, 1971; Loya, 1976; Randall & Birkeland, 1978) and the morphology of component species towards more resistant growth forms (Marshall & Orr, 1931; Maragos *et al*, 1970; Chappell, 1980; Veron, 1981). Changes in species composition or abundance have also been attributed to increases in sedimentation loads due to human activities (Brock *et al*, 1966; Marsh & Gordon, 1974; Dodge & Vaisnys, 1977), and recently it has become clear that general degradation of reefs as a result of sediments from anthropogenic sources is of serious concern worldwide (UNEP/IUCN, 1988a-c).

Sediments may influence corals in a number of ways. Suspended and/or overlying sediment may result in tissue death from smothering (Marshall & Orr, 1931; Roy & Smith, 1971; Rogers, 1983) or disease (Hodgson, 1990), and in direct disturbances to a coral's energy budget through reduction in light availability (Roy & Smith, 1971; Dallmeyer *et al*, 1982; Abdel-Salam & Porter, 1988; Yamasu & Mizofuchi, 1989), by interfering with the capacity to capture food (Szmant-Froelich *et al*, 1981; Chapter 2), and by increasing the energy demand for active sediment rejection (Aller & Dodge, 1974; Dallmeyer *et al*, 1982; Chapter 2). Reductions in growth and calcification rates resulting from these influences have been documented by a number of authors (Aller & Dodge, 1974; Dodge *et al*, 1974; Dodge & Vaisnys, 1977; Bak, 1978; Rogers, 1979; Hudson & Robbin, 1980; Dodge, 1981; Hudson *et al*, 1982), and have also been attributed to the effects of abrasion from suspended sediments in turbulent waters (Johannes, 1975; Loya, 1976; Rogers, 1983). Furthermore, layers of sediment on the substrate may inhibit settlement of juveniles (Edmondson, 1928; Harrigan, 1972; Maragos, 1972; Dodge & Vaisnys, 1977; Babcock & Davies, *in press*).

Thus increased sediment can threaten a coral's growth and survival through a wide range of different influences. Since corals differ in their dependence on autotrophic and heterotrophic feeding, and in their tolerance to wave energy and other environmental factors (e.g. Sheppard, 1982), it is reasonable to hypothesise that they may also differ in their sensitivities to the individual effects caused by sediments. If

the influence on corals of sediments from anthropogenic sources is to be effectively assessed and managed at an early stage, it is necessary to understand the effects of differing sediment quality and quantity on a range of coral species. Once differences in species sensitivities to sediments are identified, monitoring studies can be focussed on key species or 'indicators' of particular types of stress. In this context, indicator species are those which show a detectable response to a stress before it is widespread in the community at large.

Sediment rejection efficiency and tolerance to single or sustained sediment influxes are two measures of the ability of a species to cope with settling sediments. In the long-term there will be a trade-off between the advantages of strong rejection activity to prevent initial smothering by sediments, and depletion of energy reserves that would follow if this strong activity were sustained.

Rejection efficiency of a majority of Caribbean corals has been examined in the laboratory (Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976: Lasker, 1980; Logan, 1988; Abdel-Salam & Porter, 1988) and for a few species in the field (Rogers, 1979, 1983). The information about Indo-Pacific species is more dispersed and, with the exception of the fungiids, less comprehensive[1]. Some general indications of the rejection abilities and tolerance of Indo-Pacific genera were reported in early studies by Mayer (1918), Mayor (1924a&b), Marshall and Orr (1931) and Manton and Stephenson (1935). More recently, the fungiids have been studied in considerable detail by Schuhmacher (1977, 1979) and Fisk (1981).

The present study was undertaken to broaden the understanding of sediment rejection to include a wider range of Indo-Pacific taxa. Specifically it investigates the sediment rejection efficiency (the speed of sediment rejection over time) of 22 Australian corals from

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1. Only a few genera are found in both the Atlantic and Indian Ocean/Pacific regions (*Acropora, Porites* and *Montastrea* are important genera in both regions; *Siderastrea, Madracis, Leptoseris,* and *Favia* tend to be conspicuously more abundant in one region than the other). At the species level, *Siderastrea radians* is the only hermatypic coral common to both the Atlantic and Indo-Pacific (Porter, 1972; Veron, 1983). (The number of ahermatypic corals with global distributions is much greater.)

LIZARD ISLAND

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0        0.5        1        1.5
KILOMETRES
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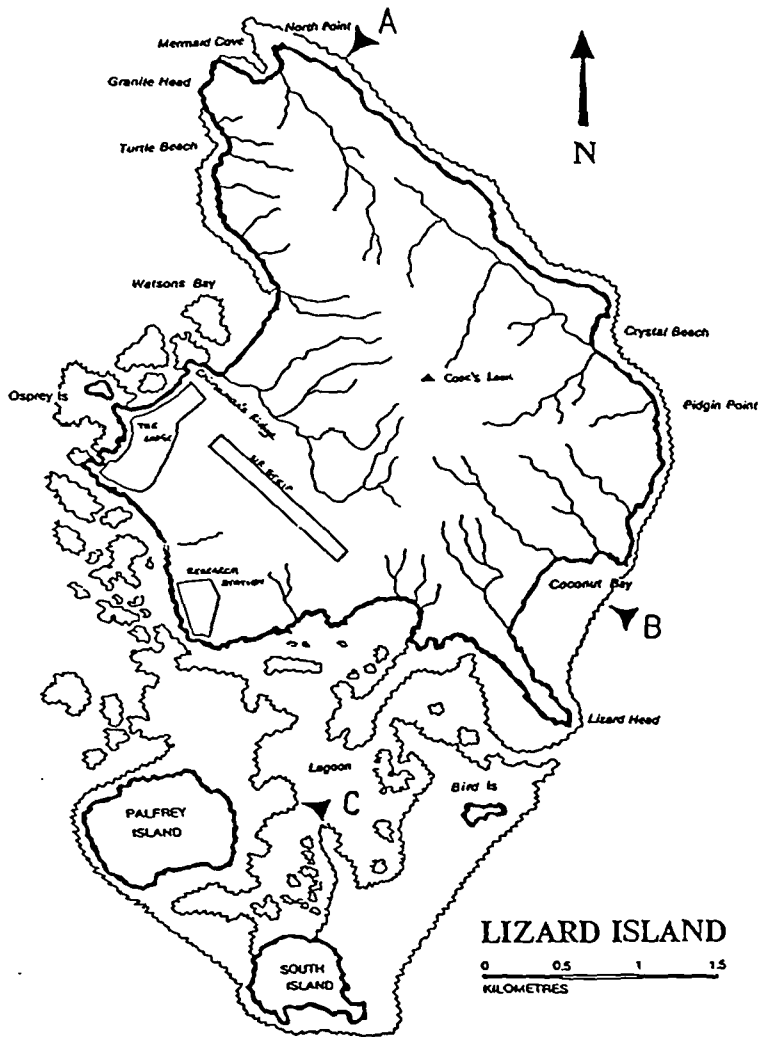
Figure 3.1. Lizard Island: locations of field sites for rejection efficiency experiments. Principal experiments were carried out at Sites A & B. Tests on ramose species were undertaken at Site C in the lagoon.

6cm-diameter screw-top central petri-dish, weighted and sealed

Test sediment

Outer sediment-collecting 'moat'
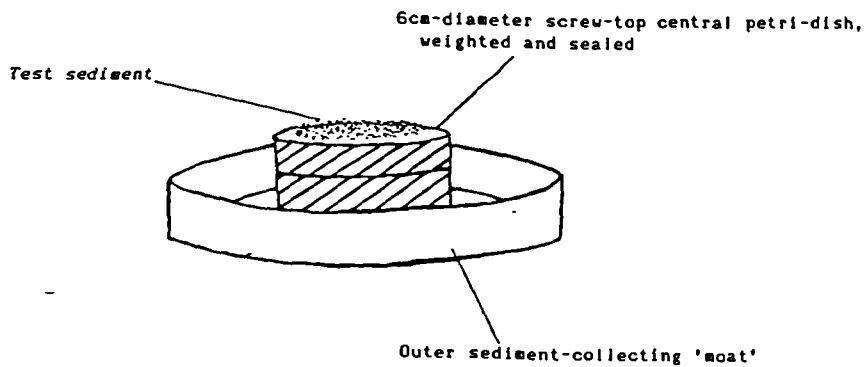
Figure 3.2 Petri-dish design for categorising the level of local turbulence.

Lizard Island. northern Great Barrier Reef. With the exception of three highly ramose species (*Porites cylindrica*, *Pachyseris rugosa* and *Psammocora contigua*), the active rejection mechanisms of all species described here are summarised in Chapter 2, Table 2.1 and Appendix A.

METHODS

Study area. These investigations were undertaken at Lizard Island. northern Great Barrier Reef. Australia[1]. Field experiments were carried out at two principal sites: Site A, on the exposed side of North Point: and Site B. on the exposed reef front at Coconut Beach (Figure 3.1). Ramose species were examined at Site C in the lagoon.

Sediment. The sediment was a local intertidal sand characteristic of the immediate region, which had been washed in fresh water, oven-dried for 4-8 hours, and sieved through a series of stainless steel Endicott sieves to *fine* (63-250um) or *coarse* (500um-1mm) grain sizes. The composition was approximately 70% sub-angular to rounded, reef-derived calcium carbonate, and 30% more angular quartz sand. Heavy minerals (represented by very fine (<100um) dark grains) *were rare and formed less than 2% of the fine sediment.* The carbonate fraction principally comprised foraminifera, shell and aragonite debris, and some red algae.

Measures of turbulence. Meteorological information and on-site observations were used to categorise conditions as Still, Light, Moderate. Strong or Very strong (approximately 0-5 [0-9], 10 [19], 15 [28], 20 [37], and 25 [46] knot [km/hr] winds respectively), and Calm, Mild, Moderate, Rough and Very rough seas.

Local water turbulence was also assessed independently for each experimental period, determined by examining the loss of a known weight of sediment from a smooth flat surface of known dimension. Sealable, 6cm-diameter, smooth-topped petri dishes were weighted, sealed, glued to the interior of larger petri dish lids (Figure 3.2)

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1. For a further description of Lizard Island, see General Introduction and Chapter 5.

ACCURACY OF VISUAL ESTIMATES

Untrained observer

Trained observer
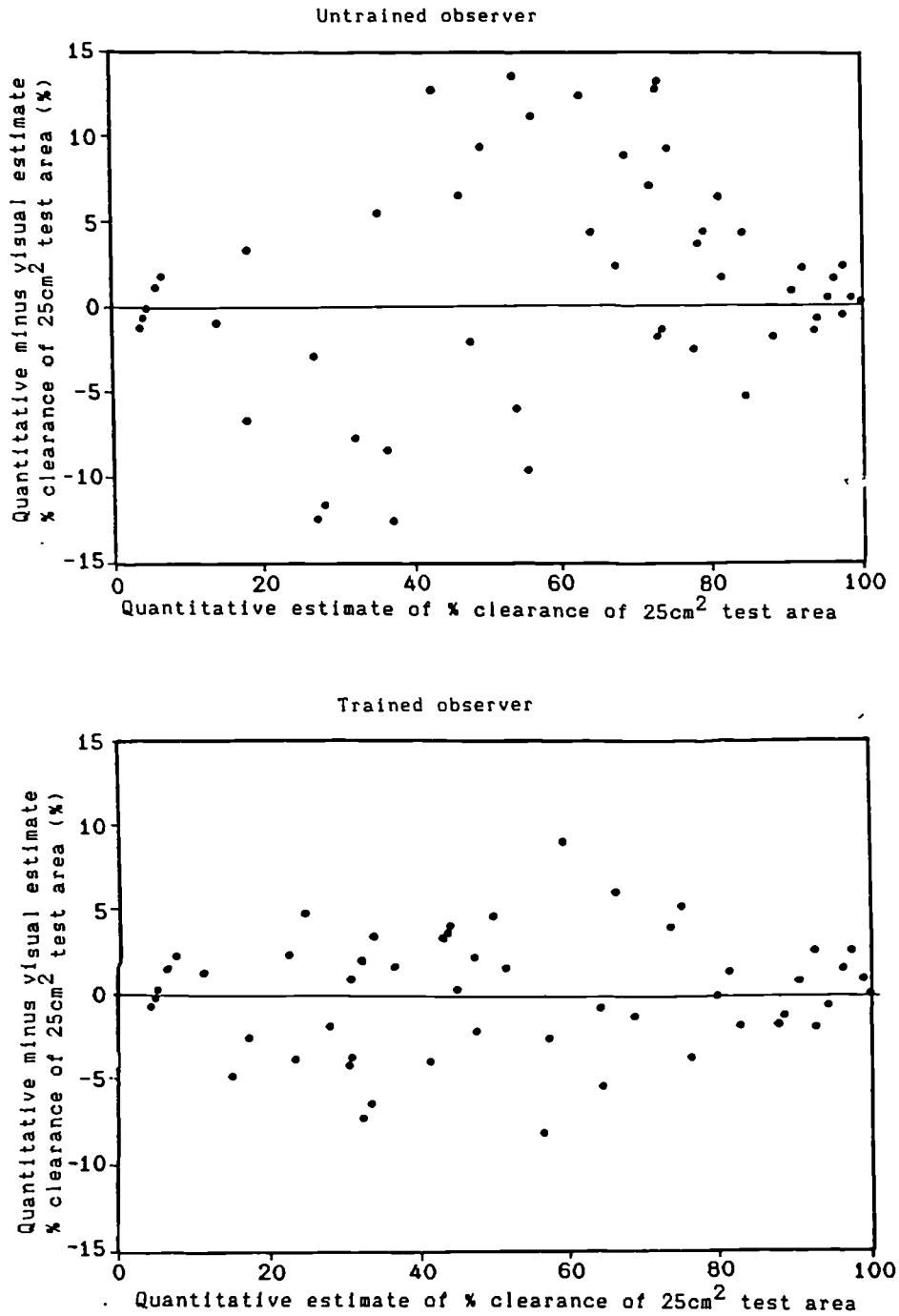
Figure **3.3.** Accuracy of visual estimates of percentage sediment cleared from $25cm^2$ test areas of *Diploastrea heliopora*: (a) prior to training; (b) following training of observer (see text). The *y*-axis is calculated as the difference between the mean of three quantitative estimates and the visual estimate. Visual estimates were made to the nearest 5%.

and placed on horizontal surfaces close to the experimental corals. $200mg.cm^{-2}$ of fine sediment was evenly spread across a 5cm diameter circle on the surface of the inner petri dish. The larger dish served as a collecting 'moat' for sediment lost from the centre. The time taken for complete clearance of the inner petri dish was recorded. A minimum of four replicates was used for each experimental period.

Tests of methodology. The accuracy and consistency of visual estimates of area covered by sediment were evaluated and observer training was undertaken. Colonies of a number of species were brought into the laboratory where _diment was evenly applied to a flat area of 5cm x 5cm. The percentage of this $25cm^2$ test area cleared over time was visually estimated to the nearest 5%, and concurrently photographed onto black-and-white film with a fixed camera. Photographic negatives were projected onto a grid of 250 points at a known scale. Quantitative estimates of percentage clearance were calculated from the ratio of points falling on sediment to those falling on clear polyp or coenosarc within the original $25cm^2$ area. A sufficient number of point-counts was carried out to provide 95% confidence intervals of $<\pm1.5\%$ around the mean for each photographic negative. The difference between the visual estimate and the quantitative estimate was plotted against the quantitative estimate to examine the level of inaccuracy and bias.

Training greatly improved the accuracy and precision of visual estimates. Pre- and post-training estimates using *Diploastrea heliopora* are illustrated, as an example, in Figures 3.3a&b.

Without training, visual estimates were within 5% of true values at high and low percentages but were less precise within the middle range. There was a bias in the estimations with a tendency to underestimate low clearance and overestimate high clearance. After training, visual estimates were always within 9% (normally within 5%) across the middle range (30-70%), and always within 5% throughout the rest of the range (Figure 3.3b).
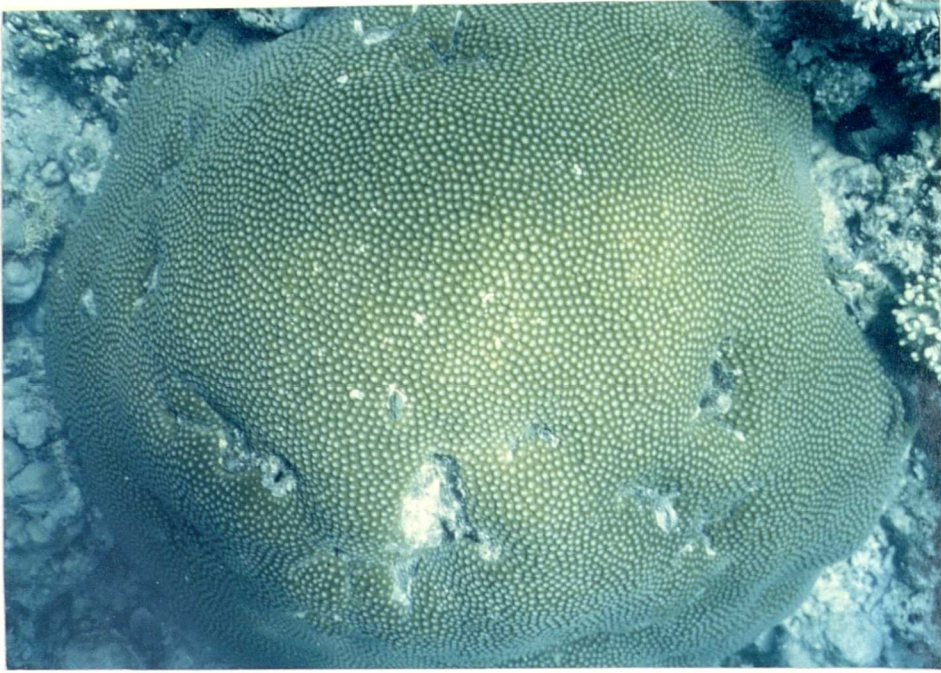
<u>Plate</u> <u>3.1</u>.   *Diploastrea heliopora* illustrating
                        massive morphology (x 0.1).

<u>Plate</u> <u>3.2</u>.   *Porites   cylindrica*   illustrating
                        ramose morphology (x 1.5).

Active rejection efficiency

Interspecies comparisons of active rejection efficiency were made for a core group of ten species (Group I, Table 3.1). Of these, eight were massive species (Plate 3.1) and two were free-living fungiids. Colonies of all ten species selected had at least some flat areas on their upper surface so that, for those areas, sediment loss under non-turbulent conditions would require active rejection. Sediment rejection was examined under Calm sea conditions to evaluate active rejection efficiency. Calm conditions were defined as those during which less than 5% of sediment was lost from turbulence petri dishes in 24 hours. Under these conditions, wind speeds were less than 10 knots, generally 0-5 knots.

A total of twenty[1] colonies of each species at a depth of 1.5-6m (measured from Low Water Mean Tide) were selected and tagged. All corals had a minimum diameter of 20cm (with the exception of *Fungia repanda* for which minimum diameter was 15cm) and had at least 10cm x 10cm of flat surface. Ten individuals of each species were then randomly allocated to each of two treatments. Within the portion of flat surface, either fine or coarse sediment was evenly applied to a centrally located area of 5cm x 5cm at a dose of $200mg.cm^{-2}$ between 0930 and 1200 hours. Using a wire quadrat of 5cm x 5cm divided into a grid of 1cm x 1cm, the percentage of the $25cm^2$ area cleared at 1, 2, 4 and 24 hours was estimated by eye to the nearest 5% for each coral. Additional observations were made after 48-54 hours, but as sea conditions had sometimes altered these observations are treated separately. Estimates of the proportion of sediment remaining by weight were made to aid the interpretation of clearance data. No individual was disturbed in any way during the course of rejection.

In general, a maximum of 30 individuals could be tested per day and a stratified randomisation schedule was used to control for bias. In all cases, the number of fine and coarse sediment treatments for each species was identical for any one 24 hour period.

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1. Additional replicates of *Porites* were tested because of field identification problems, and the required number of replicates was selected randomly following later identification.

Species Code	Species name	Replication (n) Fine/Coarse	
		Still Conditions	Increasing Turbulence
GROUP I			
Acan	*Acanthastrea echinata*	10/10	--/--
Ast	*Astreopora myriophthalma* (*)	10/10	10/10
Coel	*Coeloseris mayeri* (*)	10/10	10/10
Dipl	*Diploastrea heliopora* (*)	10/10	10/10
Fav	*Favia stelligera*	10/10	--/--
Fung	*Fungia repanda* (*)	10/10	10/10
Lept	*Leptoria phrygia* (*)	10/10	10/10
Por	*Porites lobata* (*)	10/10	. 10/10
Sand	*Sandolitha robusta*	10/10	--/--
Sym	*Symphyllia radians*	10/10	--/--
GROUP II			
Emam	*Echinopora mammiformis*	10/10	--/--
Prug	*Pachyseris rugosa*	10/10	--/--
Pcyl	*Porites cylindrica*	10/10	--/--
Psam	*Psammocora contigua*	10/10	--/--
GROUP III			
Cyph	*Cyphastrea serailia*	5/5	--/--
Galx	*Galaxea fascicularis*	10/10	--/--
Gard	*Gardineroseris planulata*	5/5	--/--
Hydn	*Hydnophora microconos*	6/6	--/--
Mont	*Montipora aequituberculata*	6/6	--/--
Oulo	*Oulophyllia crispa*	6/6	--/--
Ples	*Plesiastrea versipora*	6/6	--/--
Plut	*Porites lutea*	4/6	--/--

Table 3.1 Checklist of species (with species codes) tested in sediment rejection experiments. All experiments were carried out *in situ*. Group I: core group species involved in interspecies comparisons in Calm conditions; Group I (*): species tested in increasing turbulence; Group II: ramose species tested for comparison; Group III: species excluded from core group because of morphology (*Galaxea*) or lower replication.

Influence of passive factors

Morphology. A group of four finely branching species (Group II. Table 3.1: Plate 3.2) from the lagoon were tested in Calm conditions for comparison with Group I. Replication levels and treatments were identical. Estimates of the proportion of projected surface area cleared over time were made from above at 10, 20, 30, 60 and 120 minutes.

Turbulence. The effect of water movement was investigated for six core group species (Group I, highlighted (*), Table 3.1) for which turbulence conditions could be categorised into Calm, Moderate and Rough. The three treatment conditions were defined as follows:

a) Calm (<⁼5 knot winds, <5% loss of sediment from turbulence petri dishes in 24 hours)
b) Moderate (⁼15 knot winds, all sediment lost from turbulence petri dishes in 2-4 hours)
c) Rough (⁼25 knot winds, all sediment lost from petri dishes in 30-60 minutes)

For all species except *Leptoria phrygia*, the same 10 replicates for each sediment grain size were re-tested in Moderate and Rough sea conditions. As three colonies of *L. phrygia* suffered some mortality during initial tests, further colonies were substituted and were tested in all three conditions. For all species, tests of the same colony in different turbulence conditions were more than seven weeks apart.

Additional species

Eight corals (Group III, Table 3.1) were examined in the field but were analysed separately from Group I because of differences in experimental protocol.

For all Group III species except *Galaxea fascicularis*, logistic constraints resulted in reduced overall replication (4-6 per sediment grain size and 10-12 in total, Table 3.1). *G. fascicularis* was excluded from Group I on the grounds of morphology and the occasional need for interpolation of data. Colonies, though flat overall, have very exsert

corallites with tentacles extended day and night. Estimates of sediment loss were uncertain on six occasions because a proportion of the underlying tissue was obscured. In these cases, the percentage was estimated by interpolation.

Statistical analyses

The mean percentage clearance and 95% confidence intervals plotted on graphs have been calculated on arcsin-squareroot transformed data but are presented back-transformed. Although transformations improved normality of data on a species by species basis, variances were very heterogeneous and parametric analysis of variance was inappropriate. Hypotheses were therefore tested by non-parametric ranking procedures. Interspecies comparisons under Calm conditions and for the 4-hour timepoint under Rough conditions were analysed by Kruskal-Wallis 2-way analysis of variance by ranks (e.g. Zar, 1984: pp. 219-222). Subsequent pairwise comparisons followed a non-parametric equivalent to Tukey's test (Zar, 1984: p. 199). Data for Calm and increasing turbulence levels were paired (the same colony was tested in each of the three turbulence treatments) and Wilcoxon's paired sample ranking procedure was employed. Error rates were adjusted for multiple comparisons using the Dunn-Sidak equation

$$\alpha' = 1 - (1-\alpha)^{\frac{1}{k}}$$

where k=number of contrasts, and α'=the individual test error rate required in order to achieve the desired experimentwise (overall) error rate α (see Sokal & Rohlf, 1981: pp. 241-2). Comparisons between Group III species were restricted to Kruskal-Wallis one-way analysis of variance between species because of unequal cell sizes and the relatively low replication levels. To ensure equal replication of coarse and fine treatments for this analysis two data for coarse sediment were selected at random for *Porites lutea* and excluded from the analysis. Other standard tests are indicated in the text where relevant.

SEDIMENT CLEARANCE - CALM CONDITIONS

Group I species

Hours after sediment influx
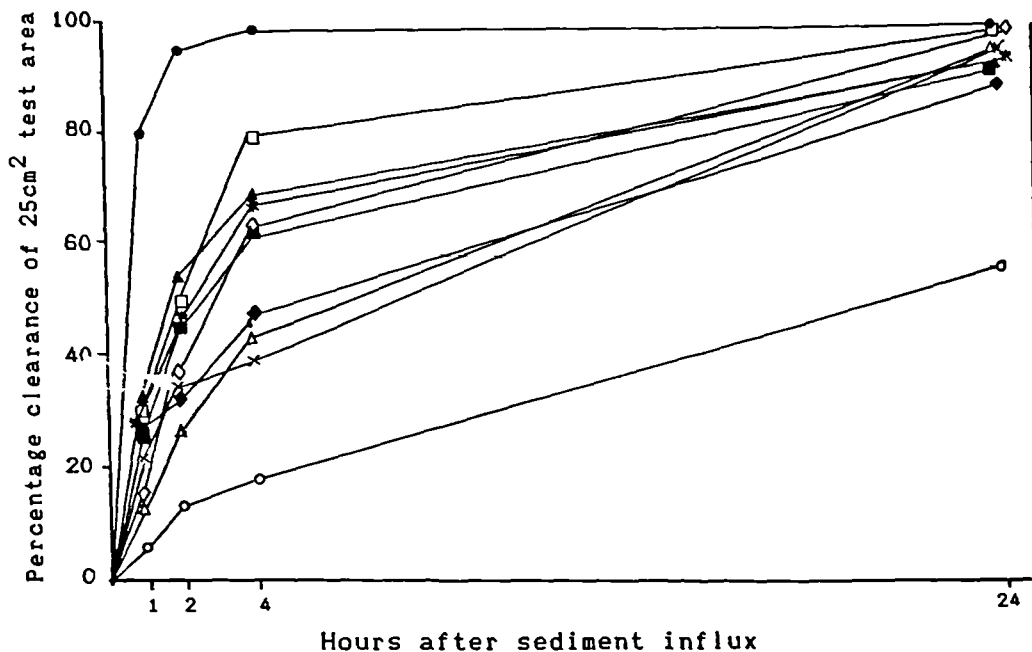
■ Acan   ◇ Ast   ▵ Coel   □ Dip   ✶ Fav

● Fung   ◆ Lept   ○ Por   x Sand   ▲ Sym

Figure 3.4. Sediment clearance by Group I species under Calm conditions (coarse and fine treatments combined). Means were calculated on arcsin-squareroot transformed data but are presented back-transformed. Confidence intervals have been excluded for clarity but are shown on summary graphs (Figures 3.9a-d). See Figure 3.5 for sediment size effects.

Active rejection efficiency

Mean clearance estimates for Calm conditions calculated for each timepoint and each species are illustrated in Figure 3.4. Untransformed raw data were analysed independently for 1, 2, 4 and 24 hours by Kruskal-Wallis 2-way analysis of variance (Tables 3.2a-d). Throughout the 24-hour period, sediment rejection of colonies inundated with fine sediment was significantly greater than that for coarse sediment. In absolute terms this difference amounted to approximately 10-20% of the tissue area during the first four hours, reducing to less than 10% after 24 hours (Figure 3.5), although individual species showed substantial variation. There was no interaction between species and sediment (p>0.1) indicating that no species showed a significant reverse trend[1]. Overall, however, differences between species were highly significant (p<0.001). Detailed analysis of species differences are given in significance matrices (Tables 3.3a-d).

Table 3.3d and Figure 3.4 indicate that all species but *Porites lobata* had cleared an average of 89% of the test area or greater after 24 hours. Visual estimates of the amount of sediment remaining on the tissues suggested that these species had also removed more than 90% of the sediment by weight (i.e. the weight per unit area on which sediment remained was often much less than $200mg.cm^{-2}$). In contrast, *P. lobata* had cleared an average of less than 60% of the test area and visual estimates of sediment quantity remaining on the tissues showed that often more than half the sediment by weight remained on a reduced area (i.e. the weight per unit area often increased to over $200mg.cm^{-2}$).

Over the first four hours *Fungia repanda* showed significantly greater clearance than other species with a minimum of 60% of all test areas cleared after one hour (Table 3.3a). *Diploastrea heliopora* and *Symphyllia radians* also showed consistently high clearance rates. In

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1. As there was no interaction between species and sediment size (p>0.10, Table 3.2), details of species/sediment-size interactions are not reported here but are given in Appendix 3.1 because they may highlight useful areas for further work.

FINE/COARSE SEDIMENT CLEARANCE
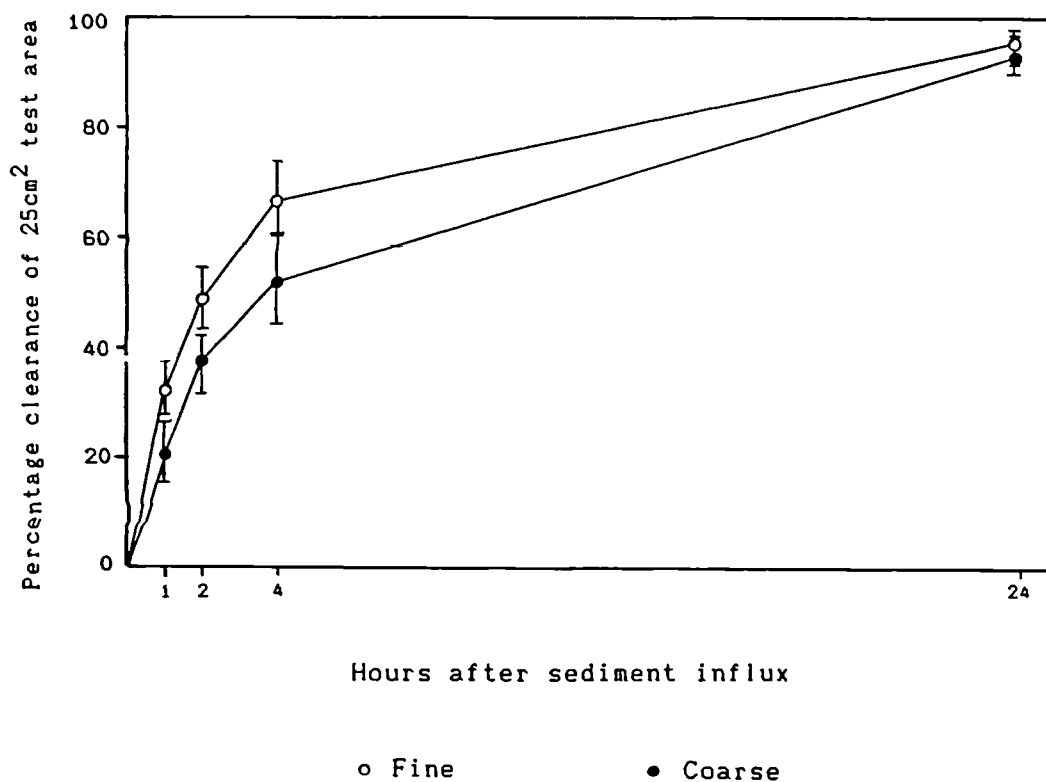
Figure 3.5. Rejection of fine and coarse
sediment under Calm conditions (all Group 1
species combined: n=100 per treatment.
mean+95%CI).

Group I species

a) Hour 1	SS	SS/MS (H)	df	p	
Sediment	48298.3	14.8	1	<0.001	***
Species	317401.6	97.5	9	<0.001	***
Species*sediment	30325.9	9.3	9	>0.10	ns
Error MS[1]	3255.5				

b) Hour 2	SS	SS/MS (H)	df	p	
Sediment	29451.6	8.9	1	<0.005	**
Species	288094.5	87.3	9	<0.001	***
Species*sediment	37171.2	11.3	9	>0.10	ns
Error MS[1]	3301.6				

c) Hour 4	SS	SS/MS (H)	df	p	
Sediment	29939.0	9.0	1	<0.005	**
Species	329899.5	99.5	9	<0.001	***
Species*sediment	39962.1	12.0	9	>0.10	ns
Error MS[1]	3316.4				

d) Hour 24	SS	SS/MS (H)	df	p	
Sediment	13894.4	4.3	1	<0.05	*
Species	314807.3	98.4	9	<0.001	***
Species*sediment	17939.0	5.6	9	>0.10	ns
Error MS[1]	3199.9				

Table 3.2. Kruskal-Wallis 2-way analysis of variance to examine clearance of two sediment sizes by Group I species in Calm conditions.

[1] Error MS has been corrected for tied ranks.

CALM CONDITIONS

Group I species

a) **Hour 1**

	Por	Coel	Ast	Sand	Acan	Lept	Fav	Dipl	Sym	Fung
Por	-									
Coel	ns	-								
Ast	ns	ns	-							
Sand	*	ns	ns	-						
Acan	**	ns	ns	ns	-					
Lept	***	ns	ns	ns	ns	-				
Fav	**	ns	ns	ns	ns	ns	-			
Dipl	***	(*)	ns	ns	ns	ns	ns	-		
Sym	***	*	ns	ns	ns	ns	ns	ns	-	
Fung	***	***	***	***	***	***	***	**	*	-

% test area cleared

	Por	Coel	Ast	Sand	Acan	Lept	Fav	Dipl	Sym	Fung
Mean	4.79	12.9	13.5	21.7	25.5	26.9	27.2	29.8	32.0	78.9
Max	20	30	60	60	50	60	80	70	60	95
Min	0	5	0	5	10	10	10	10	10	60

	Por	Coel	Ast	Sand	Acan	Lept	Fav	Dip	Sym	Fung

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                                                          ----
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b) **Hour 2**

	Por	Coel	Lept	Sand	Ast	Acan	Fav	Dipl	Sym	Fung
Por	-									
Coel	ns	-								
Lept	ns	ns	-							
Sand	ns	ns	ns	-						
Ast	ns	ns	ns	ns	-					
Acan	**	ns	ns	ns	ns	-				
Fav	**	ns	ns	ns	ns	ns	-			
Dipl	**	ns	ns	ns	ns	ns	ns	-		
Sym	***	*	ns	ns	ns	ns	ns	ns	-	
Fung	***	***	***	***	***	***	**	**	*	-

% test area cleared

	Por	Coel	Lept	Sand	Ast	Acan	Fav	Dipl	Sym	Fung
Mean	12.3	27.0	33.1	34.0	37.0	45.0	46.0	49.1	53.5	93.5
Max	50	70	70	95	98	90	80	95	80	100
Min	0	10	10	10	0	20	10	20	20	80

	Por	Coel	Lept	Sand	Ast	Acan	Fav	Dip	Sym	Fung

```
                                                          ----
           ------------------------------------
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    ------------------------
```

c) Hour 4

	Por	Sand	Coel	Lept	Acan	Ast	Fav	Sym	Dipl	Fung
Por	-									
Sand	ns	-								
Coel	ns	ns	-							
Lept	ns	ns	ns	-						
Acan	**	ns	ns	ns	-					
Ast	**	ns	ns	ns	ns	-				
Fav	***	ns	ns	ns	ns	ns	-			
Sym	***	(*)	ns	ns	ns	ns	ns	-		
Dipl	***	**	*	(*)	ns	ns	ns	ns	-	
Fung	***	***	***	***	***	***	**	**	ns	-

% test area cleared

	Por	Sand	Coel	Lept	Acan	Ast	Fav	Sym	Dipl	Fung
Mean	17.0	39.7	43.4	47.5	62.1	62.6	66.3	68.6	78.4	97.5
Max	50	95	95	90	90	98	90	95	100	100
Min	0	10	10	10	30	10	30	30	40	85

Por Sand Coel Lept Acan Ast Fav Sym Dip Fung

d) Hour 24

	Por	Lept	Acan	Sym	Coel	Fav	Sand	Ast	Dipl	Fung
Por	-									
Lept	(*)	-								
Acan	*	ns	-							
Sym	*	ns	ns	-						
Coel	***	ns	ns	ns	-					
Fav	**	ns	ns	ns	ns	-				
Sand	***	ns	ns	ns	ns	ns	-			
Ast	***	(*)	ns	ns	ns	ns	ns	-		
Dipl	***	***	**	**	*	*	ns	ns	-	
Fung	***	***	***	***	*	*	ns	ns	ns	-

% test area cleared

	Por	Lept	Acan	Sym	Coel	Fav	Sand	Ast	Dipl	Fung
Mean	57.3	89.1	92.4	93.1	94.5	95.2	96.1	98.8	99.9	100
Max	90	100	100	100	100	100	100	100	100	100
Min	20	40	60	70	60	50	60	80	90	98

Por Lept Acan Sym Coel Fav Sand Ast Dip Fung

Table 3.3. Pair-wise comparison matrices for the 10 Group I species in Calm conditions. --- Statistically similar species are linked at p>0.05. *** p<0.001; ** p<0.01; * p<0.05; (*) p<0.10; ns p>0.10.

Group I and Group II species

a)   Analysis of variance at 1 hour including ramose species

	SS	SS/MS (H)	df	p	
Sediment	39460.6	6.1	1	<0.025	*
Species	434236.2	221.4	13	<0.001	***
Species*sediment	40948.4	6.3	13	>0.10	ns
Error MS[1]	6478.3				

b)   Contrasts among ramose corals and against Group I corals

	Por	Coel	Ast	Sand	Fav	Acan	Lept	Dipl	Sym	Fung	Prug	Pcyl	Psam	Emam
Prug	***	***	***	***	***	***	**	**	**	ns	–			
Pcyl	***	***	***	***	***	***	***	***	***	ns	ns	–		
Psam	***	***	***	***	***	***	***	***	***	ns	ns	ns	–	
Emam	***	***	***	***	***	***	***	***	***	ns	ns	ns	ns	–

Table **3.4**. Kruskal-Wallis 2-way analysis of variance to examine clearance of to sediment sizes by Group II (ramose species) and Group I species after one hour in Calm conditions. There are no differences between ramose species, but all four show significantly higher clearance than all non-ramose species but *Fungia repanda* after one hour.

[1] Error MS has been corrected for tied ranks. *** $p<0.001$; ** $p<0.01$; * $p<0.05$; (*) $p<0.10$; ns $p>0.10$.

contrast, only one individual of *Porites lobata* had cleared 20% after the first hour, and both *Coeloseris mayeri* and *Sandolitha robusta* also showed poor initial clearance. *Leptoria phrygia*, *Astreopora myriophthalma*, *Favia stelligera* and *Acanthastrea echinata* fell in the mid-range.

Influence of passive factors

Morphology. Clearance rates after one hour from branching lagoonal forms of *Porites cylindrica*, *Echinopora mammiformis*, *Psammocora contigua* and *Pachyseris rugosa* were substantially higher than Group I corals (Table 3.4). For all Group I corals except *Fungia repanda* the differences were highly significant (*Porites cylindrica*, *E. mammiformis* and *Psammocora contigua*: $p < 0.001$; *Pachyseris rugosa*: $p < 0.01$). The mean clearance after one hour for ramose corals (range 92.6-98%) was also substantially higher than that for *F. repanda* (78.9%), but the difference was not significant ($p > 0.10$). Readings made for 12 individuals of *F. repanda* after 30 minutes showed a maximum clearance of 60%, and were directly tested against those for *P. rugosa* for the same time point. The difference was highly significant ($p < 0.001$, Mann-Whitney 2-sample test, $n_1 = 12$, $n_2 = 20$). Thus, all ramose species showed significantly higher rejection rates than all Group I species.

Sediment size had no effect on clearance rates of ramose species, but there were significant differences in clearance rates between species: *Pachyseris rugosa* showed significantly lower clearance than either *Echinopora mammiformis* ($p < 0.01$) or *Psammocora contigua* ($p < 0.05$).

Turbulence. The effect of turbulence on clearance rates for each species and each sediment size is illustrated in Figures 3.6a-l. Paired differences between Calm and Moderate, and Calm and Rough conditions for the 4-hour timepoint, were examined by Wilcoxon signed ranks for all species combined.

Although turbulence petri dishes indicated substantial increases in turbulence between Calm and Moderate conditions, there were no

CALM CONDITIONS

Group II ramose corals only

a) Analysis of variance (10 minutes after sediment influx)

	SS	SS/MS (H)	df	p	
Sediment	441.80	0.84	1	>0.10	ns
Species	7904.13	15.01	3	<0.005	**
Species*sediment	671.13	1.27	3	>0.10	ns
Error MS[1]	526.4				

b) Multiple contrasts between species (10 minutes after sediment influx)

	Prug	Pcyl	Psam	Emam
Prug	-			
Pcyl	ns	-		
Psam	*	ns	-	
Emam	**	ns	ns	-

% test area cleared

	Prug	Pcyl	Psam	Emam
Mean	76.1	81.4	85.1	88.4
Max	90	95	95	100
Min	60	65	70	70

Prug Pcyl Psam Emam

Table 3.5 Kruskal-Wallis 2-way analysis of variance to examine differences between clearance by ramose species after 10 minutes. --- Statistically similar species are linked at $p>0.05$. [1] Error MS is corrected for tied ranks. *** $p<0.001$; ** $p<0.01$; * $p<0.05$; (*) $p<0.1$; ns $p>0.10$.

a) Effect of Moderate and Rough conditions on sediment clearance
    (Wilcoxon signed ranks)

	Moderate	Rough
Large sample test statistic (Z)	1.40	5.10
Sample size (total less tied pairs)	98	108
p	>0.10	.c. 1
Significance	ns	***

b) Detailed analysis of effect of Rough conditions on clearance
    for each species

Species	Significance Wilcoxon pairs (n=20)	Adjusted Significance
Astreopora	0.004	*
Coeloseris	0.011	(*)
Diploastrea	0.573	ns
Fungia	0.463	ns
Leptoria	0.000	**
Porites	0.000	**

Table **3.6** Influence of turbulence on sediment   rejection.
Percentage clearance under Calm and Rough conditions for the 4-
hour time point. The calculated significance levels for each
species are reported using combined data for fine and coarse
sediments (n=20). α' for multiple comparisons was calculated by
the Dunn-Sidak equation for k=6.

For $p<0.10$ (*), $\alpha'<0.017$: $p<0.05$ *, $\alpha'<0.0085$; $p<0.01$ **,
$\alpha'<0.0017$.

FINE SEDIMENT   COARSE SEDIMENT

Hours after sediment influx

■ Still   ○ Moderate   ▲ Rough

84

FINE SEDIMENT   COARSE SEDIMENT

Hours after sediment influx

■ Still   o Moderate   ▲ Rough
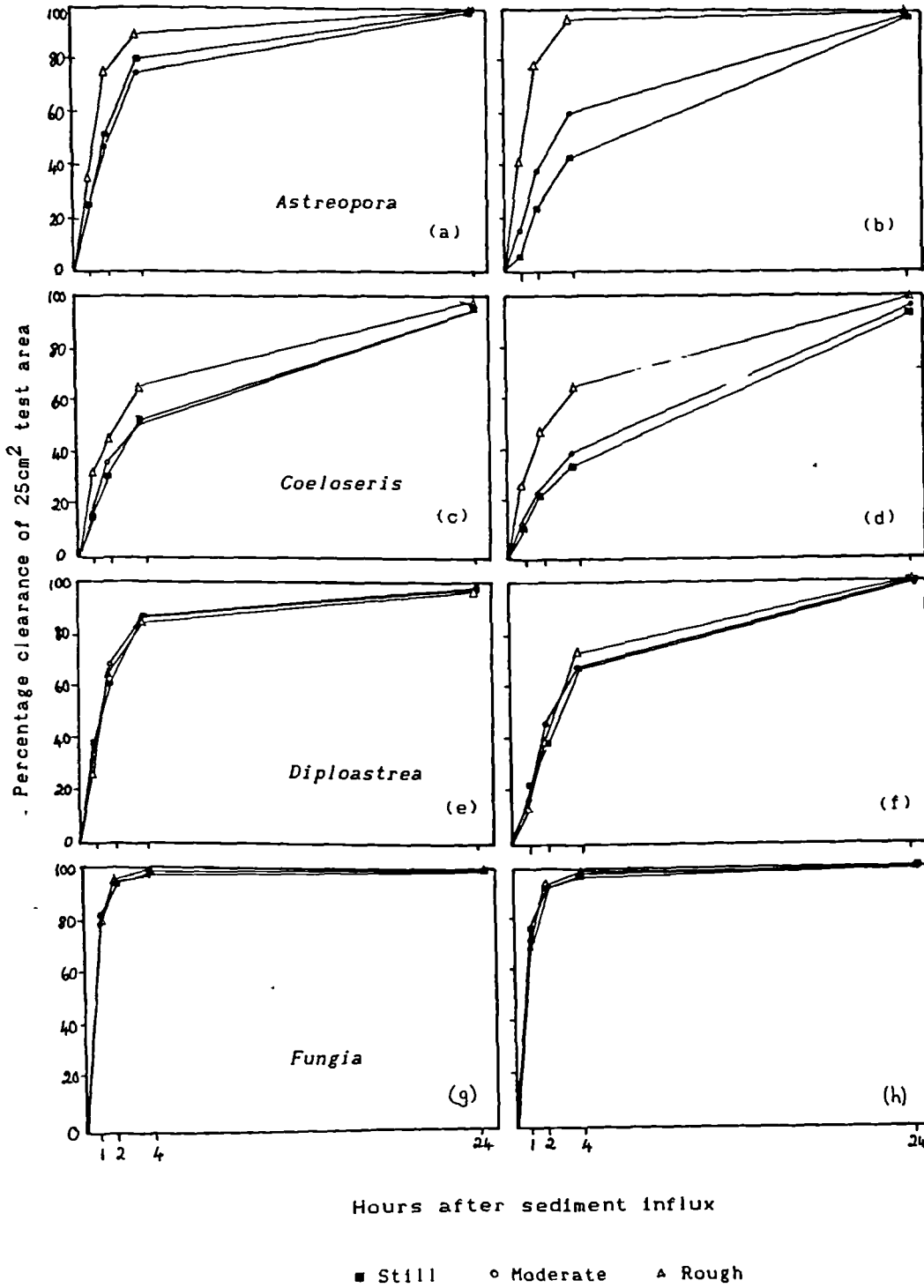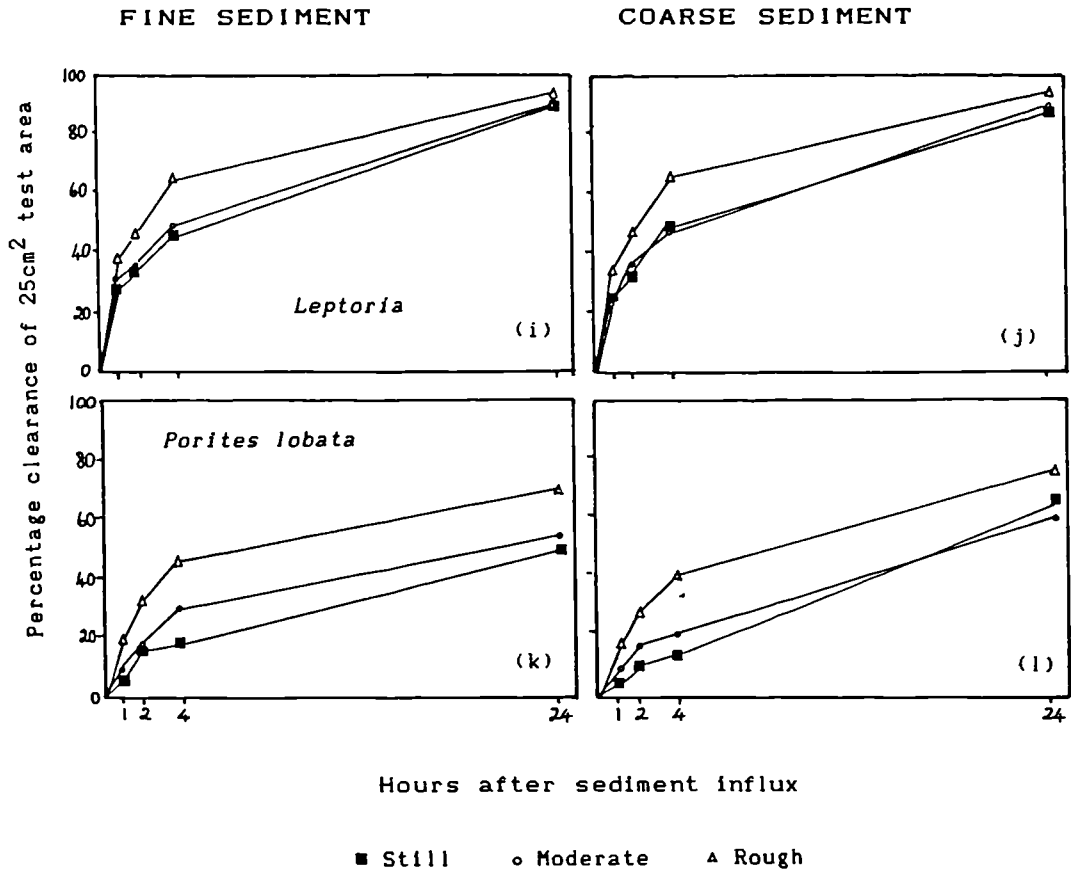
Figure **3.6.** Effect of turbulence on coarse and fine, sediment rejection for Group I (*) species after 4 hours. No significant effect of Moderate turbulence on sediment rejection could be demonstrated (see text). Sediment clearance under Rough conditions was significantly faster than in Calm conditions. For combined fine and coarse sediment treatments (n=20), turbulence was a significant factor for *Porites lobata* and *Leptoria phrygia* (p<0.01). *Astreopora myriophthalma* (p<0.05), and less so for *Coeloseris mayeri* (p<0.10). There was no effect for either *Diploastrea heliopora* or *Fungia repanda*.

Means (±95%CI for the 4-hour timepoint) are based on arcsin-squareroot transformed data but are presented backtransformed.

Group I (*) corals

a) Analysis of variance (4 hours after sediment influx)

	SS	SS/MS (H)	df	p	
Sediment	108.30	0.09	1	>0.10	ns
Species	84205.97	70.44	5	<0.001	***
Species*sediment	2081.37	1.74	5	>0.10	ns
Error MS[1]	1195.5				

b) Multiple contrasts between species (4 hours after sediment influx)

	Por	Lept	Coel	Dipl	Ast	Fung
Por	-					
Lept	ns	-				
Coel	ns	ns	-			
Dipl	**	ns	ns	-		
Ast	***	***	**	ns	-	
Fung	***	***	***	*	ns	-

% test area cleared

	Por	Lept	Coel	Dipl	Ast	Fung
Mean	42.6	65.4	65.5	79.1	93.1	97.7
Max	60	80	95	100	100	100
Min	20	40	40	30	30	85

Por Lept Coel Dipl Ast Fung

Table 3.7. Kruskal-Wallis 2-way analysis of variance to examine clearance of two sediment sizes by Group I(*) species under Rough conditions after 4 hours. --- Statistically similar species are linked at p>0.05. [1] Error MS is corrected for tied ranks. *** p<0.001; ** p<0.01; * p<0.05; (*) p<0.10; ns p>0.10.

significant differences in overall species clearance rates (p>0.10,
Table 3.6a). However. overall clearance rates were significantly
higher during Rough conditions (p<0.001, Table 3.6a), affecting
Leptoria phrygia and *Porites lobata* (p<0.01). *Astreopora
myriophthalma* (p<0.05) and, to a lesser extent, *Coeloseris mayeri*
(0.10>p>0.05, Table 3.6b).

Kruskal-Wallis 2-way analysis of variance was carried out on
data for Rough conditions on the 4-hour timepoint (Table 3.7a). In
contrast to the same Group I species under Calm conditions (see
Table 3.2), there was no difference in the clearance of fine and
coarse sedi ' but differences between species were still very
significant (p<0.001). Interspecies multiple contrasts indicated
similar trends to those highlighted in Table 3.3c with the exception
that *Astreopora myriophthalma* showed higher clearance under Rough
conditions.

Additional species

Clearance rates of Group III corals showed significant interspecies
variation (Figure 3.7 and Tables 3.8 and 3.9). *Porites lutea*. a species
very similar in form and polyp size to *Porites lobata*, showed similarly
poor clearance. *Montipora aequituberculata*, a second species with small
polyps, also showed consistently poor tissue clearance. At the other
end of the spectrum, clearance from *Oulophyllia crispa* was the greatest
for Group III corals and significantly higher than for either *P. lutea*
or *M. aequituberculata*.

Gardineroseris planulata showed a different response from all other
species. It cleared sediment well during the first hour, but this
declined rapidly and overall clearance after 24 hours was poor.

Persistence of overlying sediment, tissue damage and mortality

All colonies on which sediment remained were re-assessed for tissue
damage or death after 48-56 hours and again subsequently as logistics
and weather conditions allowed. Table 3.10 shows the number of colonies
for which clearance was complete (98-100%). almost complete (90-98%),
relatively poor (50-90%) or very poor (<50%) after 48-56 hours.

Group III corals

Hours after sediment influx

■ Cyph	● Galx	◆ Gard	▲ Hydn
□ Mont	○ Oulo	△ Ples	◇ Plut
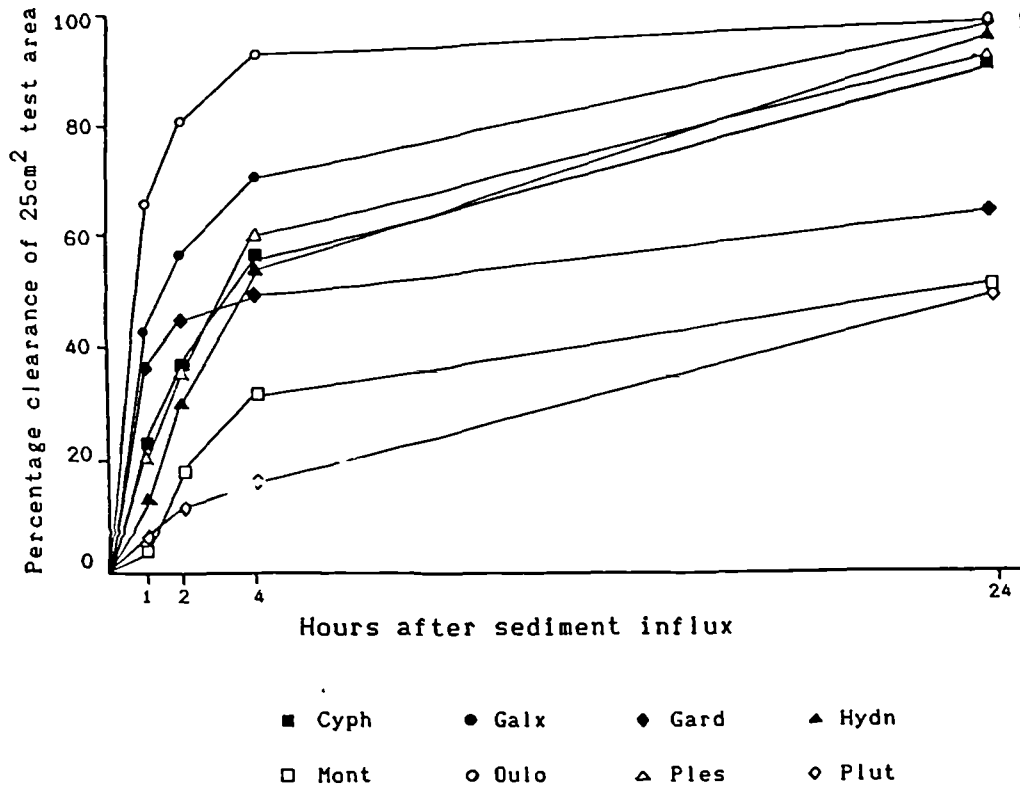
Figure 3.7. Sediment clearance by Group III species under Calm conditions (coarse and fine treatments combined). Means were calculated on arcsin-squareroot transformed data but are presented back-transformed. Confidence intervals have been excluded for clarity but are shown on summary graphs (Figures 3.9a-d).

CALM CONDITIONS

Group III species

```
┌─────────────────────────────────────────────────────┐
│                                                      │
│ One-way analysis of variance between species         │
│                                                      │
│                    H      df     p                    │
│                                                      │
│        Hour 1     64.1     7    <0.001 ***           │
│        Hour 2     53.9     7    <0.001 ***           │
│        Hour 4     47.2     7    <0.001 ***           │
│        Hour 24    57.9     7    <0.001 ***           │
│                                                      │
│        Chi-squared for df=7 and p=0.001              │
│             is 24.32                                  │
│                                                      │
└─────────────────────────────────────────────────────┘
```

Table 3.8. Kruskal-Wallis one-way analysis of variance to examine clearance of two sediment sizes from Group III species in Calm conditions. Data for fine and coarse treatments are combined.

CALM CONDITIONS

Group III species

a) **Hour 1**

	Mont	Plut	Hydn	Ples	Cyph	Gard	Galx	Oulo
n	12	8	12	12	10	10	20	12
Mont	-							
Plut	ns	-						
Hydn	ns	ns	-					
Ples	ns	ns	ns	-				
Cyph	ns	ns	ns	ns	-			
Gard	ns	ns	ns	ns	ns	-		
Galx	*	*	ns	ns	ns	ns	-	
Oulo	***	**	*	ns	ns	ns	ns	-

% test area cleared

	Mont	Plut	Hydn	Ples	Cyph	Gard	Galx	Oulo
Mean	3.77	6.23	13.7	21.1	22.7	37.1	42.5	66.1
Max	20	20	30	50	50	80	80	90
Min	0	0	0	0	10	15	10	50

Mont Plut Hydn Ples Cyph Gard Galx Oulo

----

b) **Hour 2**

	Plut	Mont	Hydn	Ples	Cyph	Gard	Galx	Oulo
Plut	-							
Mont	ns	-						
Hydn	ns	ns	-					
Ples	ns	ns	ns	-				
Cyph	ns	ns	ns	ns	-			
Gard	ns	ns	ns	ns	ns	-		
Galx	(*)	ns	ns	ns	ns	ns	-	
Oulo	***	**	*	ns	(*)	ns	ns	-

% test area cleared

	Plut	Mont	Hydn	Ples	Cyph	Gard	Galx	Oulo
Mean	11.3	18.1	30.9	36.4	37.0	45.5	56.8	81.3
Max	30	40	70	60	98	80	90	95
Min	0	5	10	5	0	20	10	70

Plut Mont Hydn Ples Cyph Gard Galx Oulo

            ----

c) Hour4

```
      Plut Mont Gard Hydn Cyph Ples Galx Oulo
Plut  -
Mont  ns   -
Gard  ns   ns   -
Hydn  ns   ns   ns   -
Cyph  ns   ns   ns   ns   -
Ples  ns   ns   ns   ns   ns   -
Galx  ns   ns   ns   ns   ns   ns   -
Oulo  ***  **   ns   ns   ns   ns   ns   -
```

% test area cleared

```
Mean 15.6 32.0 49.7 54.4 56.9 61.2 70.4 93.8
Max    30   50   85   90   98   95   95  100
Min     0   20   20   10   30   10   10   80
```

```
      Plut Mont Gard Hydn Cyph Ples Galx Oulo
           --------------------------------
        ---------------------------------
```

d) Hour 24

```
      Plut Mont Gard Cyph Ples Hydn Galx Oulo
Plut  -
Mont  ns   -
Gard  ns   ns   -
Cyph  ns   ns   ns   -
Ples  ns   ns   ns   ns   -
Hydn  ns   (*)  ns   ns   ns   -
Galx  *    (*)  ns   ns   ns   ns   -
Oulo  *    **   *    ns   ns   ns   ns   -
```

% test area cleared

```
Mean 50.6 51.6 64.3 91.5 92.1 96.6 98.9 99.1
Max    90   80   90  100  100  100  100  100
Min    20   20   50   60   50   75   60   80
```

```
      Plut Mont Gard Cyph Ples Hydn Galx Oulo
                --------------------------
             --------------------------
           --------------------------
```

Table **3.9** Pair-wise comparison matrices for Group III species under Calm conditions. Data for fine and coarse treatments have been combined. --- Statistically similar species are linked at $p > 0.05$. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; (*) $p < 0.10$; ns $p > 0.10$.

Code	Species name	Total (n) F/C	Clearance after 48 hours >98% F/C	90-98% F/C	50-90% F/C	<50% F/C	Tissue damage Blch F/C	Mort F/C
Acan	*Acanthastrea echinata*	10/10	8/6	2/1	0/3	0	0	0
Ast	*Astreopora myriophthalma*	10/10	10/9	0/1	0	0	0	0
Coel	*Coeloseris mayeri*	10/10	7/8	2/0	1/2	0	0	0
Cyph	*Cyphastrea serailia*	5/5	3/3	1/1	1/1	0	0[a]	1/0[b]
Dipl	*Diploastrea heliopora*	10/10	10/10	0	0	0	0	0
Emam	*Echinopora mammiformis*	10/10	10/10	0	0	0	0	0
Fav	*Favia stelligera*	10/10	7/8	3/1	0/1	0	0[a]	3/1[c]
Fung	*Fungia repanda*	10/10	10/10	0	0	0	0	0
Galx	*Galaxea fascicularis*	10/10	10/8	0	0/2	0	0	0
Gard	*Gardineroseris planulata*	5/5	1/0	1/0	3/5	0	2/2[a]	2/0
Hydn	*Hydnophora microconos*	6/6	5/5	0/1	1/0	0	0	0
Lept	*Leptoria phrygia*	10/10	6/6	2/3	1/0	1/1	0[a]	3/0[c]
Mont	*Montipora aequituberculata*	6/6	0	1/0	4/4	1/2	6/5[d]	0
Oulo	*Oulophyllia crispa*	6/6	6/5	0/1	0	0	0	0
Prug	*Pachyseris rugosa*	10/10	10/10	0	0	0	0	0
Ples	*Plesiastrea versipora*	6/6	4/5	1/0	1/1	0	0	0
Pcyl	*Porites cylindrica*	10/10	10/10	0	0	0	0	0
Por	*Porites lobata*	10/10	2/0	0/2	1/7	7/1	8/6	0
Plut	*Porites lutea*	4/6	0/1	1/0	1/2	2/3	4/5	0
Psam	*Psammocora contigua*	10/10	10/10	0	0	0	0	0
Sand	*Sandolitha robusta*	10/10	9/6	1/2	0/2	0	0	0
Sym	*Symphyllia radians*	10/10	8/7	2/2	0/1	0	0	0

Table **3.10.** For each species, the number of replicates of each treatment (fine and coarse sediment: F/C) showing different degrees of clearance after 48 hours. The number of replicates sustaining some bleaching (Blch) or mortality (Mort) is indicated in the last two columns.

[a] Generally colonies that suffered some mortality also bleached around the edges of the damaged tissue - these have not been included in bleaching figures (e.g. six colonies of *Gardineroseris* were affected in total).

[b] Partial mortality of this colony was almost certainly caused by incidental mechanical damage rather than from sediment (see text).

[c] These two species suffered mortality within 48 hours, whereas tissue mortality for other species was only observed after several days.

[d] Sediment accumulations remained despite the fact that weather conditions became rough on the second day.

All replicates of six species (the four ramose species, as well as *Fungia repanda* and *Diploastrea heliopora*) were completely clear of sediment after 48-56 hours, and two additional species (*Astreopora myriophthalma* and *Oulophyllia crispa*) showed complete clearance for all but one replicate. Four species (*Leptoria phrygia*, *Montipora aequituberculata*, *Porites lobata* and *P. lutea*) showed very poor clearance for a number of replicates. 17 of 20 *L. phrygia* colonies had cleared more than 90% (overall mean clearance was 96.6%) and poor rejection was limited to three individuals. *M. aequituberculata* and both *Porites* species showed uniformly poor rejection. *Gardineroseris planulata*, as noted above, shc̶w̶n̶ little sediment rejection after the first few hours.

Tissue mortality was observed in four species: *Cyphastrea serailia*, *Favia stelligera*, *Gardineroseris planulata* and *Leptoria phrygia*. In *C. serailia* this was almost certainly due to mechanical damage from falling debris, unrelated to the experiment. Tissue death in the remaining three species was clearly sediment-related. Mortality of *F. stelligera* and *L. phrygia* occurred quickly, within the first 48 hours. Six *G. planulata* individuals were affected, but did not suffer mortality immediately: all bleached for several days and some tissue of two died after 6 days. For all species, between 5-20% of tissues were affected.

Despite the heavy bleaching in both *Porites* species and in *Montipora aequituberculata*, no tissues died. Observations on *M. aequituberculata* were terminated after 3 days due to deteriorating weather conditions. Incidental observation does suggest, however, that this species has a much greater sediment tolerance than *Leptoria phrygia*, *Favia stelligera* or *Gardineroseris planulata*. No mortality was observed in one group of *Porites* after six days of calm weather. Recovery from bleaching could not be monitored regularly for *M. aequituberculata* or the two *Porites* species, but re-examination after 6 weeks revealed that all individuals had regained full colour and appeared normal.

Calice diameter

The relationship between calice diameter (or meander width for meandroid species) and sediment rejection efficiency (as measured by mean clearance rates), was examined for the 22 species investigated

REJECTION EFFICIENCY AS A FUNCTION OF CALICE DIAMETER
after 1 hour
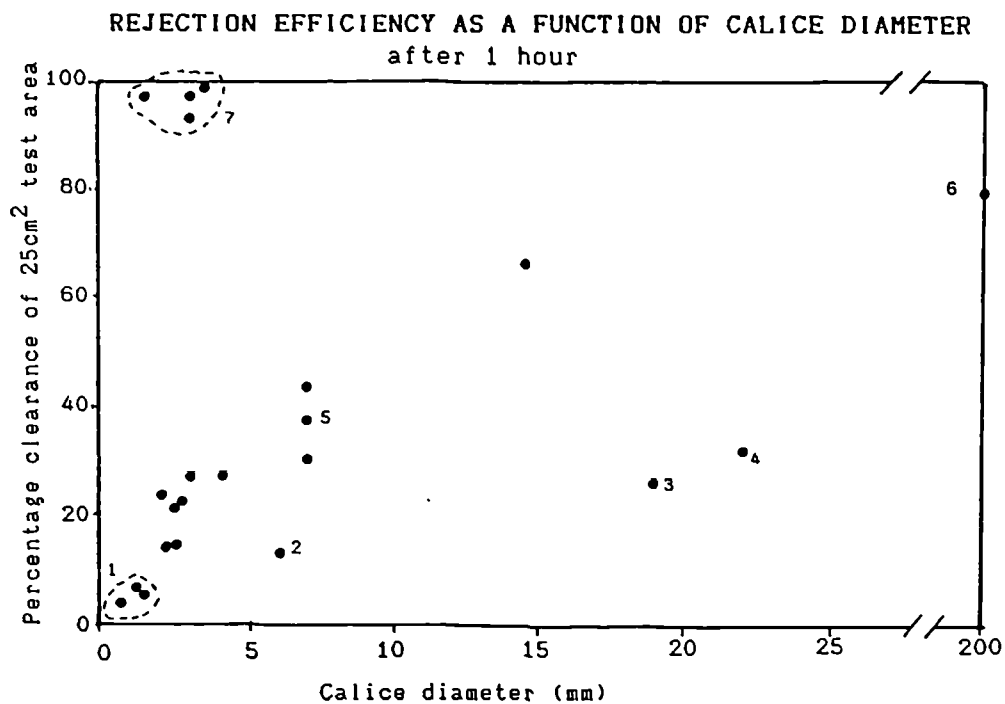
Figure 3.8. Relationship between calice diameter (or meander width for meandroid species) and mean sediment clearance after 1 hour.

[1]*Porites lobata,* *P.* *lutea* and *Montipora aequituberculata;* [2]*Coeloseris mayeri;* [3]*Acanthastrea echinata;* [4]*Symphyllia* *radians;* [5]*Gardineroseris planulata;* [6]*Fungia repanda;* [7]The four ramose species.

RELATIONSHIP BETWEEN CALICE DIAMETER AND REJECTION EFFICIENCY

	Spearman Rank Correlations			
	1 hour	2 hours	4 hours	24 hours
Coefficient	0.8467	0.8064	0.7158	0.5488
Sample size	18	18	18	18
Probability	0.0005	0.0009	0.0032	0.0236
Significance	***	***	**	*

Table 3.11. Spearman's rank correlations for calice diameter (or meander width) and mean clearance after 1, 2, 4 and 24 hours excluding the four Group II ramose species. Calice diameters are as quoted in Table 2.1 with the addition of *Pachyseris rugosa:* 3mm, *Porites cylindrica:* 1.5mm, and *Psammocora contigua:* 3mm.

(Figure 3.8). The four ramose species formed a distinct group and were excluded from the correlation analysis. The correlation between calice diameter and mean clearance rates for the non-ramose species was highly significant (Table 3.11).

Species synthesis

Analyses of species Groups I and III were carried out independently because of differences in experimental replication, but the relative sediment rejection rates of all 22 tested species are summarised in Figures 3.9a-d for each timepoint (+95% contidͤ· e intervals). ͫ· allows species to be divided into five tentative categories:

Category 1: the ramose species: *Echinopora mammiformis*, *Psammocora contigua*, *Porites cylindrica* and *Pachyseris rugosa*.

Category 2: *Fungia repanda* and *Oulophyllia crispa*.

Category 3: including most of the species with mid-range rejection rates. Four species, *Favia stelligera*, *Diploastrea heliopora*, *Symphyllia radians* and *Galaxea fascicularis*, showed a consistently higher clearance during the first 4 hours than the other species.

Category 4: *Gardineroseris planulata*, the only species to show very active rejection during the first few hours but little subsequently.

Category 5: *Montipora aequituberculata*, *Porites lobata* and *P. lutea*, all showing poor sediment rejection.

Additional subdivisions can be made on the basis of the tolerance of different species to sediment (Figures 3.9a-d).

SPECIES SYNTHESIS

Percentage clearance of 25cm² test area

1 Hour

2 Hours
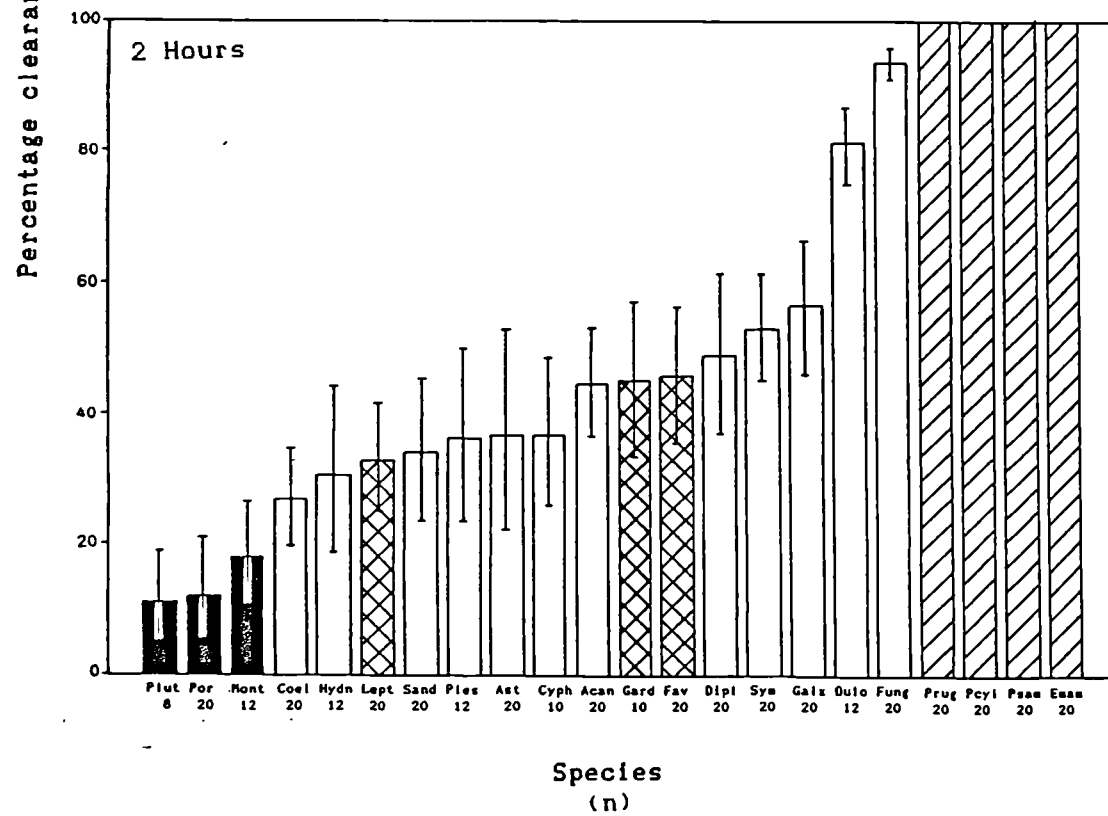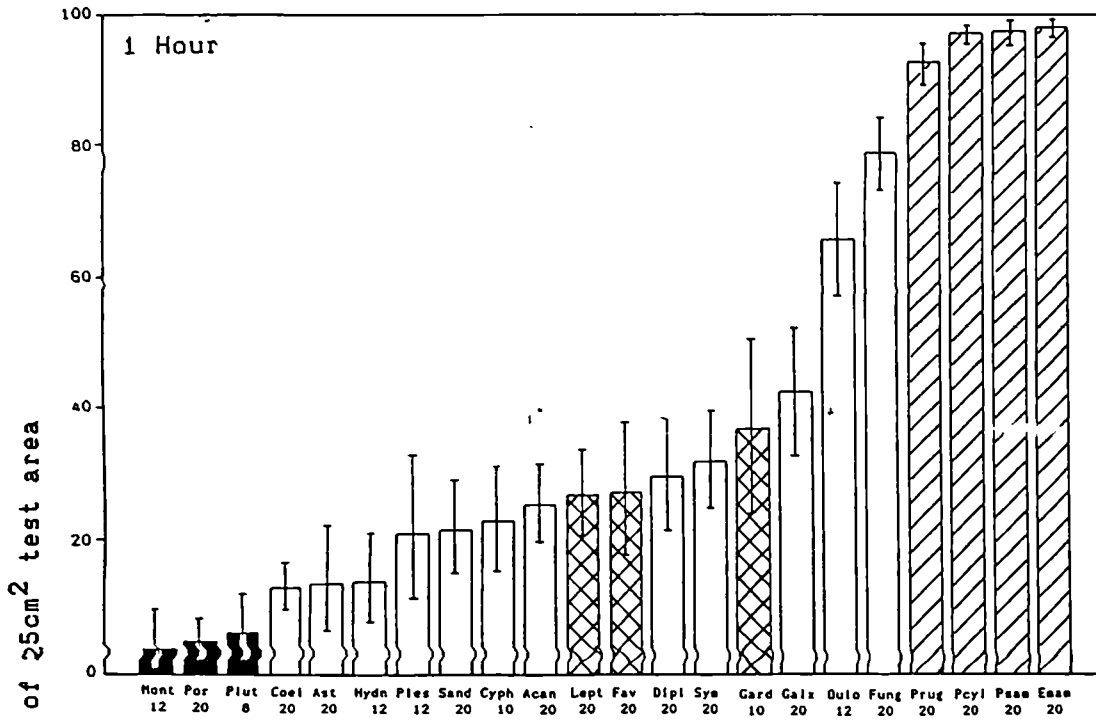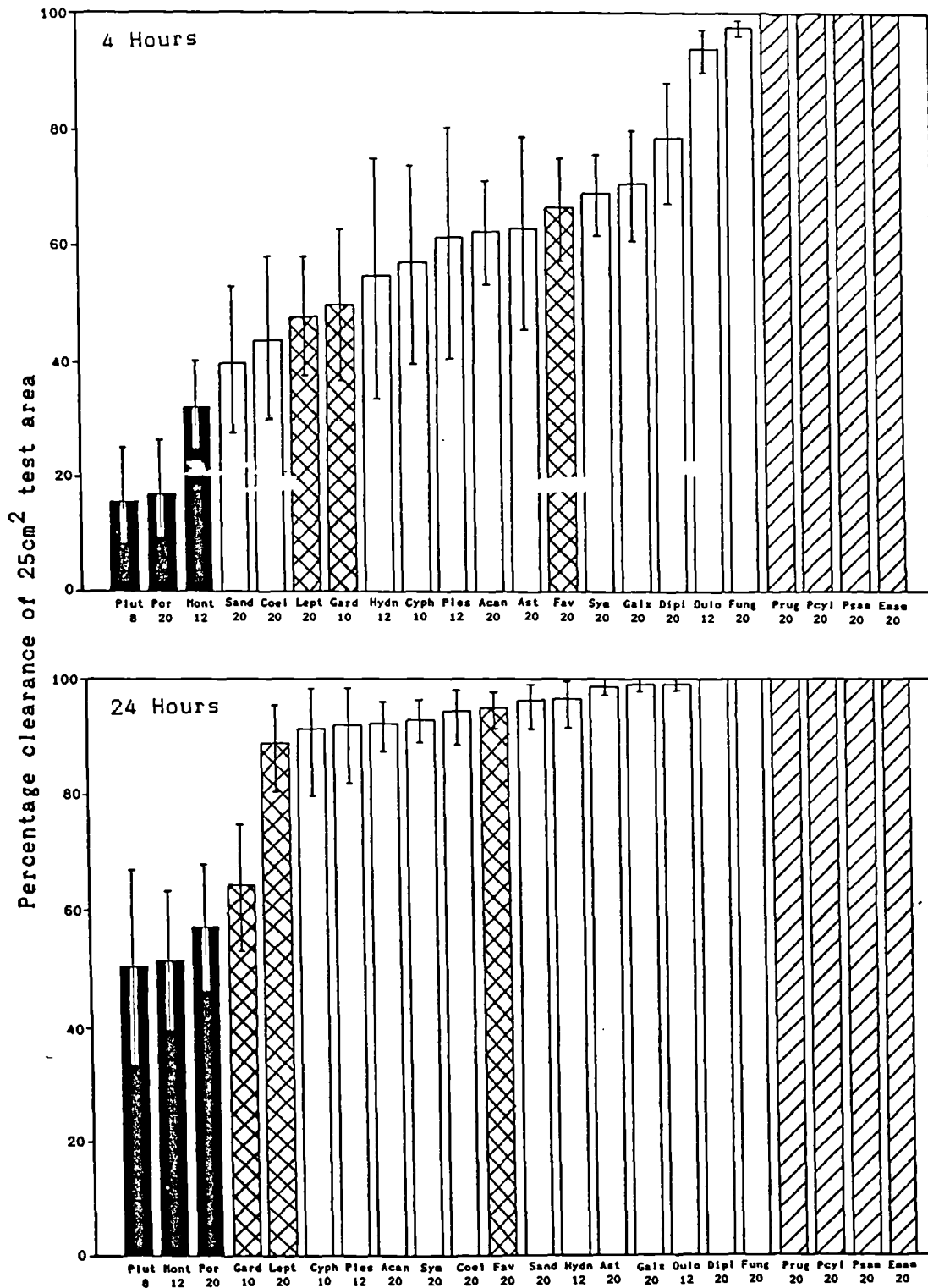
Species
(n)

Figure 3.9 Combined data from all tested species (means±95%CI).

Ramose species

Species that suffered some mortality

Species whose tissues bleached but did not die

97
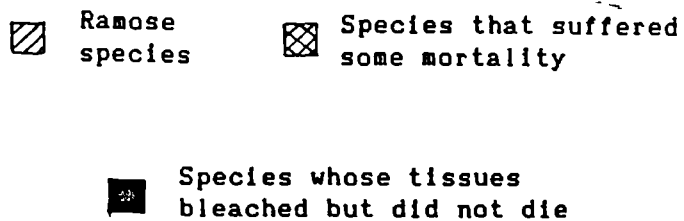
DISCUSSION

Sediment rejection occurs by both active and passive mechanisms acting separately or, more usually, in combination (Chapter 2). This study is concerned with the efficiency, or rate, of rejection, whether active or passive. As far as possible, the experimental procedures undertaken have been designed to isolate one aspect from another. When rejection efficiency is considered as a whole, however, these aspects must be interrelated in order to extract the essential combinations of factors which are of primary importance to reef corals in general and to target species in particular.

This discussion, therefore, primarily concentrates on species differences in skeletal morphology, and effects of sediment grain size and water turbulence, as the principal factors acting in various combinations which control sediment removal efficiency, and compares the present results with those of other studies.

Sediment size

This study found that active clearance of coarse sediment was significantly slower than fine (Table 3.2). Important effects of sediment size on rejection were also found for most species during behavioural investigations (Chapter 2: Table 2.1), and grain size-specific differences have been widely reported by other researchers (Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976; Schuhmacher, 1977; Logan, 1988). All 26 Caribbean species examined by Hubbard and Pocock (1972) were found to deal effectively with silt-sized particles, whereas manipulative abilities with larger sizes depended upon expansion capability and calice morphology. In his study of the Indo-Pacific fungiids, Schuhmacher (1977) found grain size-specific differences but only for those species that used ciliary currents as their principal rejection mechanism. Clearance of silts (62um) from the Caribbean coral *Scolymia cubensis* was faster than that of fine (250um) or coarse (2mm) sediment (Logan, 1988).

On the other hand, investigations of the Caribbean coral *Montastrea cavernosa* by Lasker (1980) demonstrated differences between fine (60-250um) and coarse (500um-1mm) sediment immediately after application, but not after 2 hours. This species has plocoid corallites and rounded, often convex surfaces. He attributed the differences for sediment sizes to the combined effects of convexity and polyp height and argued that fine particles would behave like a dense liquid, flowing off the tissues as they collected, but coarse sediments would be selectively retained. After 2 hours, this effect was no longer obvious. For *M. cavernosa*, therefore, the data suggested that *passive* rather than *active* rejection was a force favouring fine sediments. and that this was a short-lived (but potentially important) erfect.

Bak and Elgershuizen (1976) examined species differences in rejection of sand (0.1-3mm, mean 1.2mm) and silt-sized (carborundum powder) particles by 19 Caribbean corals. In many cases there was little difference between rejection of different particles sizes, and both were rejected in less than 4 hours. Where large differences existed, clearance of silt was generally faster than sand, with the principal exception of *Porites astreoides*.

Although previous studies have demonstrated that most species reject fine sediment more quickly than coarse, it is not clear whether differences in clearance rates are more important for some species than others. Distinctions of this nature are important in developing predictions of species responses to anthropogenic loads of different median grain size. With the exceptions of the studies of Lasker (1980) and Schuhmacher (1977, 1979) discussed above, intraspecies replication has been too low, or the research has had other aims, such that previous studies have not been illuminating on this point. During the present study, some species did appear to show greater differences between coarse and fine sediment rejection than others. *Acanthastrea echinata*, *Fungia repanda*, *Leptoria phrygia*, *Oulophyllia crispa* and *Symphyllia radians* all showed very little difference, whilst differences for *Astreopora myriophthalma*, *Gardineroseris planulata* and *Sandolitha robusta* were more substantial. However, data for within-species replicates showed very high variance, so that even with a replication level of n=10 for each sediment size for each species, no statistically clear patterns were detected (Table 3.2). This could be because there

is no real difference between species and that, for all species, coarse sediment rejection is slower than fine sediment rejection *to the same degree*; this seems very unlikely given the differences in rejection capabilities described in Chapter 2. Furthermore, there are non-significant trends apparent in the data which suggest that larger sample sizes would uncover some interesting size-specific rejection differences. These trends are not reported here, but summary graphs are presented in Appendix 3.1, as they may generate hypotheses for future research.

The impact of coarse and fine sediments on corals is worth further consideration. Coarse grains and granules may generally cause greater mechanical abrasion than fine (e.g. lesions were observed when large grains became wedged between hydnophores of *Hydnophora microconos* but fine grains caused no apparent problems, Chapter 2). Schuhmacher (1977) was able to demonstrate that sediment tolerance was related to sharpness of septa and, although he does not report grain-size related differences, it is probable that larger or more dense grains would cause greater tissue damage over sharp septa than finer or less dense grains. It might also be expected that coarse sediment would be more deleterious to corals than fine because of longer residence times on the tissues. However, this may not be so. Brafield (1964) showed that oxygen concentration in the interstitial waters of beach sands decreased as the ratio of fine sand (<250um) to coarser grains increased. These measurements were made for thicker sediment layers than are common on flat coral tissues, but some effect of sediment size is still likely, especially over concave regions of tissue. Oxygen diffusion may be further inhibited by mucus secretion which is particularly common with silts and fine sands (Chapter 2). Thus anoxia due to fine sediments and mucus may be a cause of tissue death (Chapter 2; Bak & Elgershuizen, 1976). Weight for weight, fine sediment also attenuates substantially more light than larger sediment sizes (Chapter 8: Figures 8.2 & 8.3). Ecologically, therefore, the persistence of overlying fine sediments may also be more important for species that rely heavily on autotrophy. Thus, while there may be good mechanical reasons why fine sediments are cleared more readily than coarse, it may also be in the best interest of a coral to reject fine sediments quickly due to their deleterious impact.

In view of the above points, it is interesting to note that of the nine colonies whose tissue mortality could be attributed to overlying sediment (i.e. excluding *Cyphastrea serailia*, Table 3.10), only one was due to coarse sediment.

Morphology

The influence of morphology, orientation and water movement on sediment rejection has been discussed by many authors (e.g. Marshall & Orr, 1931; Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976; Loya, 1976; Schuhmacher, 1977; Dryer & Logan, 1978; Rogers, 1983). The theoretical basis for assuming that these factors may substantially affect the degree of active rejection (and thus energy expenditure) is intuitively obvious and may explain why there have been so few quantitative evaluations of their effects. Certainly ramose species in this study showed predictably high clearance rates relative to non-ramose species, but it was interesting to note that there were significant differences even between these species. *Pachyseris rugosa* cleared sediment more slowly than either *Echinopora mammiformis* or *Psammocora contigua*. This probably reflects finer morphological differences. The morphological variant of *Echinopora mammiformis* used in these tests had extremely fine, widely-spaced branches. A very high proportion of sediment never touched living tissue, but dropped straight through. In contrast, the colonies of *Pachyseris rugosa* tested, were moderately compact with distinct ridges typical of the genus. Although much sediment fell off this ramose form rapidly, some collected in the ridges and required active rejection. In view of the fact that *Pachyseris* species do not appear to have tentacles (Yonge, 1930; Abe, 1938), have not been observed to expand their polyps (Veron, 1986; *pers. obs.*), but are very active mesenterial feeders on small particles (Yonge, 1930; Abe, 1938; Chapter 2), it may be necessary for these species to have semi-trapping regions to capture particulates raining onto the surface as a source of food.

Many corals are very plastic in their growth forms; their morphologies adapt in response to environmental parameters such as light, surge, aerial exposure, and sedimentation (Roberts *et al*, 1977; Chappell, 1980; Foster, 1980; Veron, 1981; Fricke & Schuhmacher, 1983;

Veron & Pichon, 1976, 1980, 1982; Veron *et al*, 1977; Veron & Wallace, 1984). The present study focussed on the active component of rejection efficiency and care was taken to control for the effects of gross morphology by selecting tissue regions which were flat. However, during searches for suitable subjects, it was obvious that some species displayed a range of morphologies (from domed to semi-columnar: *Leptoria phrygia*, *Favia stelligera*; or flat-plating to almost vertical: *Montipora aequituberculata*, *Echinopora lamellosa*), while others, notably *Diploastrea heliopora*, showed very little variation at all. *Echinopora mammiformis*, which displayed two totally distinct morphological forms, takes morphological variation to extremes.

The capacity of a species to display morphological variation, and the speed with which morphological change can occur in response to environmental changes, are key issues in survival, especially where physiological sediment tolerance is not high. The proportion of flat to *angled living coral tissue is one aspect of* great importance. For example, Logan (1988) found that colonies of the solitary Caribbean coral *Scolymia cubensis* at angles of 75° cleared sediment much faster than those at 0°. Colonies at 35° were not always faster than 0° so there may be a threshold angle of orientation at which point the combined effects of active rejection and gravity overcome static friction. This requires further study, but some aspects relating to the changes in predominant tissue angle with environmental conditions are explored in Chapter 5.

The relationship between calice diameter and sediment rejection capability was examined in the previous Chapter. Results from this study show that active rejection efficiency is also linked to calice dimension. Passive rejection advantages to ramose species are sufficient to overcome the disadvantages of small polyp size in this respect.

Turbulence

The effects of turbulence revealed by this study are somewhat counter-intuitive. Local turbulence under rough conditions always cleared turbulence petri-dish control sediments in less than an hour, usually less than 30 minutes. Yet no replicate of the six coral species

tested had lost all sediment during the same period. Therefore, microtopographical features of the tissue surface must have been inhibiting movement of sediment which might otherwise be destabilised and lost by water movement. More importantly, there was no effect of Moderate turbulence on sediment rejection despite the clearance of sediment from turbulence petri-dishes in 2-4 hours (p>0.10). At replication levels of n=20, Moderate turbulence had no detectable effect for any species. There may be a turbulence threshold which was not reached at wind speeds of 15 knots but which had been surpassed at 25 knots, or the relationship between turbulence and passive clearance may be inherently non-linear.

The skeletal micro-architecture of hard corals will have a profound effect on the degree of turbulence required to overcome static friction. Projections on the coral surface create obstacles which can alter characteristics of water flow across the tissues and increase boundary layers. The boundary layer effect is greatly dependent on the number, height and dispersion of the projections. The colonies of *Porites lobata* involved in turbulence tests were very smooth, and although this species showed very little active sediment rejection in comparison to other tested species, it was strongly affected by turbulence which was probably because the boundary layer was thin in comparison to other species. Koehl (1977), who studied the effects of water flow on sediment rejection of the Caribbean zoanthids *Palythoa variabilis* and *P. caribaeorum*, found that rejection rates increased with turbulence. For zoanthids, which do not have solid skeletons, the boundary layer may be under active control by body volume and shape changes through stomodaeal uptake of water. If this is the case, the concept of a turbulence 'threshold' may not be relevant although turbulence itself may still be very important. Corals whose polyps can project above relatively smooth surfaces may also have substantial active control of boundary layers. Such conditions apply to *Goniopora* spp. and *Alveopora* spp. which have large fleshy polyps, but may also apply to species with small polyps such as *Porites* spp.

Hard corals whose polyp and/or tissue expansion capacity is small in relation to skeletal projections (such as *Montipora aequituberculata* or *Hydnophora microconos*), probably have less control on their boundary layers and require higher turbulence levels before passive rejection from turbulence will occur.

Micro-architecture, however, is only one of several influences. At Lizard Island, *Hydnophora microconos* was generally globular in shape, while *H. exesa* had a complex shape. These gross morphologies would be expected to create respectively low and high boundary layer effects. The scale of the skeletal projection in relation to the sediment grain size will also modify these responses. Furthermore, mucus tends to build up over time if sediments remain stationary on tissue surfaces (Chapter 2). In moderation, especially to active sediment rejectors, mucus can be advantageous because it links sediment particles. But a heavily agglutinated mass trapped in a concave region of tissue offers much greater resistance to water movement than single grains. In the case of *Porites* spp., although the loss of thin, light, naturally occurring mucus sheets was assisted by water movement, the *lack* of mucus within sediment accumulations which had been lying on the tissues for several days seemed to be an advantage as sediment particles could be picked up more easily and at lower current velocities.

In addition to *Porites lobata*, three other species (*Leptoria phrygia*, *Astreopora myriophthalma* and *Coeloseris mayeri*) showed significant increases in clearance rates under Rough conditions. Both qualitative and quantitative observations indicate that turbulence is important for sediment rejection in *Leptoria phrygia*, but there is an important ecological distinction between this species and *P. lobata*: the latter appears to be sediment-tolerant whereas *L. phrygia* does not. Thus *P. lobata* can afford to wait for several days for turbulent conditions to recur and cleanse its tissues, whereas tissues of *L. phrygia* cannot (Chapter 4).

Although the test areas of *Astreopora myriophthalma* colonies were flat, this species is normally mildly or strongly convex at Lizard Island, with relatively widely-spaced, plocoid corallites. Such growth forms are probably well-adapted for exploiting local turbulence as boundary layer effects would be reduced. *Coeloseris mayeri*, which showed the weakest positive response to turbulence, has cerioid corallites in which sediment can collect. This would require relatively high turbulence to resuspend accumulated sediment.

Clearance rates for both *Diploastrea heliopora* and *Fungia repanda* showed no significant increase under strong turbulence. For *Diploastrea*

heliopora this was counter to predictions based on behavioural observations which suggested that mucus sheets or strands were fairly commonly wafted off colonies by slight water movement, but not under calm conditions (Chapter 2). In the present study, sediment rejection was limited to flat $25cm^2$ test areas rather than the whole colony. It is therefore possible that water movement would be more important on convex surfaces which are more common on this species.

Diurnal variations

Species show variations in their sediment rejection behaviours which relate to polyp expansion and feeding activity (Bak & Elgershuizen, 1976; Chapter 2). As a result, sediment rejection efficiency for some species (e.g. *Astreopora myriophthalma*) may show diurnal patterns correlated with these behaviours. In support of this view, the Caribbean coral, *Scolymia cubensis*, appears to show increased rejection at night (Logan, 1988).

Limited nighttime studies were undertaken *in situ* during the present work, but their scope and reliability were constrained both by logistics and by difficulties related to experimental protocol[1]. Of six species tested in the laboratory (*Acanthastrea echinata, Astreopora myriophthalma, Sandolitha robusta, Diploastrea heliopora, Fungia repanda* and *Leptoria phrygia*; n=5), three showed small non-significant increases in rejection rate from dusk to early night in comparison to those during the day (*A. echinata, A. myriophthalma* and *Sandolitha robusta*). However, the results are ambiguous and should be treated with caution because both nighttime and daytime rejection rates were higher in the laboratory than *in situ* for these three species.

The cost of sediment rejection and the consequences of not rejecting sediment may be different at different times of day. Sediment rejection during the dusk and early evening may have a lower marginal respiratory cost than during the day for most species because the polyps and tissues

---

1.   (a) expanded polyps wholly or partially obscured sediment accumulations still remaining on the tissues; (b) characteristics of the colonies, used to exactly relocate $25cm^2$ test areas, were obscured.

are active. On the other hand, there may be a decrease in energy input due to repression of heterotrophic feeding. The presence of sediments on the tissues during the day will cause light attenuation (Chapter 8) and therefore has the potential to affect photosynthesis. These considerations lead to the tentative hypothesis that sediment rejection from flat tissues of predominantly autotrophic feeders may be highest during the day. Those of predominantly heterotrophic feeders may be higher at night (or whenever the principal feeding period is for that species) or may be more even. Differences in behaviour between the laboratory and the field necessitate *in situ* studies to examine these possibilities.

Significance of sediment rejection to species distributions

A basic and important result from these experiments is that they reveal a distinct difference between sediment rejection *efficiency* and sediment *tolerance*. *Gardineroseris planulata* was a competent sediment rejector of all four sediment sizes tested in previous experiments (Table 2.1). However, its sediment clearance rates suggest that energy is channelled into rejection during the first hour or so, but that rejection soon ceases (perhaps through exhaustion). Nevertheless, only bleaching occurred initially, and no tissue mortality was observed for 6 days. In contrast, *Leptoria phrygia* and *Favia stelligera* showed moderate clearance rates but were very sensitive to overlying sediments, with mortality occurring in 24-48 hours. The small-polyped species (*Montipora aequituberculata* and *Porites* spp.), all showed low rejection efficiency, and yet no individual showed any mortality despite frequent bleaching of tissues. These species presumably have some physiological adaptations which allow them to tolerate low light levels, reduced diffusion, etc., for substantial periods of time.

To put these observations into ecological context, *Gardineroseris planulata* was only observed in exposed regions around Lizard Island, and *Favia stelligera* and *Leptoria phrygia* were absent from the lagoon and were much more abundant in high turbulence environments than in relatively protected ones (Chapter 5). *L. phrygia* is also reported to be absent from turbid habitats on the Great Barrier Reef by Veron (1986), while Bouchon (1981) describes *Favia stelligera* as being characteristic of wave exposed areas of Reunion Island (Indian Ocean)

fringing reefs. Increases in turbulence were demonstrably advantageous to *Leptoria* (Table 3.6), and although effects of turbulence on sediment rejection by *Favia stelligera* were not tested, it is possible that these species are restricted to areas of relatively high wave action to ensure a strong passive influence on rejection. In his work on Australian corals, Veron (1986) confirms that *Gardineroseris planulata* prefers clear water. It appears that this species may only survive where the need for strong bursts of ciliary activity are infrequent. Nevertheless, observations showed that the ciliary mechanisms are strong (Chapter 2) and it would be surprising if this species were excluded from areas of light silt influx on these grounds alone.

Porites and *Montipora* are both abundant genera in regions of high sedimentation or turbidity in Australia (Bull, 1982; Veron, 1986, 1987; Ayling & Ayling, 1987) and elsewhere (e.g. Maragos, 1974). Large massive *Porites* colonies are present in all three principal regions of Lizard Island, while foliose *Montipora* appear to be more common in relatively sheltered biotopes (Chapter 5). However, field distinctions to species of these genera were not always reliable and although, for field experiments, samples were taken for later verification, this was not the case during the brief survey of species distribution around Lizard Island. Thus, distributions of *Porites lobata*, *P. lutea* and *Montipora aequituberculata* are uncertain at the species level. Within the Great Barrier Reef province, Veron (1987) records both *Porites lutea* and *Montipora aequituberculata* as being common on turbid fringing reefs of Cape Tribulation, *Porites lobata* was not recorded during his survey. Potts *et al* (1985) report *Porites* species (including *P. lobata* and *P. lutea*) as dominant in turbid waters of Pandora Reef. Bull (1982) implies that *Porites lobata* is common on turbid inshore fringing reefs of Magnetic Island, off Townsville, while Collins (1987) records all three species from the same reefs. More recently Done (1989) has also recorded *Montipora aequituberculata* from. Magnetic Island. Neither *Gardineroseris planulata* nor *Favia stelligera* are listed for the turbid reefs of Cape Tribulation or Magnetic Island. *Leptoria phrygia* is absent from Magnetic Island (Collins, 1987), and described as 'rare' for Cape Tribulation (Veron, 1987).

In conclusion, this study shows that sediment rejection efficiency is the result of a complex interrelationship of environmental influences

and species attributes which include the size of sediment, prevailing turbulence regime, colony morphology at a variety of spatial levels, and rejection capability of the species. An understanding of these influences, and in particular, species differences in sediment rejection behaviour, efficiency and tolerance, can help to explain the distributions of several common Australian species.

APPENDIX 3.1

FINE AND COARSE SEDIMENT CLEARANCE ON A SPECIES BY SPECIES BASIS

Significant differences in sediment clearance by Group I and Group III species are demonstrated in Tables 3.2, 3.3, 3.8 and 3.9. Overall, the clearance of fine sediment was significantly greater than coarse for Group I species (Table 3.2). There was no interaction between species and sediment size (Table 3.2) indicating that all species found coarse sediment harder to remove than fine *to the same degree.* In fact, however, there are trends in the data which suggest the contrary and which might be confirmed by experiments using higher replication. This Appendix presents, for each species, clearance of fine and coarse sediment for each species as they may suggest useful areas for future research.

FINE AND COARSE SEDIMENT REJECTION BY SPECIES

Group I
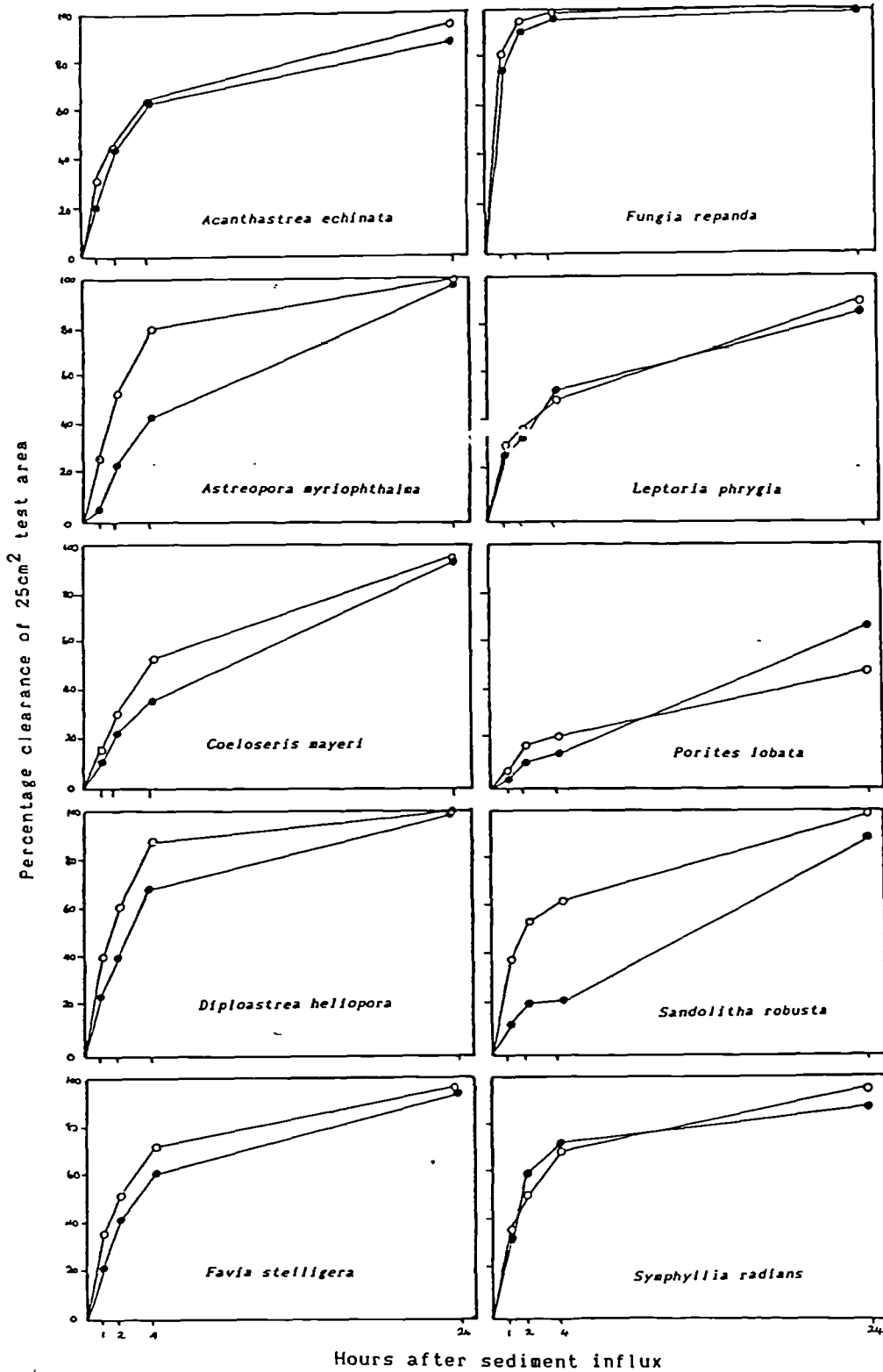
Appendix Figure 3.1. Clearance of fine and coarse sediment by Group I corals on a species by species basis. Trends were not significant, but graphs are reproduced here as they may suggest useful areas for further research.

o Fine   • Coarse

110
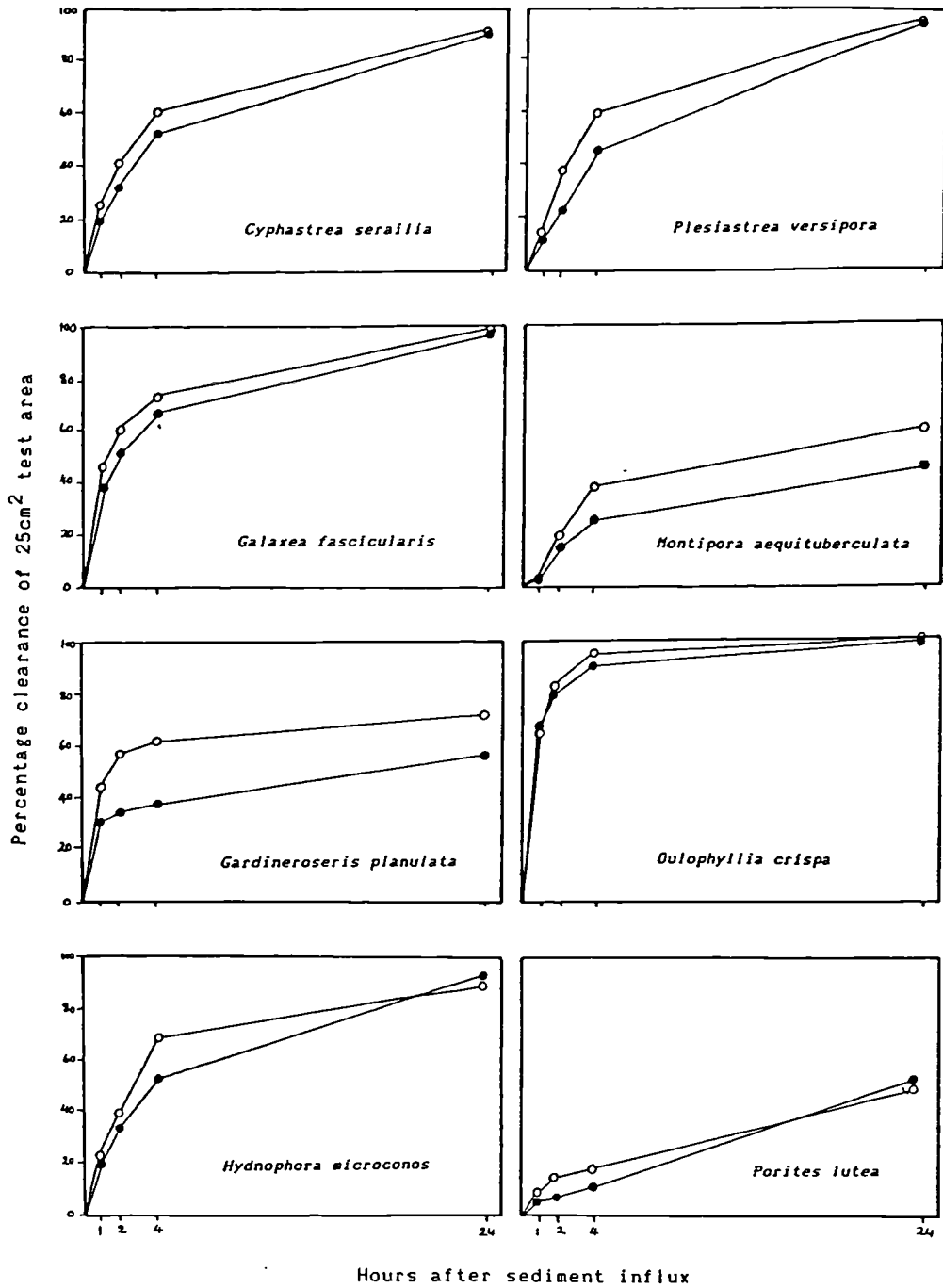
Group III

Appendix Figure 3.2. Clearance of fine and coarse sediment by Group III corals on a species by species basis. Trends were not significant, but graphs are reproduced here as they may suggest useful areas for further research. ·~

o Fine   ● Coarse

CHAPTER 4

SEDIMENT TOLERANCE OF AUSTRALIAN

SCLERACTINIAN CORALS

SEDIMENT TOLERANCE OF AUSTRALIAN
SCLERACTINIAN CORALS

SUMMARY

Ten species of Australian mid-shelf corals were subjected, *in situ*, to a daily influx of 0, 50, 200, or 400mg.cm^{-2}.day^{-1} (n=10 per treatment per coral) of fine sediment (63-250um) for eight days to investigate sediment tolerance over time. Sediments were applied to a 25cm^2 area of more or less flat tissue between 0900 and 1100 hours. Sea conditions were very calm during the first four days but turbulence increased abruptly on the fifth day.

Some tissue damage or mortality from sediment had occurred after 4 days for 7 species. No previously unaffected colonies showed mortality ᵃfter the fifth day when turbulence increased.

Of the ten species, *Fungia repanda*, *Sandolitha robusta* and *Acropora hyacinthus* showed no tissue bleaching or necrosis and all sediment was removed from the tissues each day. Considerable quantities of sediment accumulated on many colonies of the remaining species. *Echinopora lamellosa*, *Merulina scabricula*, *Leptoria phrygia*, *Mycedium elephantotus*, and *Pectinia lactuca* all experienced tissue death (in decreasing order of effect). With the exception of one replicate (for which damage was <1cm^2 and later recovered), all *Diploastrea heliopora* were completely unaffected.

The response of *Porites* sp. was quite unlike that of other taxa. Sediment rejection was minimal and accumulations of 5mm occurred during the first four days. Tissues of almost all colonies bleached severely but only one showed any mortality and this subsequently recovered. As water turbulence increased, sediments were dispersed and tissues of all colonies completely recovered in 3-6 weeks.

Species mortality was independent of water turbulence (mortality occurred during initial calm conditions when differences in local turbulence of each colony were negligible). However, mortality was significantly correlated with input sediment load (p<<0.001): 50mg.cm^{-2}.day^{-1} for 4 days was sufficient to cause tissue death in many *Echinopora lamellosa* and *Merulina scabricula*, and one *Leptoria phrygia* and *Mycedium elephantotus*, but mortality was substantially higher for these species as loads increased to 200 and 400mg.cm^{-2}.day^{-1}. Mortality was also significantly correlated with minor variations in local convexity (p<0.001). Differences in interspecies convexity could not account for species variations in mortality, indicating that other factors (such as physiological tolerance to overlying sediments) must also be involved.

The data suggest that, for some species, measurements focussing on the periodicity and persistence of intense but relatively short-term sedimentation events may be as, if not more, important to the understanding of species distributions, as measurements of mean sedimentation rates over monthly or yearly cycles.

North Point

Mermaid Cove
Granite Head
Turtle Beach
Watsons Bay
Osprey Is
THE LODGE
Crystal Beach
Cook's Look
Pidgin Point
AIRSTRIP
RESEARCH STATION
Coconut Bay
Lizard Head
Lagoon
Bird Is
PALFREY ISLAND
SOUTH ISLAND

LIZARD ISLAND

0   0.5   1   1.5
KILOMETRES
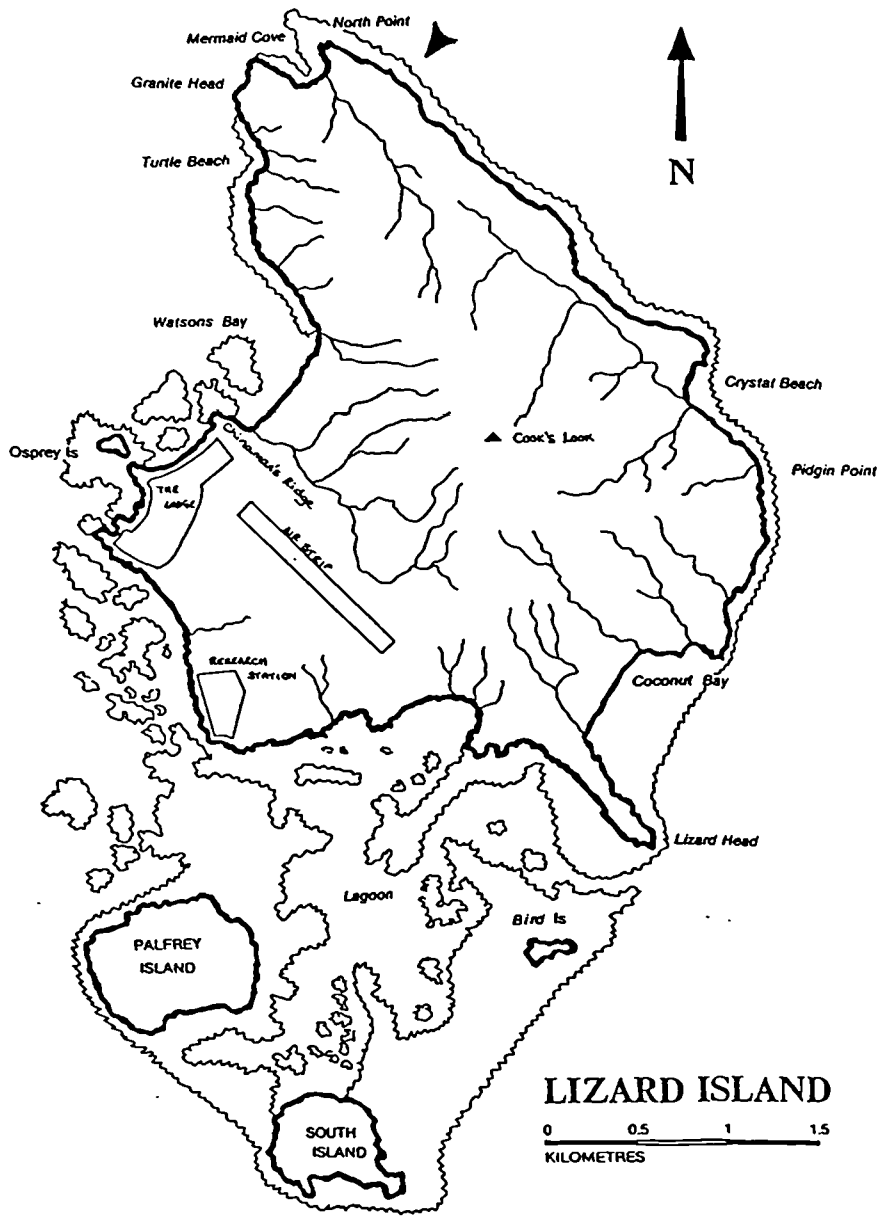
Figure 4.1. Location of field site at North Point.

INTRODUCTION

Studies of survival times of colonies buried in layers of mud or sand have provided some information about differences in sediment tolerance of corals (Mayer, 1918; Mayor, 1924b; Edmondson, 1928; Marshall & Orr. 1931). However, as Marshall and Orr (1931) point out, sudden burial may be an uncommon event in nature and gradual burial, or exhaustion from sustained rejection of lesser quantities of sediments, is more likely. The effects of persistent sediment influxes have been examined for Caribbean corals (Kolehmainen. 1974: Rogers, 1979, 1983; Peters & Pilson, 1985; Rice, 1985) and for a few Indo-Pacific species (Mayor, 1924a&b: Edmondson. 1928; Marshall & Orr, 1931: Schuhmacher, 1977, 1979; Hodgson, 1990).

Previous experiments (Chapters 2 & 3) highlighted potential differences in sediment tolerance between species. *Porites lobata*, *P. lutea* and *Montipora aequituberculata* were all found to be poor sediment rejectors, but seemed to have relatively high sediment tolerance. *Gardineroseris planulata* was a very active sediment rejector for limited periods, following which rejection ceased but death did not occur for several days. *Leptoria phrygia* and *Favia stelligera*, were moderately active sediment rejectors with mid-range rejection efficiencies, but both were very intolerant of sediment accumulations.

The present experiments were carried out during 1988 to investigate the tolerance of 10 species of Australian corals to continuing daily sediment influxes *in situ*. Based on observations from the previous Chapter, five species were chosen to represent a range of expected tolerance. The sediment rejection mechanisms for all ten species are described in Chapter 2 and Appendix A.

METHODS

Study area. This investigation was undertaken at Lizard Island, northern Great Barrier Reef, Australia[1]. The location of the field

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1. For a fuller description of Lizard Island, see the General Introduction and Chapter 5.

SPECIES AND THEIR DOMINANT MORPHOLOGY

Code	Species	Dominant morphology
Acrop	*Acropora hyacynthus*	Corymbose plates (composed of fine branchlets, Figure 4.1), colonial
Por	*Porites lobata/lutea*	Massive, colonial
Fung	*Fungia repanda*	Free-living, solitary
Sand	*Sandolitha robusta*	Free-living, colonial
Myc	*Mycedium elephantotus*	Encrusting to laminar or foliaceous, colonial
Pect	*Pectinia lactuca*	Laminar to foliaceous, colonial
Meru	*Merulina ampliata*	Encrusting to laminar or foliaceous, colonial
Lept	*Leptoria phrygia*	Massive, colonial
Dipl	*Diploastrea heliopora*	Massive, colonial
Ech	*Echinopora lamellosa*	Laminar or foliaceous, colonial

Table **4.1**. List of species involved in tolerance tests with their species codes and dominant morphology.

site was 200m SE of North Point, on the exposed reef front (Figure 4.1).

Experimental procedure. The sediment tolerances of ten coral species at depths of 0.5-6m[1] were tested simultaneously under uniform weather conditions (Table 4.1). Species were divided into two groups according to abundance. The first group comprised the common species *Acropora hyacinthus* (Plate 4.1), *Leptoria phrygia*, *Porites lobata/lutea* (Plate 4.2), *Diploastrea heliopora*, *Sandolitha robusta*, and *Fungia repanda*. Forty colonies with minimum diameter 20cm (16cm for *F. repanda*) were selected for each species. With the exception of colonies of *Acropora hyacinthus* which was corymbose (composed of fine branchlets, Plate 4.1), each colony included a more or less flat area of at least 10cm x 10cm. Ten colonies of each species were allocated to each of four treatments according to a stratified randomisation schedule (based on minor differences in convexity, see below). Within the flat portion of tissue, fine sediment (63-250um) was evenly applied to a centrally located area of 5cm x 5cm at a dose of 0mg (controls), 50mg, 200mg or 400mg.cm^{-2}.day^{-1} (i.e. n=10 per treatment per species).

The remaining four species, *Echinopora lamellosa*, *Merulina scabricula* (Plate 4.3), *Mycedium elephantotus* and *Pectinia lactuca* (Plate 4.4), were less common but colonies were often very extensive (with surface areas greater than 2m^2). For this reason, only ten colonies were tagged and different portions of the same colony were tested with each treatment. Test areas on the same colony did not necessarily have either the same convexity, turbulence rating or depth (several *Mycedium* colonies covered a vertical depth range of 1.5-2m), and for the purposes of the analyses, test areas have been considered independent.

Starting on the 15 June 1988, sediments were applied to test colonies between 0930 and 1130 each morning for a total of eight days. Approximate wind speeds for the period of the experiment are plotted in Figure 4.2. Exceptionally rough conditions began on 22

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1. Measured from Low Water Mean Tide.

Plate **4.1**.   *Acropora hyacinthus* showing corymbose plates composed of compact upright branchlets (*x 0.25*).

Plate **4.2**.   Close-up of *Porites* sp. (*x 7*).
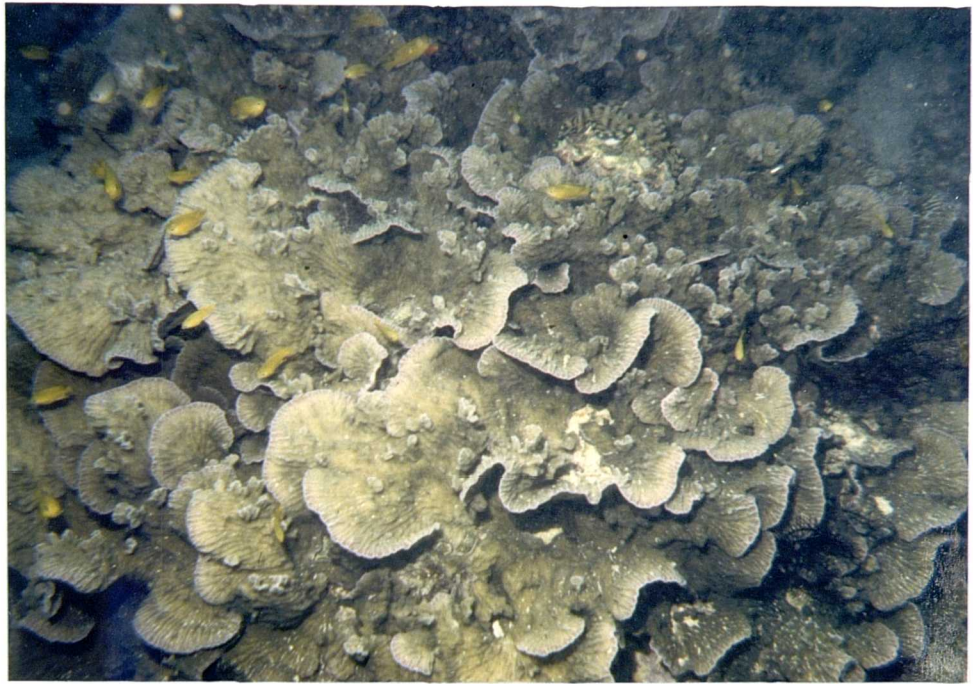
Plate 4.3.   Encrusting   to laminar or   foliaceous
             growth form of *Merulina scabricula*
             (*x 0.07*).

Plate 4.4

Pectinia lactuca
showing horizontal
laminar areas (*x
0.1*).
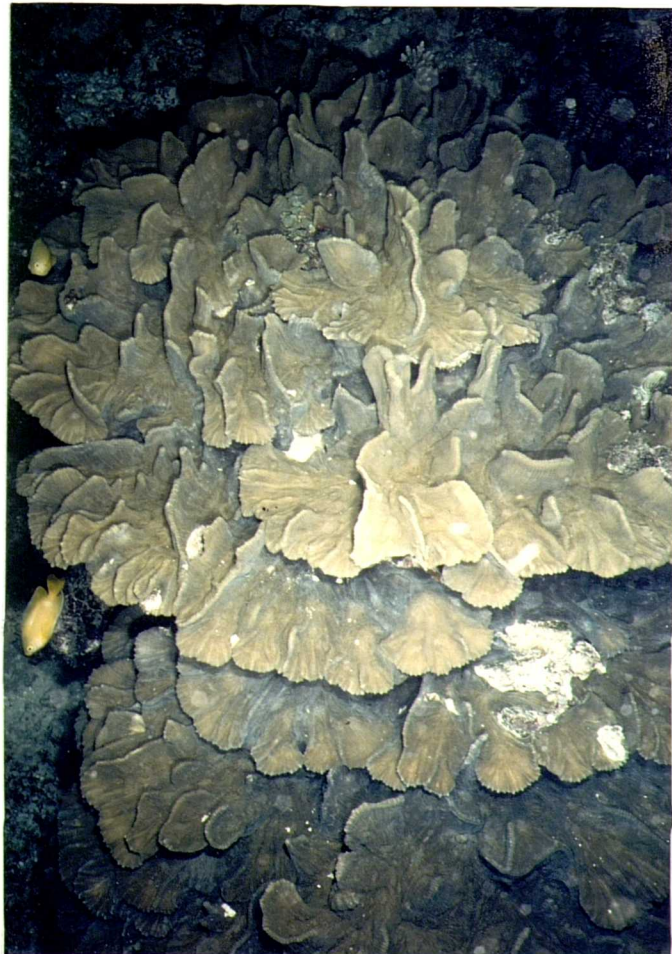
TISSUE MORTALITY CATEGORIES

Category	Description	
0	No damage	
1	Temporary:	Bleaching only, with full recovery by 23 July
2	Temporary:	Minor tissue death observed 19 and 30th June, but full recovery by 23 July
3	Permanent:	$<1cm^2$
4	Permanent:	$<5cm^2$
5	Permanent:	$<10cm^2$
6	Permanent:	$<20cm^2$
7	Permanent:	$>20cm^2$

Table 4.2. Definition of mortality categories used in the text and in Figures.
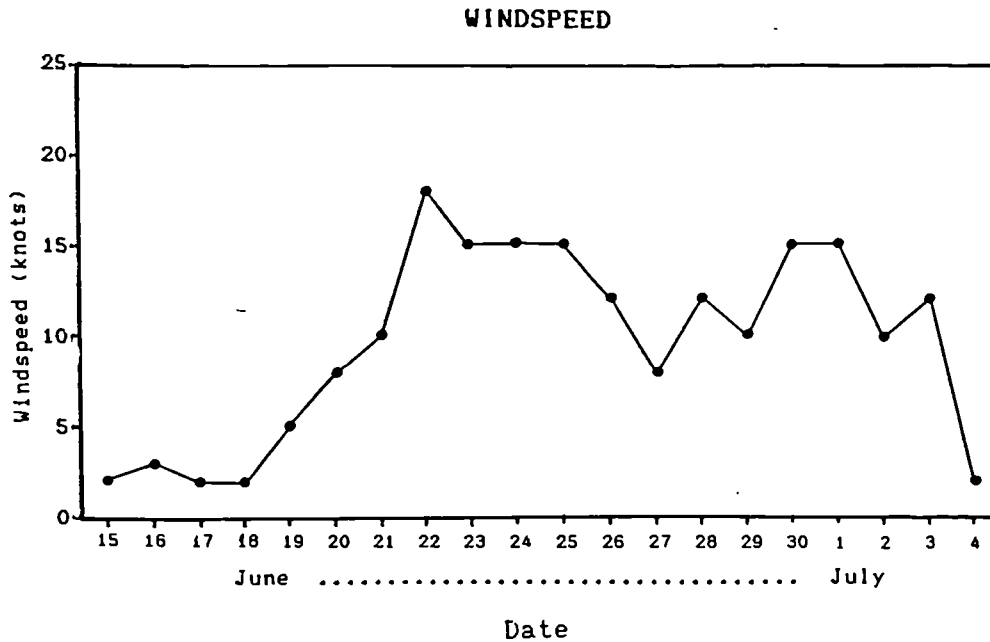
WINDSPEED

Figure 4.2. Winds speeds for Cooktown over June/July 1988. Lizard Island showed the same pattern but speeds were generally 5-10 knots higher.

June (Day 8) and artificial applications of sediment were stopped
after Day 8 although the presence of overlying sediment was checked
on Day 9. Using a fine paint brush, corals were gently examined for
tissue death and damage on 19th June (Day 5, after four daily
applications). To avoid major disturbance, sediments were moved as
little as possible and detailed measurements of the extent of the
damaged area were postponed until daily applications had been
stopped and sediments on most colonies had been washed away or
removed actively.

The degree of tissue damage was divided into four principal
categories: no damage, bleaching, tempuraiy ~nd minor damage
(existing for less than 5 weeks), and permanent damage (existing for
more than 5 weeks). The final category was subdivided according to
Table 4.2 and thus eight levels of tissue damage were distinguished.

Turbulence. Meteorological information and on-site observations were
used to categorise sea and wind conditions. Local water turbulence
was assessed independently for each experimental period as described
in Chapter 3, using replicate turbulence petri-dishes. On two calm
and three rough days, the relative local turbulence for each
experimental coral was estimated on a scale of 0-10. Estimates were
based on a subjective evaluation of passive loss of sediment from
test areas (due to water movement rather than behavioural activity)
and on timed loss of sediment from turbulence petri-dishes placed
close to each test colony.

Tests carried out immediately prior to the start of the
experiment indicated that turbulence around all corals was
negligible under very calm conditions. During the first four days
of the experiment, local turbulence in calm weather continued to be
negligible for all colonies except those of *Acropora hyacinthus*.
For this reason, this species is excluded from some interspecies
analyses below.

From day five, wind speeds began to increase (Figure 4.2) and by
day eight sea conditions were very rough. For most species,
therefore, active sediment rejection was required during days 1-4,
but turbulence became increasingly important from then on.
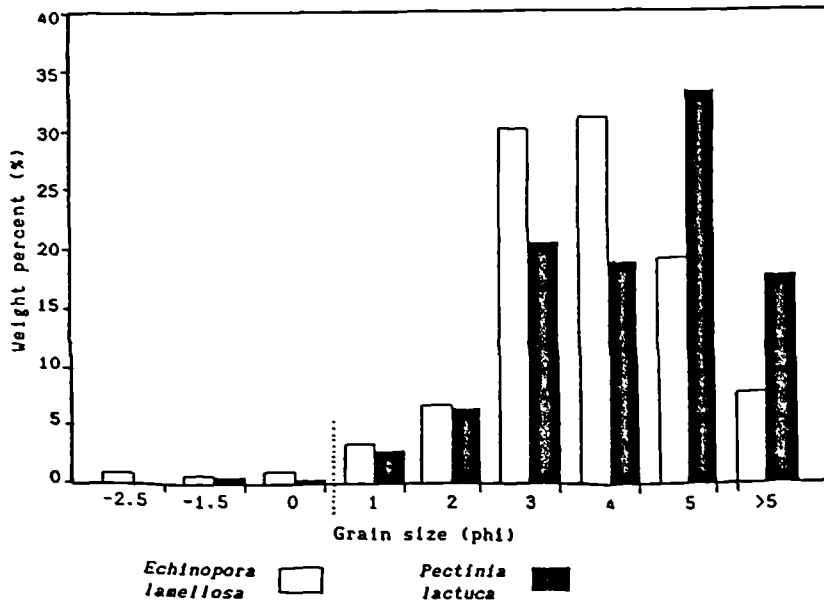
Figure 4.3. Typical grain size distribution for sediments occurring naturally in concave portions of *Echinopora lamellosa* and *Pectinia lactuca* at the North Point field site. NB: note that size categories for negative phi (>1mm) are broader than for positive phi (at the dotted line).

Size equivalents phi to um: -2.5=5mm, -1.5=2.8mm. 0=1mm, 1=500um, 2=250um. 3=125um, 4=63um, 5=31um.

MEASUREMENT OF CONVEXITY
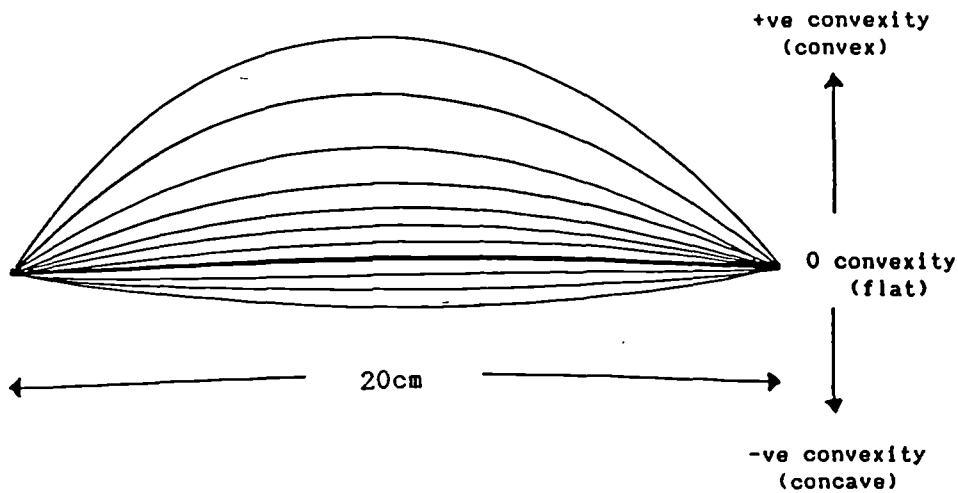
Figure 4.4. Example of sample curves used to estimate convexity of coral colonies underwater. Curves were drawn on perspex on a base of 20cm and held at 20cm from the subject.

Sediment. Analysis of sediments found naturally on a number of coral colonies at the site (particularly *Echinopora lamellosa* and *Pectinia lactuca*) predominantly yielded fine grain sizes (Figure 4.3). For this reason, fine sediments (63-250um, from the same source as those discussed in earlier Chapters) were used for this experiment.

Convexity of colonies. As far as possible, near-flat regions of tissue were selected for testing. Nevertheless, overall convexity varied slightly between colonies and constituted a potential influence on tissue mortality. Approximate convexities (+ve=convex, 0=flat, -ve=concave) of the test areas were measured against a series of ellipses with in 'easing curvature ^ a base of 20cm (Figure 4.4). Curves were drawn on perspex and held 20cm from the colony in the horizontal plane to estimate convexity *in situ*. Many colonies did not neatly fit convexity categories and in these cases classification was biased towards minimum rather than mean convexity. *Acropora hyacinthus*, being corymbose, was arbitrarily assigned a convexity of "20". As far as possible, test areas were divided into convexity groups and a stratified random allocation of treatments was carried out within groups for each species. Allocation of treatments to *Acropora hyacinthus* was random.

Effects of sediments on tissues outside the test area. Sediments removed from test areas were often lost from the colony completely, but were sometimes trapped in other areas. When this occurred, tissues were monitored for tissue damage.

RESULTS

Effects of treatments on test areas

No control colony suffered any mortality from 15 June to 22 July with the exception of one *Echinopora lamellosa* and one *Acropora hyacinthus*, both of which were caused by falls of other colonies after the storms. Although occasional very lightweight (possibly faecal) material was recorded in dips of control corals, there was no build-up

SEDIMENT ACCUMULATION
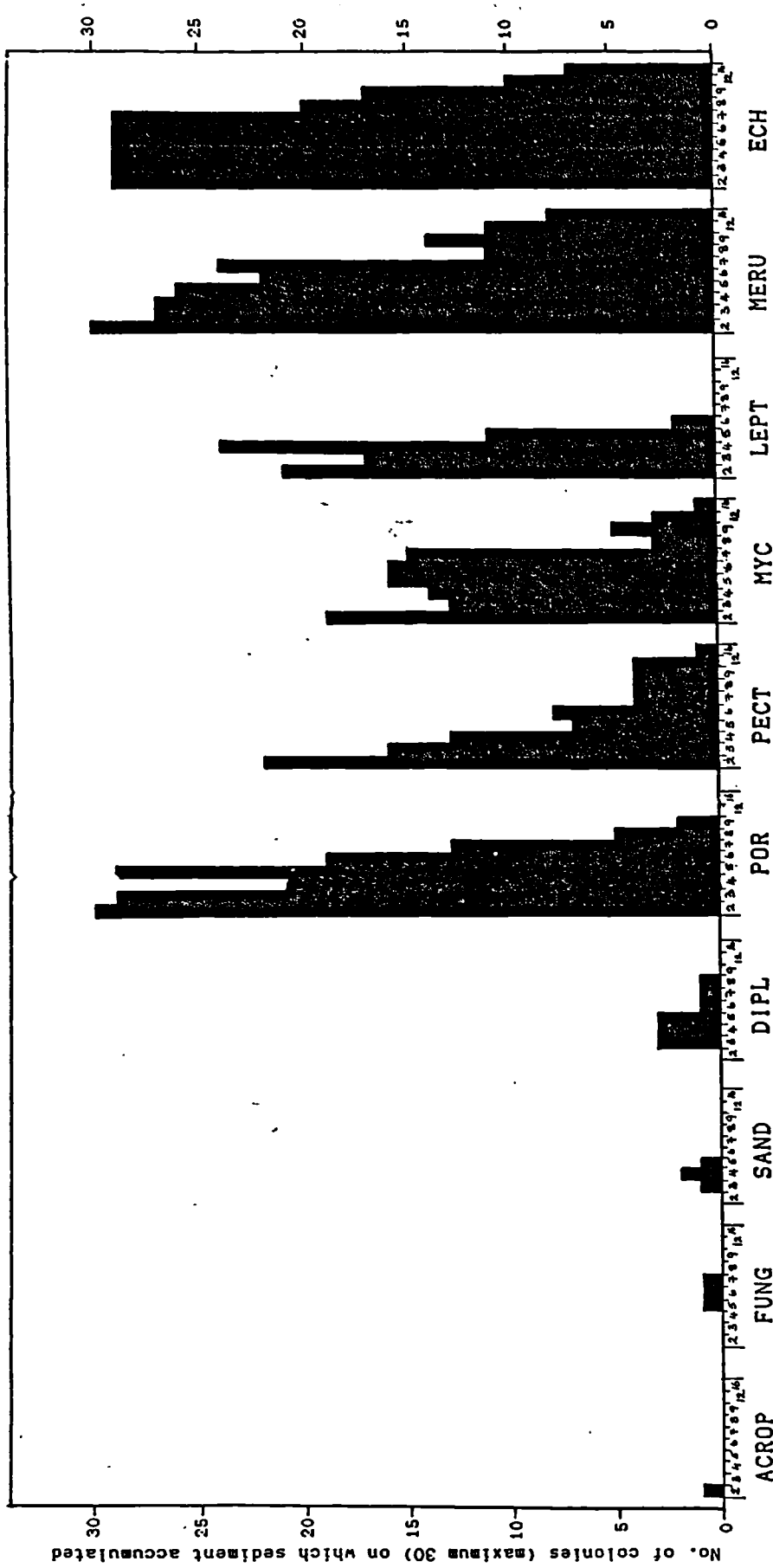
Figure 4.5. Number of colonies of each species on which sediment had accumulated from Day 2 to Day 9 consecutively (16-23 June), and on Day 12 (26 June) and Day 16 (30 June). Controls not included (i.e. total n=30 per species).

of sediment on control colonies during the period of sediment application to treated corals, and no bleaching or other observable damage to tissues. It was therefore assumed that all tissue mortality and bleaching occurring on sediment-treated corals was caused by experimental sediment loads.

Sediment accumulation. With the exception of one colony (after 24 hours), all *Acropora hyacinthus* were entirely clean of sediment at the beginning of each day (Figure 4.5). At least half of all sediments deposited on this species fell through the colony and mild water turbulence assisted loss of the remainder in mucal strands, even uu..ng still conditions. Turbulence was not observed to assist sediment loss in other species during the first four calm days. During this period, most *Fungia repanda*, *Sandolitha robusta* and *Diploastrea heliopora* were consistently free of sediment, and remaining sediment on the few exceptions was very minor. The other six species, *Porites* sp., *Pectinia lactuca*, *Mycedium elephantotus*, *Leptoria phrygia*, *Merulina scabricula* and *Echinopora lamellosa* accumulated sediments on a majority of colonies during the first calm days. There was a substantial decrease in the number of colonies with overlying sediment between the fifth and eighth day as wind speeds increased (Figure 4.5) and the quantity of sediment remaining on each colony also greatly decreased.

Tissue damage. Although the area of tissue damage was not well-defined when tissues were first examined for damage on Day 4 (19th June), all corals that showed dead patches at later dates, when detailed measurements were made, showed some tissue necrosis when first examined on Day 4. Three species, *Acropora hyacinthus*, *Fungia repanda* and *Sandolitha robusta*, showed no observable ill effects from any treatment. The remaining seven species each had at least one incidence of tissue damage (Figure 4.6). Damage to *Diploastrea heliopora* was very minor: tissues over two septa showed necrosis but recovered completely by 5th July (Day 21). One *Porites*, two *Pectinia lactuca*, almost half the *Leptoria phrygia* and *Mycedium elephantotus* and a very high proportion of *Merulina scabricula* and *Echinopora lamellosa* suffered at least some tissue death, and in a majority of colonies this damage was permanent. The extent of

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MORTALITY OF COLONIES IN SEDIMENT TREATMENTS
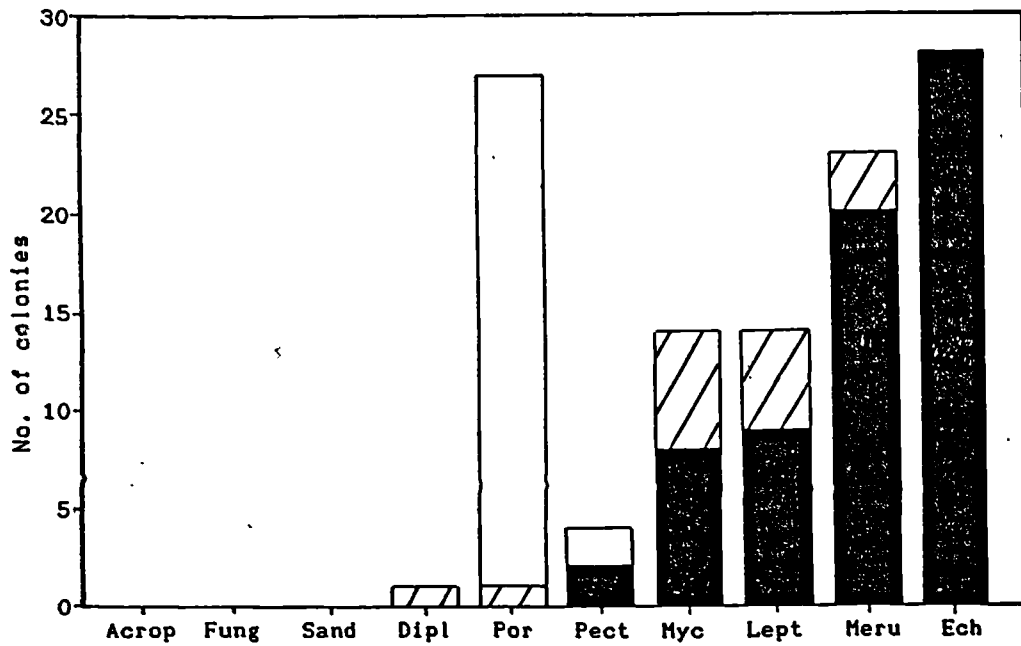
Figure 4.6. Number of colonies of each species suffering tissue damage and mortality. All sediment treatments combined (controls excluded; n=30).

■ Permanent damage

▨ Minor mortality which subsequently recovered

□ Bleaching only

tissue damage also dramatically increased as the number of affected colonies increased across this sequence of species (Figure 4.7a-g).

Effects on *Porites* sp. were quite unlike other species. Almost all replicates bleached severely and extensively (Figure 4.7b-inset), but only one colony showed any tissue death and this later recovered. As turbulence increased, sediments that had accumulated on *Porites* tissues were passively dispersed and, within a month, tissues of all but three colonies had completely recovered their colour and could no longer be distinguished from their neighbours. The three remaining colonies fully recovered after six weeks. Although bleaching occurred at the peripheries of damaged tiss extensive, long-term (several ..ys) bleaching wit..... tissue deatn was very uncommon in all other species.

Sediment load. There was a clear increase in the number of colonies showing permanent tissue damage (Figure 4.8), and an increase in the extent of that damage (Figures 4.7a-g), as the sediment load increased. Although there was a great deal of scatter, correlation between mortality and sediment load· for the six permanently affected species (*Porites* sp., *Pectinia lactuca*, *Mycedium elephantotus*, *Leptoria phrygia*, *Merulina scabricula* and *Echinopora lamellosa*) was highly significant (Spearman's rank correlation, $r=0.34$, $n=180$, $p<0.001$).

Turbulence. The overall mean depth and relative local turbulence in rough conditions for each species is plotted in Figure 4.9. Although individual colonies showed some variation, there was, predictably, an overall inverse relationship between depth and turbulence. However, there was no correlation between turbulence and mortality (Spearman's rank correlation, $r=-0.022$, $n=270$ *A. hyacinthus* excluded, $p>0.7$). With the exceptions of *Acropora hyacinthus* and *Leptoria phrygia*, turbulence levels across species were similar.

Convexity. Minor variations in local convexity were inversely correlated with the extent of tissue damage for the six species with permanent effects (Spearman's rank correlation, $r=-0.28$, $n=180$,

EXTENT OF TISSUE DAMAGE

Mortality category
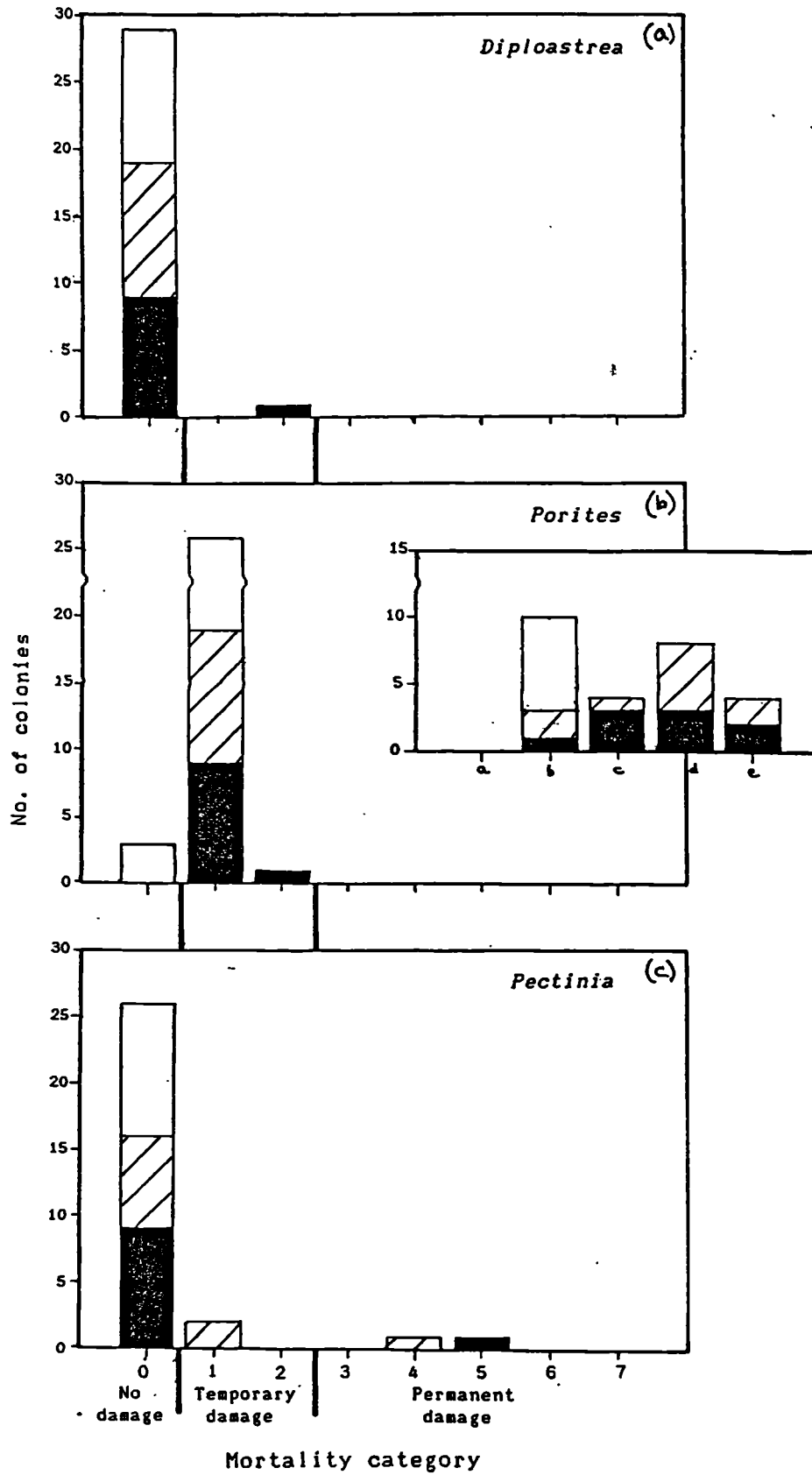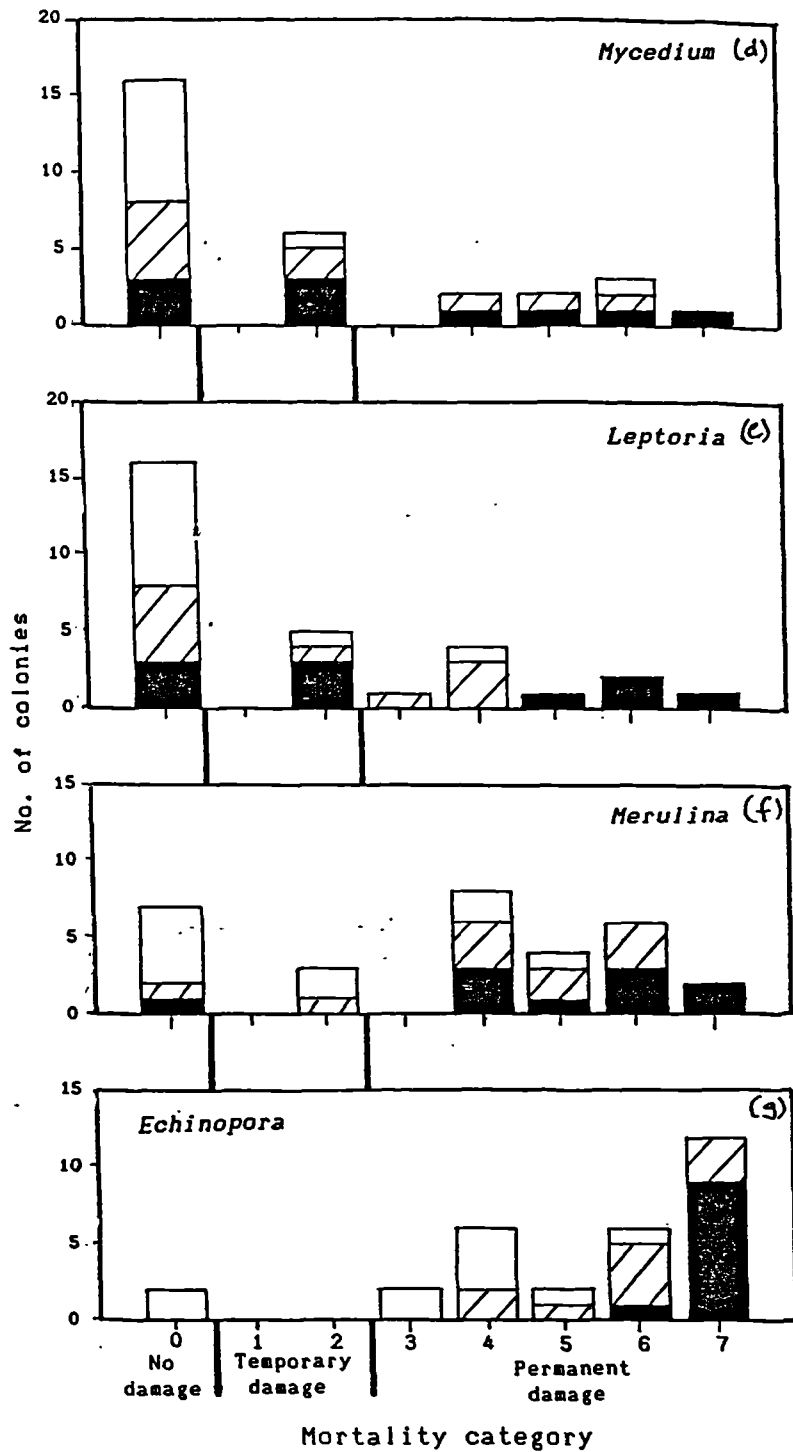
Figure 4.7. Extent of tissue damage for each species. No control regions showed any tissue damage and are excluded from these figures (n=10 per sediment treatment, 30 in total). For explanation of mortality categories 1-7, see Table 4.2. Inset categories for *Porites* show the extent of tissue area bleached as follows: 1a: $<1cm^2$, 1b: $<5cm^2$, 1c: $<10cm^2$, 1d: $<20cm^2$, 1e: 25cm^2.

■ 400mg.cm^{-2} ▨ 200mg.cm^{-2} ☐ 50mg.cm^{-2}
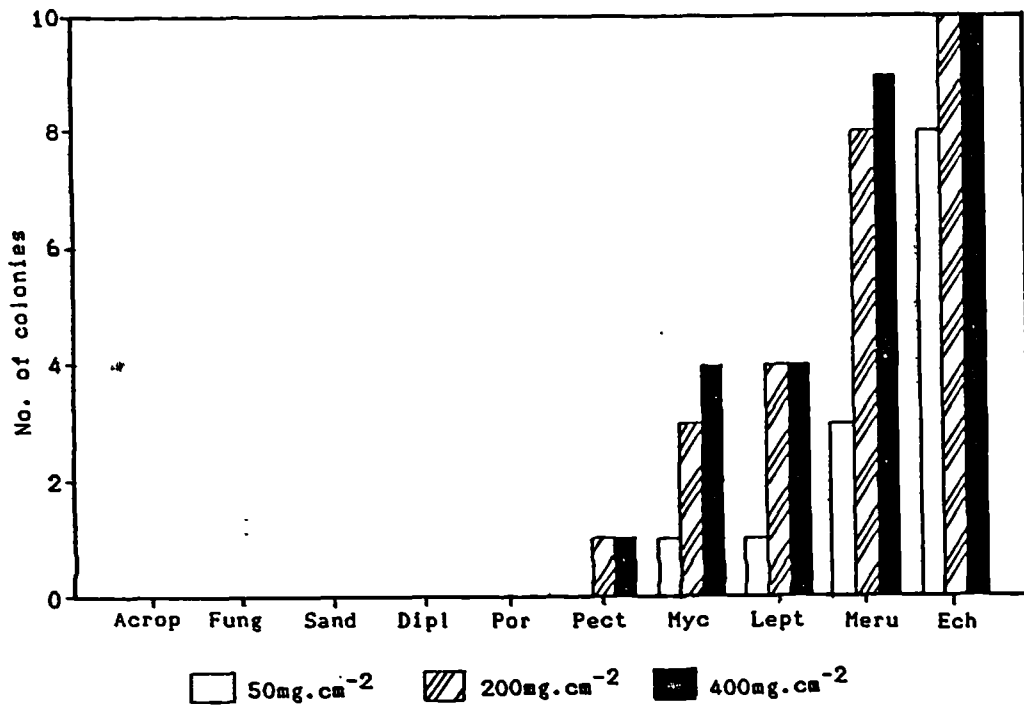
Figure 4.8. Number of colonies experiencing some permanent damage as a function of input sediment load for each species (controls excluded).

DEPTH AND TURBULENCE
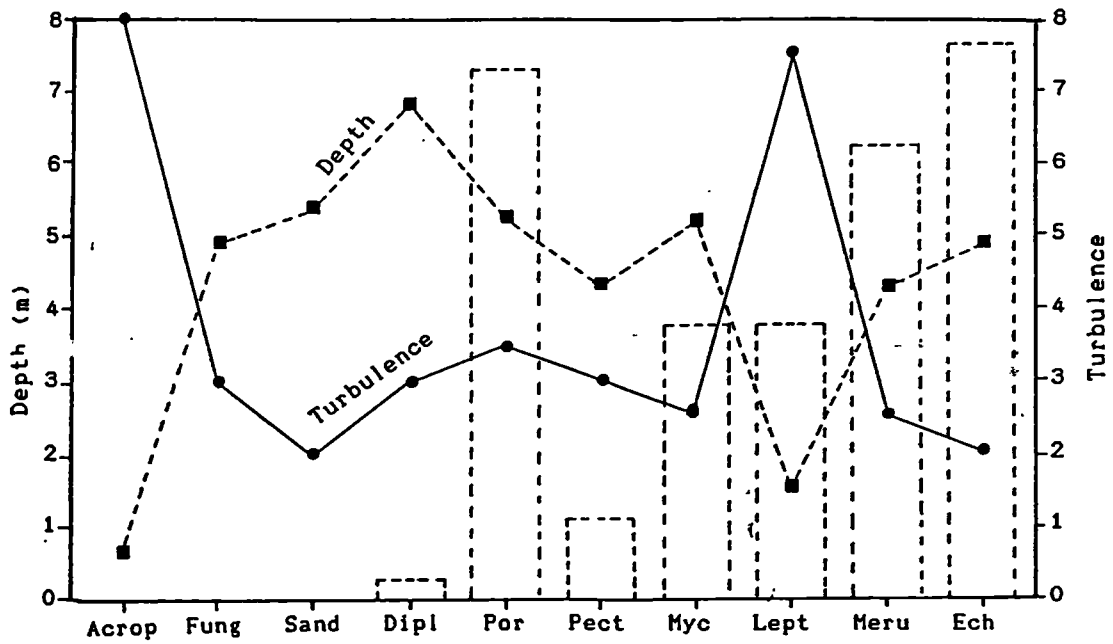
Figure 4.9. Mean depth and mean relative turbulence of colonies for each species (controls excluded). Dotted bars indicate damage levels (see Figure 4.6).
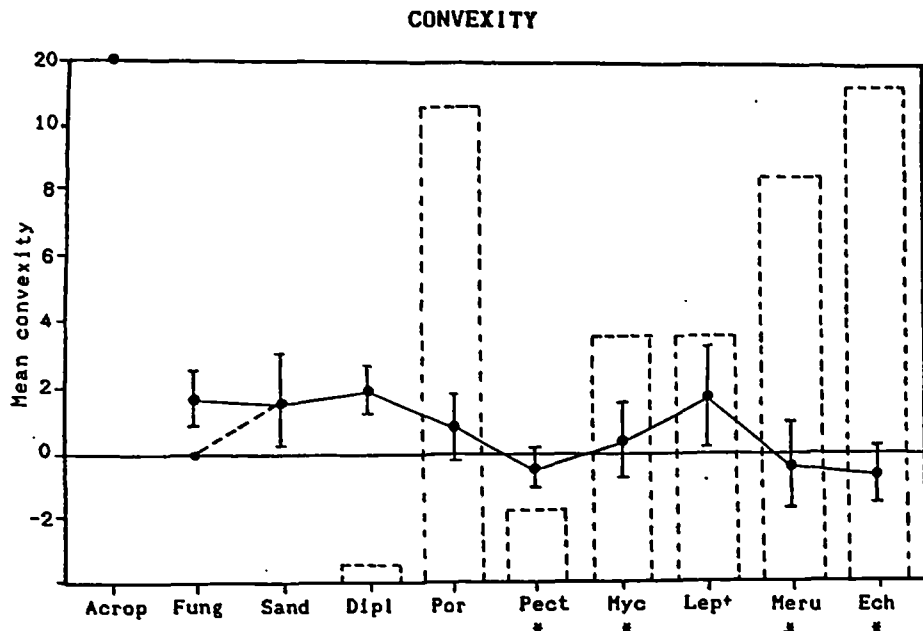
CONVEXITY

Figure **4.10.** Mean convexity (+SD) for colonies of each species used in sediment treatments (controls excluded). The plating or foliose species (*) tended to. have lower mean convexity. *Fungia repanda* has a convex profile, but sediments fall between the septa and its convexity is thus ambiguous. Dotted bars indicate damage levels (see Figure 4.6)

MORTALITY AS A FUNCTION OF CONVEXITY
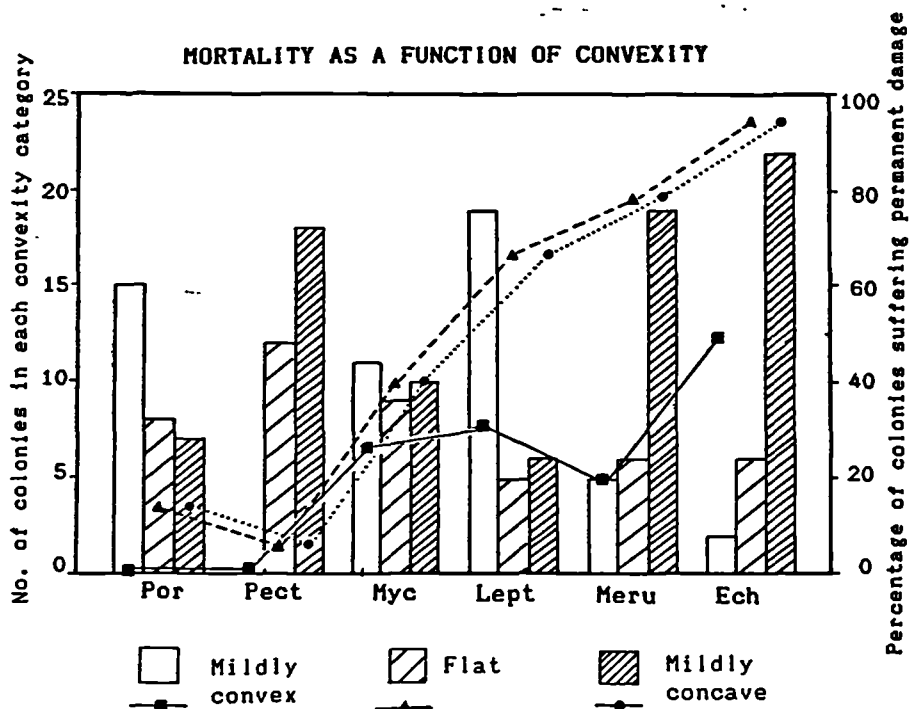
· Figure **4.11.** Mortality of each species as a function of convexity. Bars indicate the number of colonies in each convexity category. Lines show the percentage of each category that suffered permanent tissue damage.

p<0.001). There was no relationship between convexity and sediment load either overall (Spearman's rank correlation, r=.03, n=180, p=0.66) or within species (r=-0.005 to 0.151, n=30, p>0.32), indicating that the experimental procedure had been successful in distributing convexity fairly evenly between sediment treatments.

Although corals were selected to minimise potential differences in mortality due to local convexity, some interspecies variation in convexity remained (Figure 4.10). These generally reflect real morphological differences between species. The surfaces of laminar to foliaceous colonies were more variable; near-flat areas having small pockets which could act as sediment traps. Some species had few truly flat areas with alternatives either slightly convex (e.g. *Diploastrea* for which concave surfaces were very rare), or slightly concave (e.g. *Pectinia* whose surfaces were rarely convex). These variations are discussed further below.

Although interspecific differences in convexity were slight, the negative correlation between convexity and mortality (demonstrated above for all six species *combined*) suggests that even such small differences might explain some of the variation in the number of colonies of each species affected by sediment influxes during this experiment. The low mortality in *Pectinia lactuca* (which has low convexity) and high mortality in *Leptoria phrygia* (which has high convexity) seem to show genuine differences in tolerance unrelated to morphology. However, in order to separate (a) interspecific differences in the effects of convexity, and (b) other factors affecting sediment tolerance, the percentage of replicates which suffered persistent mortality (mortality categories 3-7) for each of three convexity groups (mildly concave, flat, and mildly convex)[1] was calculated (Figure 4.11). Replication in some categories was low, but when convexity is controlled in this way, the overall percentage mortality still generally increases from *Pectinia lactuca* to *Echinopora lamellosa*, strongly suggesting that factors other than convexity play a major role in sediment tolerance.

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1. Replication at finer levels of convexity was too low to make useful comparisons.

TISSUE DAMAGE OCCURRING OUTSIDE TEST AREAS

| Species | Number of colonies | | |
	Accumulating sediments	Tissue bleaching	Tissue death
Acropora hyacynthus	0	0	0
Fungia repanda	0	0	0
Sandolitha robusta	0	0	0
Diploastrea heliopora	1	0	0
Porites lobata/lutea	8	7	0
Pectinia lactuca	4	0	0
Mycedium elephantotus	3	0	3
Leptoria phrygia	4	0	4
Merulina ampliata	1	0	1
Echinopora lamellosa	11	0	11

Table 4.3. Number of colonies for which sediments accumulated outside the test area, and which bleached or later died.

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Recovery of damaged tissues

The dramatic recovery of bleached *Porites* colonies has already been noted. With other species, small bleached areas on the peripheries of larger dead areas also later recovered. Most species had the capacity to repair severe damage of less than $1cm^2$, even if the skeleton had been completely exposed (Figure 4.6, categories 2 and 3). Recovery of dead areas of a size greater than $1cm^2$ had not occurred in any species by 22 July (Day 38). Full recovery of one area of $1cm^2$, and partial recovery of two areas of $3cm^2$ and $4.6cm^2$ on *Leptoria phrygia* colonies, as well as full recovery of one area of $1.6cm^2$ on *Merulina scabricula* was recorded afte _hree months. All four of these larger test areas showing recovery had in common the fact that damage occurred in a long strip rather than a circular or square area. *Echinopora lamellosa* was the only species for which no repair of $<1cm^2$ of dead areas was recorded, although such areas did occur (Figure 4.7g).

Tissues on the periphery of dead areas generally recovered from injury after two to three weeks. Edge tissues of *Echinopora lamellosa* in particular, but also *Mycedium elephantotus* and *Merulina scabricula*, had grown at an angle away from any remaining sediment accumulations, within three months. Unfortunately, a majority of test areas of *E. lamellosa* had died from storm damage after 8 months and only six test areas which had suffered substantial death from experimental sediment influxes were still intact. However, in all six, growth of the new edge tissues and skeleton (several millimetres) was angled at 40-60° upwards from the horizontal. Edge tissues of all damaged *M. elephantotus* also grew at an angle. In contrast, although *L. phrygia* edge tissues recovered at a similar rate to plating species, growth was not angled away from damaged areas.

Effects of sediments on tissues outside the test area

Damage to tissues outside the test areas, but resulting from applied sediments, provides additional information (Table 4.3). No damage occurred to any region of *Acropora hyacinthus*, *Fungia repanda* or *Sandolitha robusta* colonies. Sediments accumulated to approximately 2mm depth in an area of 1.5cm x 1.5cm on one *Diploastrea heliopora* colony

and remained for seven days without causing underlying tissues to bleach or show necrosis. Sediments applied to *Porites* sp. colonies usually spread outwards from test areas and on several occasions resulting bleaching extended across the test area boundary. No such areas died.

Natural accumulations of sediments were common on *Pectinia lactuca* colonies at the study site. These were heavily matted with mucus and, in a few cases, some of the underlying tissues appeared recently dead (skeletons were white and neither eroded nor overgrown with algae). In others, tissues were bleached. A number of bleached areas were monitored during the course of the experiment and no death was recorded during the period from 15 June to 11 July. Applied sediments in combination with natural sediments were not observed to cause any additional bleaching or tissue death. Naturally occurring sediments were very rare on *Mycedium elephantotus* and *Leptoria phrygia*. Test sediments occasionally collected on other parts of colonies of these species for four to seven days and in all cases some tissue death was recorded. Naturally occurring sediments were found on a few plate-like *Merulina scabricula*, particularly at the centres of whorls. Generally, these regions appeared to have been dead for some time with heavily eroded skeletal microstructure overgrown with alga. Naturally occurring sediments were present on *Echinopora lamellosa* but were less thick than those on *Pectinia lactuca*. Again the skeletons were somewhat eroded and some algae were observed.

With the exception of many *Porites* sp. and *Echinopora lamellosa*, in all cases where sediments accumulated outside the test areas the local morphology was substantially more concave than any test section.

One to three opportunistic collections of sediments resulting from the storms were made from *Pectinia lactuca*, *Merulina scabricula* and *Echinopora lamellosa*. The particle size spectrum was very similar to that shown in Figure 4.4, with predominant size range of 63-250um indicating that sediment used in experiments was similar to that which naturally accumulated on these species at the study site.

For species that have moderate or poor sediment rejection mechanisms, sediment tolerance is of paramount importance in controlling the extent to which they can colonise regions of high sedimentation. It is also critical to an understanding of the effects of human-induced changes in sedimentation regime. The necessity for species to tolerate overlying sediments is, however, very strongly controlled by local morphology. This study demonstrates that there are major interspecies differences in tolerance and that some aspects of tolerance are independent of morphology.

The significance of sediment tolerance to species distributions

Under field experimental conditions *Acropora hyacinthus*, *Fungia repanda* and *Sandolitha robusta* suffered no tissue damage of any kind from heavy sediment influxes.

Acropora hyacinthus colonies are corymbose and all replicates used in this experiment were shallower than any colonies of other species. It was the only species to show significant passive loss of sediment due to water movement in very calm conditions. At Lizard Island, this species is restricted to very shallow, turbulent regions of the reef (Chapter 5) at significant vertical distance from sandy bottoms (normally >1m). Sediment trap data (Chapter 5) from Coconut Bay, at a depth at which this species occurs, indicates that natural sediment movement or resuspension can be high during storm events. Such influxes of sediments (from sublittoral origins) would normally occur in conditions of very high turbulence, but water movement would then ensure prompt removal. Once storm conditions abated, the morphology of the coral would not trap sediments. Under normal conditions, therefore, sediment abrasion may be a more important stress factor for this species.

Fungia repanda is capable of removing heavy loads of sediment very effectively. However, Schuhmacher (1977, 1979) found that sediment clearance rates of several fungiids which have strong ciliary mechanisms, decreased and finally ceased altogether when continuous

sediment influxes were maintained for a few days. He does not report the actual daily sediment dosage for these endurance experiments, but he covered the surface of corals with 1mm of sediment and it appears that he re-applied sediment as soon as complete clearance of the previous load had occurred, which would result in variable overall daily loads. Assuming that a 1mm depth of sediment over an area of $1cm^2$ weighs approximately 135mg[1], and given that during the initial period most corals cleared all sediment within 5 hours, the daily loads may have been more than $600mg.cm^{-2}.day^{-1}$. During the present study *Fungia repanda* (which was not one of the many fungiids studied by Schuhmacher) showed no signs of exhaustion and was apparently able to cope with single pulses of $400mg.cm^{-2}.day^{-1}$ for at least 8 days. In the previous chapter, *Fungia repanda* was shown to clear more than 90% of test areas inundated with 200mg sediment.cm^{-2} within two hours, thus this species in the present study would have had almost 22 hours to recover after active sediment removal. At Lizard Island this species was most common in semi-protected sections of exposed reef on partially consolidated coral rubble well away from sand patches. It is possible that it, and other fungiids with strong ciliary rejection, are better able to deal with single isolated pulses of sediment than with more continuous, smaller, influxes.

Almost all *Sandolitha robusta* observed *in situ* at Lizard Island had some sporadic, naturally occurring sediment grains on their surface at all times. Strongly concave areas were never observed on the colonies of this species, although mildly concave areas were rare and flat sections were fairly common. Although this species occurs on sand, natural accumulations of sediments on the tissues almost never occurred. It is not a strong active sediment rejector (Chapter 2), nor does it remove sediments quickly (Chapter 3). Nevertheless, colonies rid themselves of a mean of >95% of $200mg.cm^{-2}$ in 24 hours (Chapter 3) and have been shown in this study to be competent rejectors in the longer term. It is probable, therefore, that this species constantly moves sediment slowly, and that sediment rejection is a normal part of its routine and energy budget.

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1. This figure is based on approximate weights of Lizard Island sediments and may not, of course, correspond to those used by Schuhmacher.

The remaining seven species examined during this study all showed varying degrees of tissue damage in response to the experimental treatments. Damage to *Diploastrea heliopora* was minor; with one exception (where very minor damage was subsequently repaired), no area of any colony, either within or outside the test area, showed signs of stress. As discussed in the previous Chapter, this species shows very little morphological variation at all around Lizard Island; all colonies are flat or domed, and rarely had large concave areas. However, colonies can collect sediments between corallites on flat areas if active rejection does not occur. Nevertheless, in all but very few cases, sediments did not accumulate on the tissues of this species. Given that this species efficiently rejected sediments from test areas and that tissues were not permanently affected even when accumulations occurred (outside the test areas) for several days, it is concluded that the natural distribution of this species is unlikely to be significantly sediment-controlled.

Porites sp. showed very high sediment tolerance in comparison to other species tested during this study, especially given the extent and persistence of overlying sediment. In contrast, Hodgson (1990) examined the response of Hawaiian colonies when exposed to $30mg.cm^{-2}.day^{-1}$ of 'fine marine sediment' for ten days in aquaria, and observed substantial tissue necrosis. As tissue damage was less extensive when antibiotic was added to the water medium, he concluded that bacteria played a significant part in the extent of damage. Sediment loads used during the present study were much higher than Hodgson's, and yet on the few occasions where sediments remained for more than 10 days, tissues still showed no death. The substantial difference between Hodgson's results, and those of the present study, could be due to several factors including (a) trans-Pacific genetic variation, (b) the nature of the sediment (especially if Hodgson used a fine clay fraction or sediment with higher levels of terrigenous contaminants), and (c) additional stress associated with aquarium conditions.

Concave, flat and gently convex regions are very common on *Porites* sp. colonies around Lizard Island which would be susceptible to extensive tissue damage if sediment accumulations were not removed or tolerated. After stormy weather, natural sediment accumulations were observed in shallow depressions and bleaching of tissues was not

uncommon. Both *Porites lobata* and *P. lutea* are known to occur in very turbid inshore waters (Bull. 1982; Collins, 1987; Veron, 1987). Nevertheless, *Porites* species are poor sediment rejectors (Chapters 2 & 3). With the exception of only one replicate in the present experiment, this genus has tolerated very significant accumulations of sediments (>5mm which is equivalent to 780mg.cm^{-2} for this sediment grain size) on its tissues for periods of many days. As the tissues bleached they also withdrew well back into the skeleton so that without close examination it could appear that they were dead. All accumulations beyond a certain limit (about 1mm depth) caused this reaction, but although heavier input sediment loads increased the area of tissue that subsequently bleached, they did not cause mortality. Assuming that mortality does eventually occur if the sediment accumulations remain on the tissues for long enough, the occurrence of mortality in this species group is likely to be correlated with the *time that sediments of more than a critical depth are static on the tissues* rather than an intimate synergism between *weight per unit area and time*, as appears to be the case for other species. Ecologically, this distinction is important because the distribution of *Porites* sp. may not be closely correlated with sedimentation rates. Instead, the critical factor (at least for uncontaminated sediments of the size range tested) may be the length of calm periods following a period of sediment suspension. As turbulence decreases, sediments will settle out of suspension and permanent damage would then depend on whether calm conditions continued for long enough for death to occur.

Echinopora lamellosa, Mycedium elephantotus, Merulina scabricula and *Pectinia lactuca*, all being foliaceous, are relatively difficult to control for convexity, minor differences in which could explain at least some, but not all, of the observed interspecific differences in mortality.

Pectinia lactuca colonies at the study site were large (>50cm x 50cm) with relatively flat central regions and short vertical walls (more open, with flatter peripheral and central sections than observed elsewhere at Lizard Island or other regions of the Great Barrier Reef, see Plate 4.4). Test colonies, therefore, had relatively few channels for removal of sediments (see Chapter 2) and more sediment-trapping regions. Not all test sections of this morph consistently cleared all

sediments (Figure 4.5) although strong active rejection was common. The persistence of sediment accumulations may be typical only of this particular morph, but it was selected for interspecies comparison of tolerance rather than its abundance relative to other morphs. Although all test sections were flat or slightly concave (Figure 4.11) only two colonies showed any long-term tissue damage. Even non-test areas that were bleached before the start of the experiment as a result of natural sedimentation and on which sediments persisted, did not die during the experimental period.

Not only is *Pectinia lactuca* a very strong sediment rejector (Chapter 2), but it is tole ⱼ ' of sediment accumulations for considerable periods of time. Such accumulations can, however, cause mortality. Colonies of *P. lactuca* were rare in the central lagoon area of Lizard Island (Chapter 5), but *Pectinia* species are reported by Veron (1986) to be common in turbid regions elsewhere. This study indicates that this species is generally well adapted for life in areas with high sedimentation.

Given that many more *Leptoria phrygia* colonies were slightly convex than flat or concave, the mortality of this species was very high. Sediments were lost quickly as turbulence increased, but this species is very sediment-sensitive (as concluded in the previous Chapter). The distribution of colonies and prevalence of sediment-trapping tissues is considered in further detail in Chapter 5 where it is concluded that the distribution of this species may be largely sediment related.

Of the three remaining species studied, *Mycedium elephantotus* is relatively fairly rare around Lizard Island, occurring only in isolated patches (Chapter 5). Veron (1986) describes the species as common over a wide range of habitats, and Lovell (1989) and Wells (1955) describe it as occasional from the turbid waters of Moreton Bay, Queensland. The intolerance shown by this species in the present study is not wholly compatible either with its habitat distribution or its rejection capability (Table 2.2). It is possible that near-flat surfaces in turbid areas is absent, or that this species (having strong ciliary rejection mechanisms) can deal effectively with moderate to high sediment loads of silts, but not with larger sizes.

Neither *Echinopora lamellosa* nor *Merulina scabricula* were found to be strong sediment rejectors in previous work and the sediment-tolerance of these species seems very low. However, both can occur in abundance in lagoons or turbid regions (Veron, 1986). They were also both present in Lizard Island lagoon, but tissues were predominantly vertical or sub-vertical and accumulations of sediment would have been uncommon. Each of these *vulnerable species* may rely on changes in colony orientation through a growth strategy to resist sedimentation stress.

Sediment load

Sediment loads of $50mg.cm^{-2}.day^{-1}$ for only 4 days were sufficient to cause mortality in four of the species examined (*Echinopora lamellosa, Merulina scabricula, Mycedium elephantotus* and *Leptoria phrygia*). This sedimentation rate *is well within those quoted for* coral reefs (see General Introduction) and these four species must either modify their morphologies to be able to colonise such reefs, or be restricted to reefs with lower sedimentation rates. *E. lamellosa* and *Merulina scabricula* modify their growth forms; *L. phrygia* is generally restricted to reefs with low sedimentation rates; the position of *Mycedium elephantotus* is less clear, but it may be substantially more tolerant of smaller sediment sizes.

Relationship between sediment tolerance and morphology

The correlation between convexity and mortality found during this experiment was not unexpected, but it provides confirmation that even minor variations in convexity may be critical to tissue survival. Flat or concave tissues of sediment-intolerant species will die unless morphological adaptation can occur. It follows that the range of morphology, and the speed with which morphological adaptation can occur, are critical in the longer-term.

Variation in the gross morphology of some species is likely to be primarily determined by sediment loads, either by affecting light availability or by causing selective tissue death. When the latter

occurred in *Echinopora lamellosa*, damaged edges always grew upwards. The final expression of this process could be the tubular growth form that colonies of this species frequently develop in turbid environments. Similar growth responses occur in *Mycedium elephantotus* and, less so, in *Mycedium scabricula*. A similar redirection of growth has also been seen on two colonies of *Pachyseris speciosa* whose tissues had been killed by natural sediment influxes. This was not the case in the massive *Leptoria phrygia*, but other changes in morphology related to environment are explored further for this species in the next Chapter.

Management implications

Significance of species tolerances. *Acropora hyacinthus* is very well adapted to exploit a particular habitat, in this case shallow, turbulent reef flats with high light levels where, under normal circumstances, ambient sediment loads are low. However, increased sediment resulting from human activities can severely impact these habitats. *A. hyacinthus* is difficult to maintain in aquaria, being sensitive to lack of water movement. It has also been observed to secrete substantial quantities of mucus in the presence of suspensions of very fine (silt-sized) particles in calm water (*pers. obs.*). Thus it would be inappropriate to suggest that it is not vulnerable to sediment. At Lizard Island, its distribution and abundance is probably not sediment-controlled, and its morphology would most likely protect it from adverse effects of settling sediments under natural sedimentation regimes. On the other hand, both at Lizard Island and elsewhere, it is very abundant on reef flats (e.g. Broadhurst Reef, as illustrated in Veron, 1986), and it may be very vulnerable to continuously resuspended fine sediments from anthropogenic sources (e.g. channel dredging at Heron Island, Great Barrier Reef, *pers. obs.*).

Species which are intolerant of sediment such as *Leptoria phrygia*, *Echinopora lamellosa* and *Merulina scabricula* all have potential as indicators of sedimentation, particularly where sediment-sensitive morphology is targeted.

Sediment rejection mechanisms of *Fungia repanda* are very active and almost certainly require relatively high energy investment.

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Fungia fungites, another strong ciliary rejector, can become exhausted after persistent sediment influx and is usually found on hard bottoms where sedimentation is low (Schuhmacher, 1977, 1979). Although this was not observed in the present study, the ease with which detached fungiids can be moved from place to place, suggest that further work with this genus to characterise species responses to a variety of environmental influences that may co-occur with sediment could be very fruitful. Fungiids would seem to have great potential as mobile indicators.

Effects of turbulence and periodicity of sedimentation events. During this study, mortality from sedimentation was not. correlated with local turbulence, almost certainly because sea conditions were initially very calm then abruptly became stormy. Intra- and interspecific differences in sediment residence times and mortality directly correlated with local turbulence would have been more apparent after an extended period of moderate sea conditions, when microhabitat variation in turbulence would have been less uniform.

In view of the importance of sediment residence time to resulting tissue death of corals, the *periodicity* and *persistence* of sedimentation events may, in some cases, be more significant to corals than the *average* sedimentation rates over monthly or yearly cycles. Particularly dangerous conditions could result if very strong turbulence ceased very quickly, and was then followed by a long period of calm. High winds and turbulence result in much resuspension and transport of sediments to nearby corals. Fast cessation of turbulence (say half a day[1]) would lead to additional sedimentation of finer fractions and this could result in extreme conditions of sediment stress, especially if followed by a long period of calm and lack of passive sediment removal. Artificially introduced sediments (e.g. from construction or dredging) during periods of calm are potentially more dangerous for similar reasons.

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1.   Outer reefs of the Great Barrier Reef, situated at the top of the continental slope, effectively break open-ocean ground swell.   Almost all turbulence on mid-shelf reefs is therefore wind-generated and is very responsive to wind changes.

CHAPTER 5

LIZARD ISLAND: HABITATS AND SPECIES DISTRIBUTIONS

SUMMARY

Relevant aspects of the physical environment of Lizard Island are described with respect to three regions categorised as Exposed, Moderately-exposed and Lagoon. Substrate sediments were found to be predominantly large (>1mm) in Exposed sites, mixed and fairly poorly sorted (63um-1mm) in Moderately-exposed sites, and predominantly fine (<125um) in Lagoon sites. Sedimentation rates were generally less than $22mg.cm^{-2}.day^{-1}$ in all sites except during very heavy sea conditions. Light attenuation was similar in Exposed and Moderately-exposed regions (K_d=0.118±0.010m^{-1} and 0.114±0.014m^{-1} (±SE) respectively) but was significantly higher in the Lagoon (K_d=0.171±0.008m^{-1}). Horizontal visibility measured by Secchi disc at 4m depth was highest at Exposed sites and lowest in the Lagoon. Visibility in summer was higher than winter in all regions although the difference was less marked at Moderately-exposed sites than elsewhere.

Surveys of coral cover were carried out on six 20m-transects at each of 12 principal sites, four in each region. Mean coral cover on available hard substrate varied from a minimum of 17.9% in Watson's Bay (Moderately-exposed) to a maximum of 68.8% at one Lagoon site. This Lagoon site was dominated by finely branching and strongly inclined foliaceous species in a solid multispecific stand. Overall coral cover was significantly lower in the Moderately-exposed north-western sites (24.1%) than at either Exposed (46.3%) or Lagoon sites (49.6%). There was no statistical difference in coral cover between these latter regions.

A survey of species cited in other sections of this thesis was undertaken. Gardineroseris planulata, Hydnophora microconos, Acanthastrea echinata, Favia pallida, Leptoria phrygia, Montastrea curta, Plesiastrea versipora, and Turbinaria peltata were absent from the central lagoon. Of these, G. planulata and H. microconos were restricted to Exposed sites. Acropora hyacinthus, Favia stelligera, Leptoria phrygia and Montastrea curta were substantially more abundant at Exposed sites than elsewhere. In contrast, branching Porites species (particularly P. cylindrica and P. nigrescens but also P. rus) were very much more abundant in the lagoon than elsewhere. In some cases these distributions can be at least partly explained by their sediment rejection or tolerance, as described in earlier chapters.

The distribution, and some aspects of morphology and population dynamics of one species, Leptoria phrygia, were examined in detail. This species was found to be very common in Exposed sites, substantially less common on Moderately-exposed sites, and absent from the Lagoon. The ratio of projected to total surface area and the total 'sediment-trapping' area of tissue of colonies was significantly less in Moderately-exposed sites than Exposed sites. In view of its sediment sensitivity as well as the importance of turbulence to this coral, it is probable that morphological variation may result from different sedimentation and turbulence regimes of the two areas.

Morphological characters of key species may prove to be useful indicators of ambient sediment-related environmental conditions.

INTRODUCTION

Publications resulting from the Lizard Island Metabolic Exchanges on Reefs (LIMER) expeditions in 1975 and 1977 (LIMER 1975 Expedition Team, 1976; Barnes & Crossland, 1983; Crossland & Barnes, 1983) describe the physical conditions prevailing on a transect from the exposed outer reef between South Island and Bird Islets, across the comparatively protected lagoon, to the less-exposed shallow reef between Research Point and Palfrey Island (Figure 5.1). Alldredge and King (1977) describe the distribution of zooplankton along a transect in the same vicinity. With the exception of Leis (1986) who examined surface current speeds for several sites, there is relatively little detailed information on environmental conditions in other parts of the island.

Published accounts of coral species distributions around Lizard Island are also surprisingly lacking. During the LIMER expeditions, Pichon and Morrissey (1981) carried out studies of the ecology and distribution of species across the lagoon transect, but results are discussed only in broad terms and the individual data are not published. Unfortunately, species details from this work are not available. The presence of some species from a site near Palfrey can be inferred from taxonomic accounts reported in the Scleractinia of Eastern Australia (Veron & Pichon, 1976, 1980, 1982; Veron & Wallace, 1984; Veron et al, 1977).

A general description of the reef habitats in three principal regions of Lizard Island has been given in the General Introduction to this thesis. The present Chapter is designed to expand on relevant aspects of the physical and ecological environments of the island. Studies include topographical descriptions of a number of selected sites, secchi disc measurements, examination of settling and substrate sediment grain sizes, photosynthetically active radiation (PAR) profiles with depth, and descriptions of the coral cover and dominant genera. No attempt is made to *comprehensively* describe the sedimentation regimes or turbidity around Lizard Island as such an undertaking would require, at least, seasonal replication. Present studies were logistically constrained but, nevertheless, are designed to augment qualitative observations and to put the results described in this thesis into broad ecological context.

In parallel with surveys of species distributions, a small study of the distribution, abundance and morphological variation of *Leptoria phrygia* was carried out to test hypotheses raised by earlier work. Differences in the response and tolerance of corals to settling sediments have been the subject of Chapters 2-4. Small-scale variations in morphology have been shown to be critically important in determining the extent of mortality caused by a given sedimentation regime. Synergistic influences of turbulence, light, turbidity, and biological factors all modify a species response. Nevertheless, if sedimentation is a strong forcing factor in determining the abundance and morphological characteristics of a species, changes in the overall abundance of sediment-sensitive species, together with changes in their sediment-trapping characteristics, should occur along sedimentation gradients. The direct relationship between sedimentation rate and abundance or morphological characteristics of coral species, could not be tested definitively during this study because historical records of sedimentation rates do not exist for sites around Lizard Island, and long-term comprehensive sedimentation rate studies were beyond the scope of this research. Nevertheless, the opportunity was taken to examine the abundance and morphological characteristics of the sediment-sensitive species, *Leptoria phrygia*, with respect to the three above-mentioned broad environmental categories (Exposed, Moderately-exposed, and Lagoon), to test the potential of this approach for future studies.

Based on the response of *Leptoria* to sediments observed in previous studies, (a) the overall abundance, (b) the ratio of horizontal to total surface area, and (c) the area of sediment-trapping tissue were all expected to decrease as sedimentation stress increased. As an initial hypothesis, it was assumed that the influence of settling sediments would be most severe in the lagoon (where fine sediments were continuously resuspended and visibility was normally poor), and least severe on exposed reef fronts (where turbulence was high), with effects in the Moderately-exposed region being intermediate.

LIZARD ISLAND
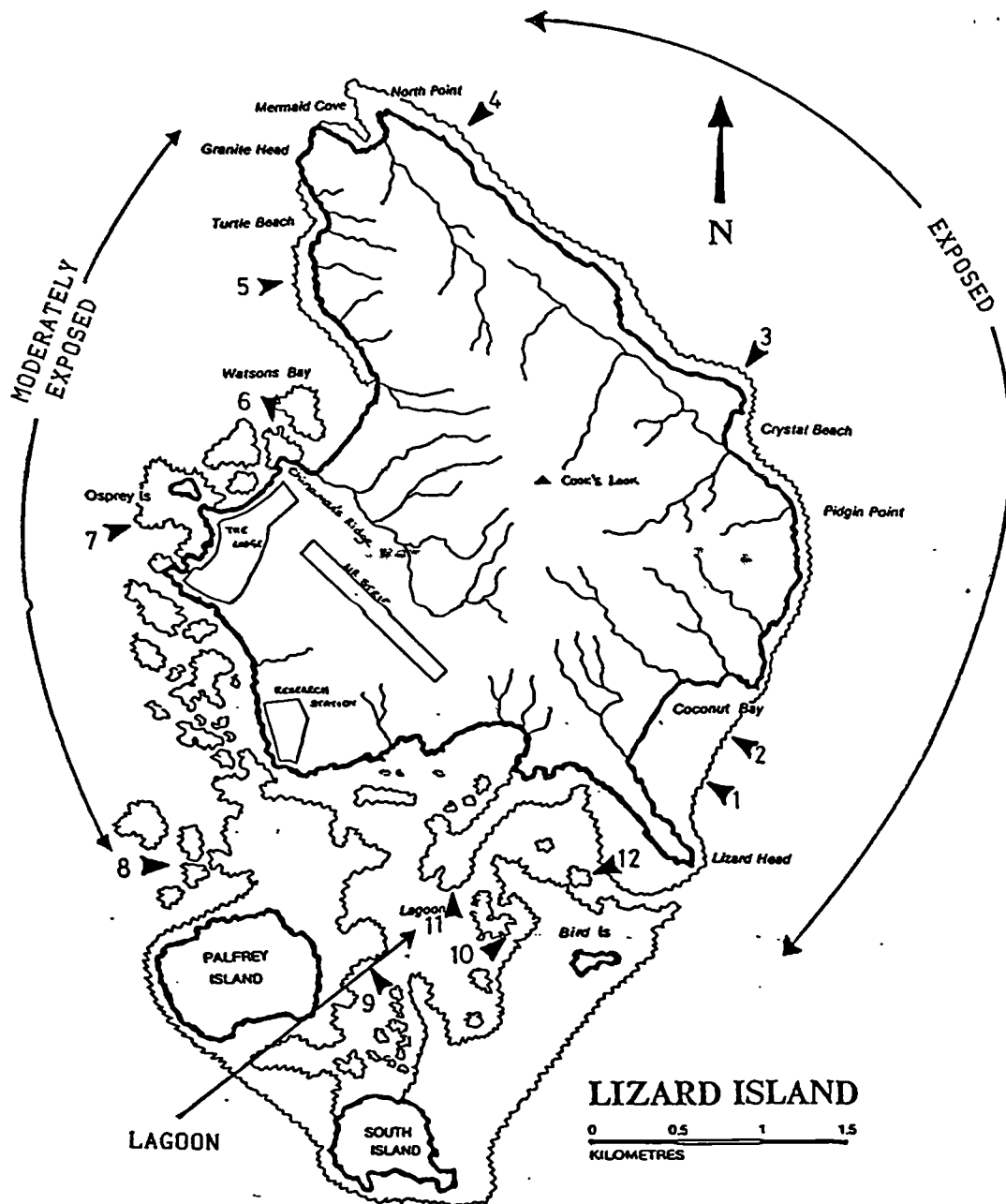
	Site	
Region	Number	Site Name
Exposed	1	Coconut1
	2	Coconut2
	3	Crystal
	4	North Point
Moderately	5	Turtle
exposed	6	Chinaman's Ridge
	7	Osprey Island
	8	Research
Lagoon	9	Palfrey
	10	Bird Island
	11	S-Bend
	12	No.2 Bommie

Figure 5.1. Location of principal sites for secchi disc, bottom sediment samples, and coral distribution and abundance studies around Lizard Island.

METHODS

Environmental parameters

Secchi disc measurements. As vertical visibility measured by Secchi
discs usually surpassed maximum depths adjacent to reefs of interest
around Lizard Island, horizontal readings were made at a fixed depth
of 4m. Twelve sites were selected, 4 in each of the three principal
Exposure regions and coinciding with sites for companion surveys of
coral distributions and abundance (Figure 5.1). In addition to
periodic measurements at these sites through all seasons, readings
were made at 9 sites (3 in each Exposure region) on the same day on
four occasions to control for temporal variation. The data for
these four days are used to provide a direct comparison between the
three Exposure regions by 2-way analysis of variance (Factors:
Exposure region, Date).

Attenuation of photosynthetically active radiation (PAR) with depth.
Measurements of PAR were made with a Stipe Underwater Lightmeter (a
cosine collector using a selenium photocell, with approximately
level response between 400 and 700nm, Drew, *pers. comm.*).
Replicate measurements of irradiation were recorded just below the
water surface and at depths of 2m, 4m, 6m, 8m, 10m, and, where
possible, deeper, at three sites in each of the three Exposure
regions (Figure 5.2). All measurements were taken within one and a
half hours of solar noon on clear, cloudless days.

On three moderate to very calm days in summer (16 November 1988,
31 January 1989 and 7 February 1989), PAR profiles of all nine sites
were measured on the same day to provide a comparison of light
attenuation coefficients in the three Exposure regions.

The vertical attenuation coefficient for downward irradiance
(K_d) is described by the equation:

$$E_d(x) = E_d(0) \cdot e^{-K_d(x)}$$

(Kirk, 1983)

or $\ln E_d(x) = -K_d(x) + \ln E_d(0)$
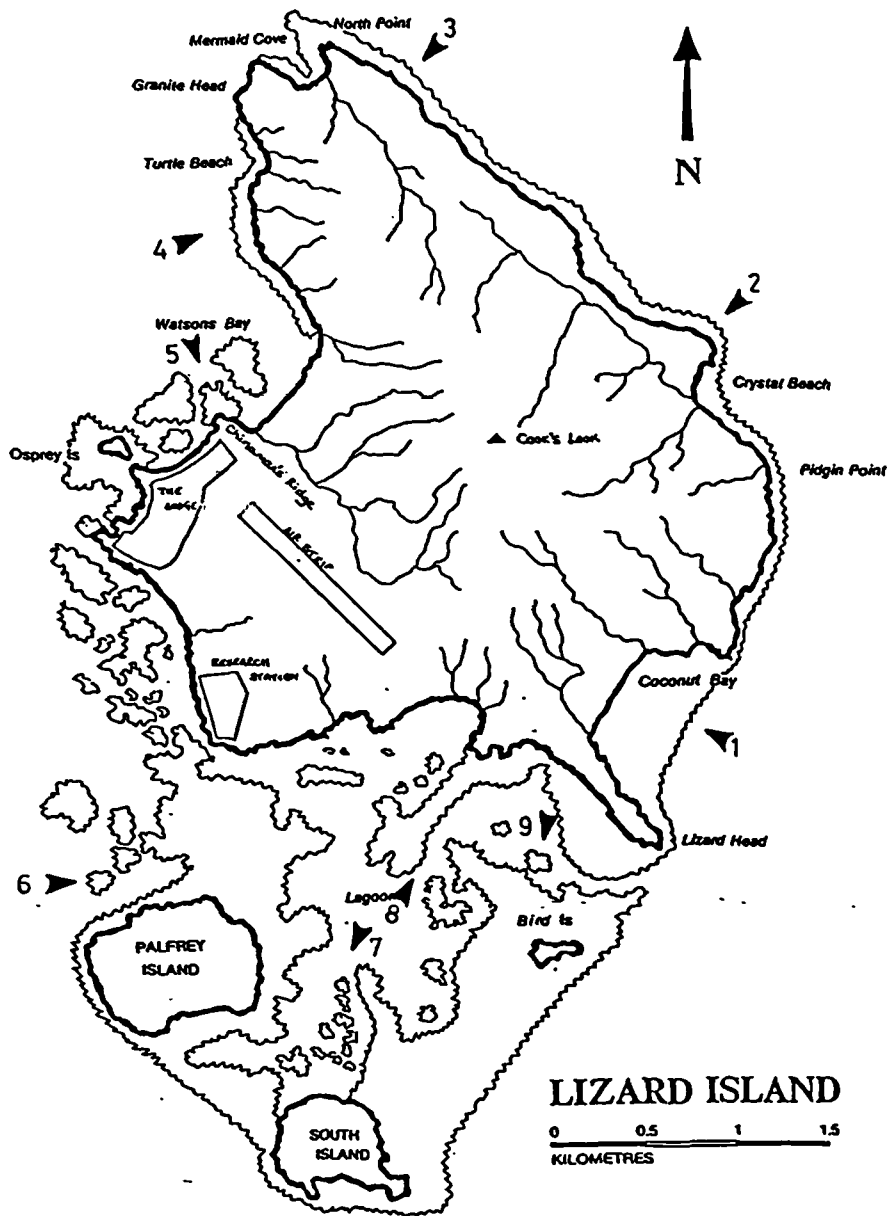
Figure 5.2. Locations of field stations for PAR measurement with depth.

where $E_d(x)$ and $E_d(0)$ are the measured values for irradiation ($umol(photons).m^{-2}.s^{-1}$) at depth x and 0m (just below the surface) respectively. The attenuation coefficient (K_d) can therefore be estimated from the slope of the regression of $lnE_d(x)$ on depth in metres. Multiple comparisons between attenuation coefficients for each region were made by the T-method (Sokal & Rohlf, 1981: p.507).

Substrate sediments. Replicate samples (approximately 80cm^3) of the top 1.5cm of substrate sediments were collected from 3-4m and 7-9m depth at each of the 12 sites selected for coral distribution studies (Figure 5.1, a total of 4 samples per site). All samples were taken during summer months following periods of variable winds from sediment patches of a minimum depth of 3cm and a minimum area of 1m^2. Each sample was washed in fresh water, and the sediments allowed to settle[1]. The overlying fluid was decanted, sediments were dried to constant weight, sieved through a series of Endicott sieves, and each grain size fraction reweighed.

Downward sediment flux. Sediment traps were deployed at four locations around Lizard Island: (a) Coconut Bay (between Sites 1 and 2); (b) North Point (close to Site 4); (c) Watson's Bay (close to Site 6); and (d) the Lagoon (close to Site 11) (Figure 5.1). Traps were standard jars with an aperture of 38cm^2 and height of 20cm. The ratio of height to aperture diameter (2.86:1) conformed to dimensions of between 2 and 3:1 recommended by Gardner (1980), but the jars did not contain baffles. The traps were located within 5cm of the substrate (i.e. trap apertures were approximately 20-25cm above the substrate), and situated on sand directly adjacent to living coral at 2-3m. Traps were deployed over four periods in January and February 1989, encompassing moderate and strong south-easterly winds, strong north-westerly winds, and light weather of variable wind direction.

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1. For early samples, the overlying fluid was decanted and filtered through pre-weighed Whatman GF/C glass fibre filters, which were subsequently dried to constant weight. However, as the residue was less than 0.2% of the total, this step was later omitted.

Sediments and seawater were filtered through pre-weighed Whatman GF/C glass fibre filters, washed thoroughly with fresh water, dried to constant weight, sieved into required grades and reweighed.

Ecological Parameters

Coral cover, and abundance of target species. In each Exposure region, 4 sites were selected where suitable reefal substrate was known to exist (Figure 5.1). For each site, a brief description of the site and its most dominant taxa was recorded, and three 20m line transects were deployed in each of two depth bands: shallow 1-2m; and deep 4-6m. With the exception of Site 11, where large coral outcrops and bommies were interspersed with short intervals of sand (approximately 1m), all transects were located across continuous hard substrate. The line intercept method (Loya & Slobodkin, 1971; Loya, 1972) was used to obtain an estimate of live coral cover. Recordings were made between the 10 and 30m marks of transect tapes to avoid any potential bias relating to the choice of start point. In addition, within a 2m band transect centred on each 20m line transect, the abundance of each of 36 species and species groups was estimated visually on an abundance scale.

Living coral cover is reported as 2-dimensional projected (or areal) cover of substrate (i.e. the percentage of horizontal reef area covered by living tissue ignoring both layered colonies and other living tissues in the vertical dimension). The transect tapes were laid in straight lines across the top of colonies and did not follow topographic irregularities. Parallax problems were reduced by the use of frequent line anchors and great care was taken to prevent observational bias.

Percentage hard coral cover for each 20m transect at each depth and site was arcsin-squareroot transformed and analysed by mixed nested analysis of variance. Exposure and Depth were fully crossed while Sites were nested within Exposure and three replicate transects examined for each depth at each site. Transformed data showed improved normality and conformed to the assumption of homogeneity of variance (Cochran's test: Winer, 1971). In all

cases, means and other statistical parameters were calculated on the arcsin-squareroot transformed data and back-transformed. Parameters such as standard deviations and standard errors are therefore asymmetrical about the mean.

Abundance, size distribution and morphology of *Leptoria phrygia*. A methodical and exhaustive search for all *Leptoria* was carried out within each 2m x 20m band transect. Estimates of both projected and total living surface area were obtained by taking as many height, width and breadth measurements as necessary (including the dimensions of dead sections). For each colony, the ratio of projected surface area to total surface area was calculated. A ratio of '0' indicates that the colony had no horizontal surface area and was entirely vertical; a ratio of '1' indicates that the colony was entirely horizontal. Colonies under overhangs with tissues facing downwards which would not be exposed to raining sediments, were considered as vertical (with ratios of '0') for the purposes of this analysis.

Surface area that could be considered 'sediment-trapping', as well as dead regions within the colonies, were also recorded.

A brief survey of 11 colonies at the Cod Hole on the outer barrier reef some 20km south-east of Lizard Island, where water clarity was much higher and sedimentation much lower, was made for comparative purposes.

Two distinct forms of small colonies were recognised: recruits and remnants. In almost all cases remnants of a single colony could be distinguished with confidence from recruits. *Leptoria phrygia* colonies are distinctly different from one another in meander shape, width and wall height and also in colour, shade and texture, allowing remnants of a single colony to be readily distinguished from recruits by their similarity in appearance. In addition, the eroded skeletal remains can usually be identified between remnants. Dead areas between remnants were recorded separately from dead patches completely surrounded by coral tissue.

SECCHI DISC MEASUREMENTS
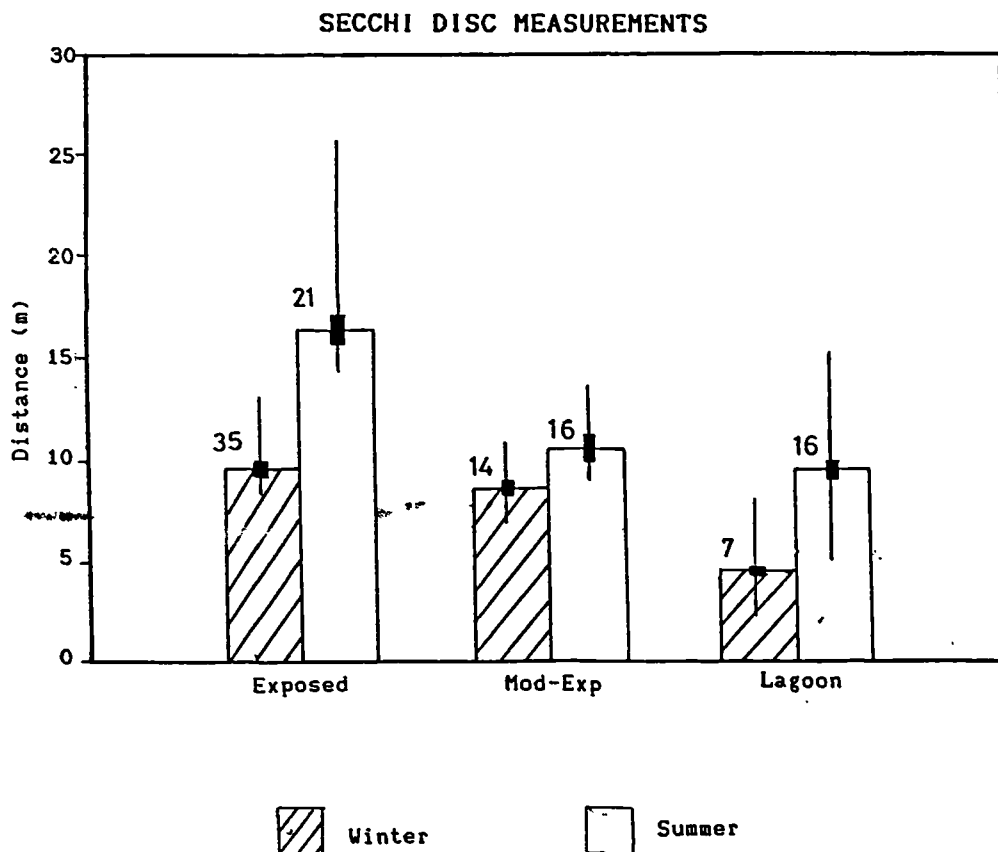
Figure 5.3. Horizontal Secchi disc measurements (mean±SE, and range) recorded for sites in each exposure region and for both summer and winter. The number of independent days on which each mean is based is given above each bar. Data for winter in Exposed sites includes records from 1987, otherwise data are for winter 1988 and summer 1988/9. These data suggest that there may be very significant differences both between all regions and between seasons. Full analyses have not been carried out as readings were not normally made in all regions on the same day. Table 5.1 provides a more limited analysis of four days in summer on which readings were taken from several sites in each region on each day.

Many *Leptoria phrygia* colonies are homes to commensal crabs and a few to barnacles. The number of these symbionts was recorded for each colony within the 2m x 20m band transects.

RESULTS

Physical parameters

Secchi disc measurements. Means of all-horizontal secchi disc readings for each region around Lizard Island divided into winter and summer seasons are summarised in Figure 5.3. Underwater visibility was usually better during summer months than winter months in all regions which was almost certainly due to lighter winds and extended periods of calm weather. In winter, the lagoon was always turbid, with a normal horizontal visibility range of between 4.5 and 6.5m. After one rare 6-day period of calm weather in April 1988, maximum horizontal visibility reached 8.5m and conversely, on one occasion visibility was only 3m. In summer, visibility was variable and depended strongly on the number of preceding calm days. A maximum of 15m was recorded after a period of calm or north-west light variable winds for 10 days, but visibilities were normally between 7 and 11m. Mean visibility in winter was only slightly greater at Exposed sites than at Moderately-exposed sites, while in summer the difference was substantial. Between seasons, Moderately-exposed sites showed a more stable pattern than other regions of Lizard Island. The highest visibilities were recorded in Coconut Bay during summer (25m), but values greater than 15m were common at all Exposed sites during summer.

Analysis of data for the four summer days on which readings were taken from replicate sites in all regions showed that visibility in Exposed sites was significantly higher than in either Moderately-exposed or Lagoon sites but that there were no overall differences between the latter regions (Table 5.1). There was, however, an interaction between Date and Exposure, almost certainly due to differential effects of weather conditions on visibility, depending

Model: 2-Way Mixed Model III analysis of variance (Exposure=fixed, Date=random)

Source	SS	df	MS	F	p	
Exposure	201.55	2	100.78	11.08_6^2	0.0096	**
Date	173.97	3	57.99	20.72_{24}^3	0.0000	***
Exposure*Date	54.56	6	9.09	3.25_{24}^6	0.0176	*
Residual	67.17	24	2.80			

Exposed   Moderately-exposed   Lagoon

Table 5.1. Comparison of horizontal Secchi disc readings between regions on each of four days in summer 1988/9. Secchi disc measurements were made at nine sites on each date, three from each region. Multiple contrasts between regions were examined by Tukey's HSD test at $p < 0.05$ and indicated that the visibility at Exposed sites was significantly greater than at sites elsewhere.

upon wind direction or number of calm days. For example, south-east winds had a stronger effect on visibility in Exposed than Moderately-exposed sites, whereas north-east winds had the opposite effect. After several days of calm or very light winds the Lagoon was occasionally clearer (13m or so) than the Moderately-exposed region, where light winds from the north-west could maintain higher suspended particle loads; when winds were stronger (either north-west or south-east), visibility in the Lagoon quickly became lower than Exposed or Moderately-exposed sites.

Attenuation of PAR with depth. The mean percentage of incident light penetrating to each depth (i.e. PAR at depth 'x' as a proportion of that measured just beneath the surface) is presented in Figure 5.4a for each of the three regions. Resulting regression lines of (ln(light) on depth) were highly significant in all cases ($p < 0.001$, Figure 5.4b). The attenuation of light, K_d, in the Lagoon was significantly greater than in other regions ($p < 0.01$), but no significant differences were detected between Exposed and Moderately-exposed sites (Table 5.2).

Substrate sediments. Size distribution patterns of substrate sediments were different at different sites and depth (Figures 5.5a-l). Distributions at Exposed sites were generally positively skewed[1], those of Moderately-exposed sites were much more evenly distributed, and those of Lagoon sites were negatively skewed. Between 50 and 58% of sediments at 3m from Coconut Bay were between 1 and 2.8mm (principally 1-2mm) and the same trend was apparent at 7m. Size distributions at Crystal and North Point were much less skewed particularly at greater depth, although there was still a higher proportion of large sediment sizes than in samples from other Exposure regions. Sediments of Moderately-exposed sites were rarely greater than 2.8mm or less than 63um, most falling fairly evenly in between. Lagoon sites were all dominated by sediments of less than 125um.

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1. i.e. distributions are not normal and show a longer tail towards positive phi (smaller grain sizes). This indicates that the modal sediment size is large - see Figure 5.5a.

LIGHT ATTENUATION

Incident irradiance (PAR) (umol(photons),m^{-2},sec^{-1})

Percentage of just-subsurface irradiance

1500

1000

500

0

100
80
60
40
20
0

0   2   4   6   8 ± 10

Depth (m)

LIGHT ATTENUATION COEFFICIENTS

Ln(light)

7.5
7.0
6.5
6.0
5.5
5.0

0   2   4   6   8   10

Depth (m)

—■— Exposed sites (slope: -0.118±0.0098)
—●— Mod-exposed sites (slope: -0.114±0.0137)
—▲— Lagoon sites (slope: -0.171±0.0076)
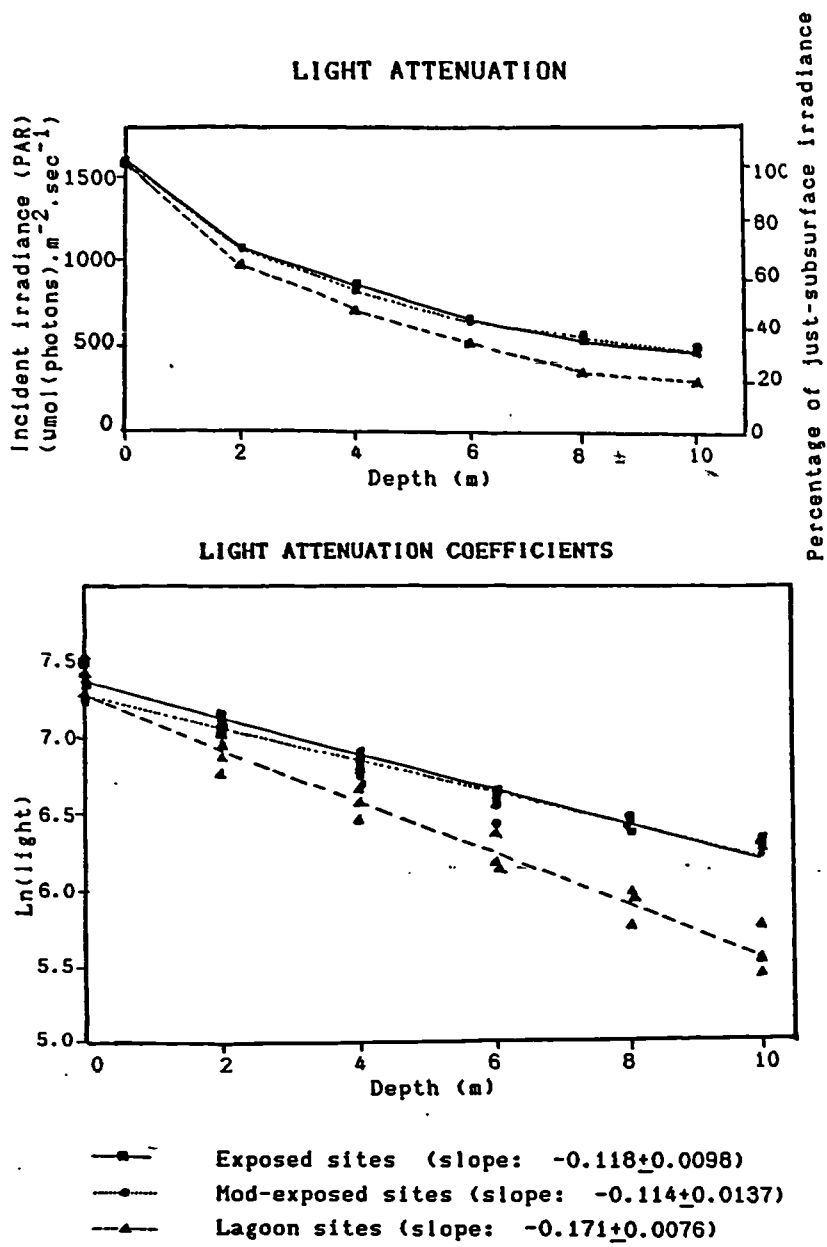
Figure 5.4. Light attenuation in each of the three exposure regions of Lizard Island. (a) Attenuation of light with depth expressed as absolute quantum flux (left scale) or percentage of just sub-surface irradiation (right scale). (b) Regression curves for calculation of light attenuation coefficient (K_d). There was no difference in the attenuation coefficients of Exposed and Moderately-exposed regions, but these were significantly different from that of the Lagoon.

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Source	SS	df	MS	F	p
Among slopes	0.500154	2	0.250077	10.48^2_{12}	<0.01 **
Error	0.286256	12	0.023855		

K_d	0.118	0.114		0.171
(SE)	0.010	0.014		0.008
	Exposed	Moderately-exposed		Lagoon

Table 5.2. Comparison of regression slopes ($-K_d$) between regions for three days in summer 1988/9 (Sokal & Rohlf, 1981, p.507; multiple comparisons by T'-method at p<0.05).

SUBSTRATE SEDIMENT GRAIN SIZE DISTRIBUTIONS

EXPOSED

Coconut1

Crystal

Coconut2

North Point

MODERATELY-EXPOSED

Turtle

Osprey Island

Chinaman's Ridge

Research

Weight percent of sediment
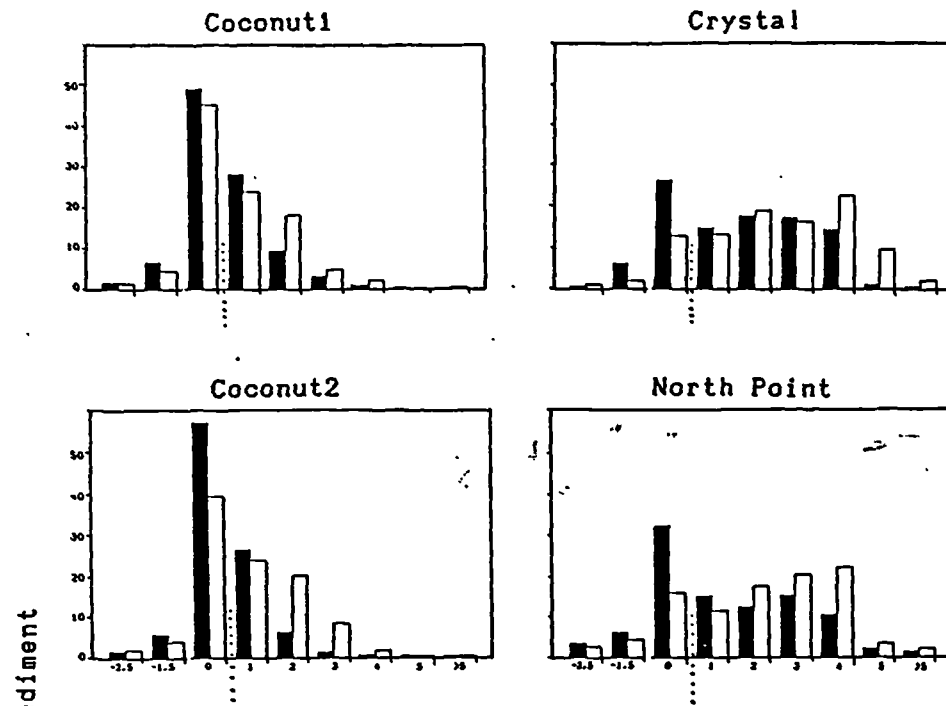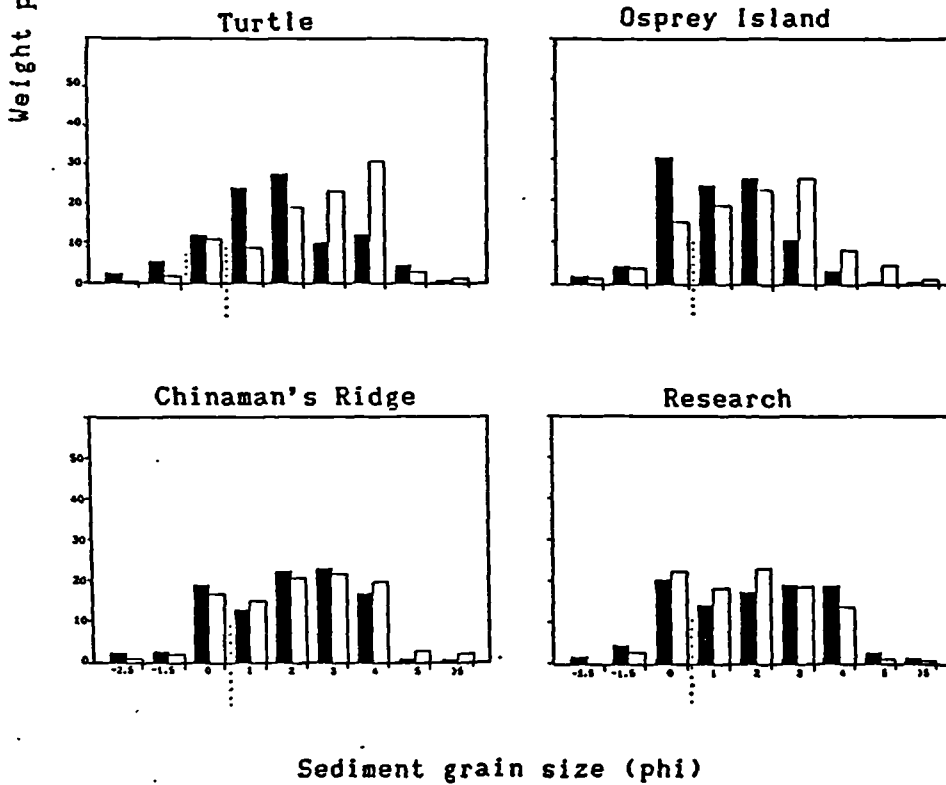
Sediment grain size (phi)
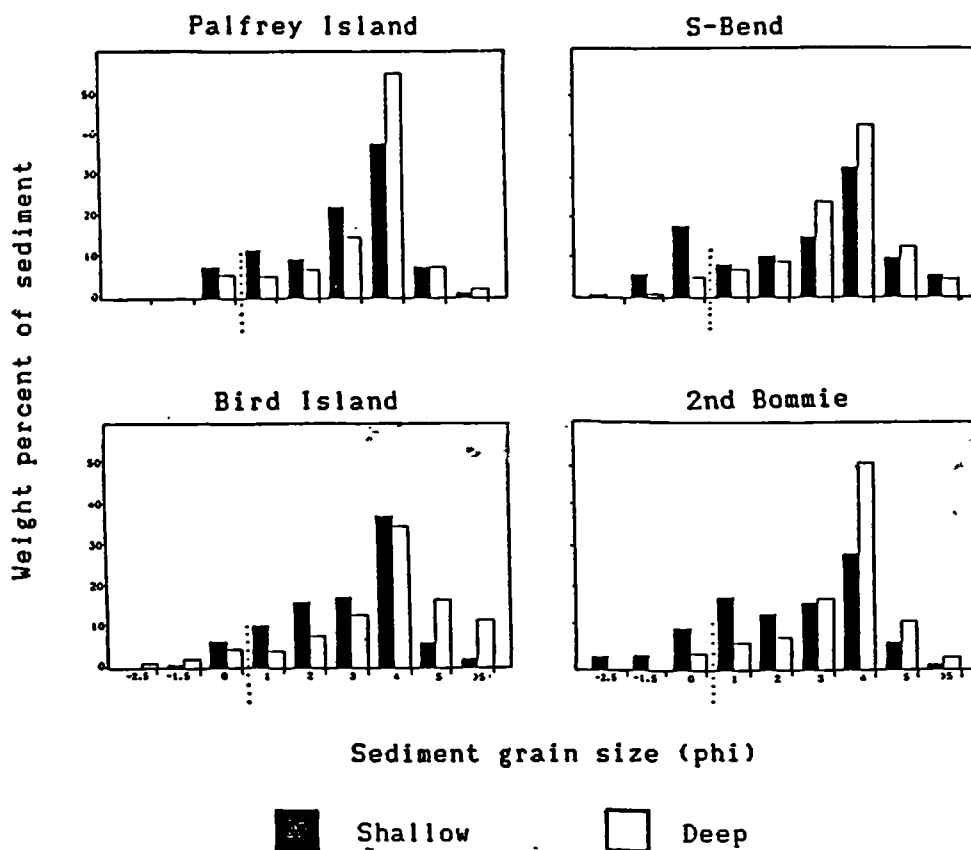
Figure 5.5. Size distributions of substrate sediments at each site in each Exposure region (n=2 per depth). NB: note that size categories for negative phi ()1mm) are broader than for positive phi (at the dotted line).

Size equivalents. phi to um: -2.5=5mm, -1.5=2.8mm, 0=1mm, 2=250um, 3=125um, 4=63um, 5=31um.

WINDSPEEDS FOR JANUARY-FEBRUARY 1989
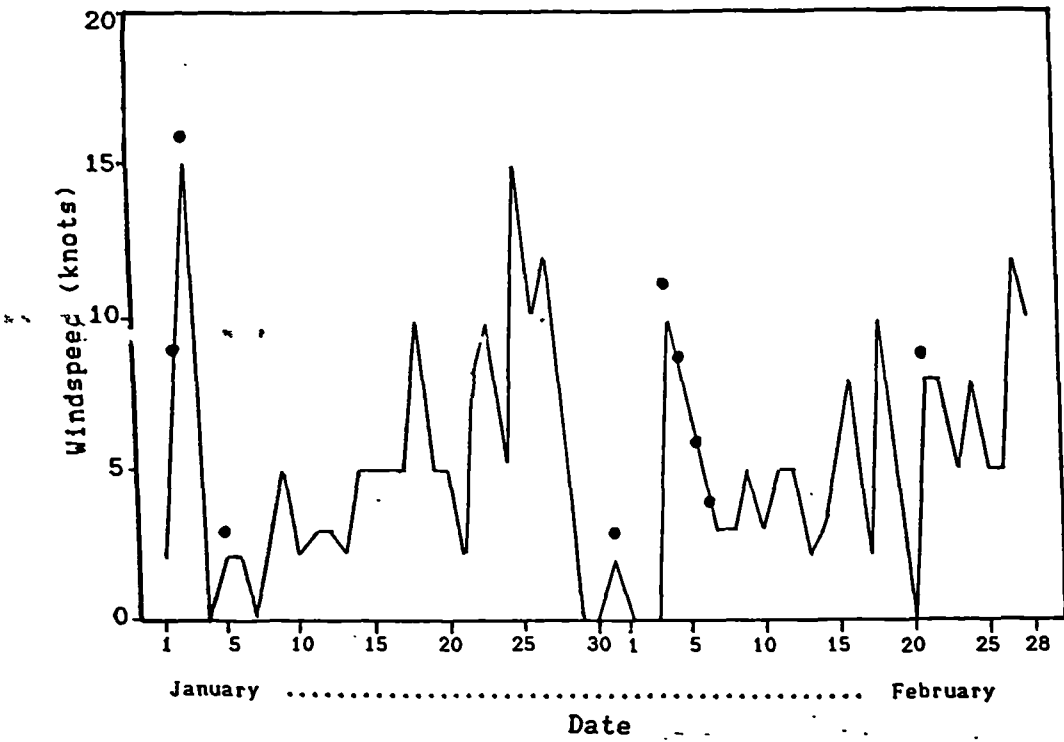
Figure 5.6. Windspeeds (knots) for Cooktown during January and February 1989. Windspeeds at Lizard Island were generally at least 5-10 knots stronger but followed a similar pattern.

• denotes NW winds. At all other times the wind direction was SSE to E.

In all regions, there was a tendency for sediments from greater depths to be comprised of a higher proportion of fine sediments than those at shallower depths.

Downward sediment flux. Recorded daily sedimentation rates were generally below $22mg.cm^{-2}.day$ (Table 5.3), but during a period of strong south-east winds towards the end of January (Figure 5.6) traps in Coconut Bay collected large quantities of sediment, more than 60% of which was comprised of foraminifera grains of between 1 and 2.8mm (principally 1-2mm). The trap was located in a section of reef that may have been subject to some surge, but target corals (including *Porites* spp., *Leptoria phrygia*, *Favia stelligera*, *Symphyllia radians*, Chapters 2 & 3) were located alongside the traps and therefore the trap location cannot be considered as inappropriate. One Watson's Bay trap collected over $50mg.cm^{-2}.day^{-1}$ during a period of strong north-west winds, but as this level was not replicated in the paired trap, it may have been a localised effect. Sampling frequency was inadequate to make detailed comparisons between the regions, but as expected, Watson's Bay sites collected more sediment during north-west winds than during south-east winds of similar force.

Ecological parameters

Coral cover, and abundance of target species. Percentage coral cover varied from 17.9% at Site 5 in Watson's Bay, to 68.8% in a multispecific thicket of densely branching corals at Site 9 in the lagoon. Mean coral covers (+SE, n=3) for each depth, at each site are given in Figure 5.7. Analysis of variance indicated that there were significant differences in coral cover between different Exposure regions, and also between Sites within each Exposure region (Table 5.4). Some interaction was present between Sites and Depth ($p<0.05$) but there were no overall differences in coral cover between the two depths. Further analysis indicated that differences between Exposure regions were primarily due to significantly lower coral cover in the Moderately-exposed sites than either the Exposed or Lagoon sites. There was no difference in cover between the latter two groups ($p>0.10$).

Site	Trap	Date	Days	Wind Speed	Dir'n	Sediment deposition $(mg/cm^2.day)$	Dominant grain size
NthPnt	1	16Jan-22Jan89	6	Mod	SE	11.1	63-125um
	2	16Jan-22Jan89	6	to		7.2	63-125um
Coconut	5	16Jan-22Jan89	6	strong		94.2	500um-1.5mm
	6	16Jan-22Jan89	6			86.7	500um-1.5mm
NthPnt	1	22Jan-28Jan89	6	Very	SE	18.6	63-125um
	2	22Jan-28Jan89	6	strong		22.1	63-125um
Coconut	5	22Jan-28Jan89	6			658.3	1-2mm
	6	22Jan-28Jan89	6			583.9	1-2mm
Watson's	9	20Jan-28Jan89	8	Very	SE	4.0	<125um
	10	20Jan-28Jan89	8	strong		6.5	<125um
Lagoon	13	20Jan-28Jan89	8			21.7	<63um
	14	20Jan-28Jan89	8			16.7	<63um
NthPnt	1	31Jan-07Feb89	7	Calm	Principally	15.2	63-250um
	2	31Jan-07Feb89	7	to	NW	21.4	63-250um
Coconut	5	31Jan-07Feb89	7	strong		11.8	125-500um
	6	31Jan-07Feb89	7			9.8	125-500um
Watson's	9	31Jan-07Feb89	7			22.0	63-250um
	10	31Jan-07Feb89	7			52.2	63-250um
Lagoon	13	31Jan-07Feb89	7			9.9	<63um
	14	31Jan-07Feb89	7			17.0	<63um
NthPnt	1	07Feb-17Feb89	10	Calm	Variable	4.7	<63um
	2	07Feb-17Feb89	10	to		3.9	<63um
Coconut	5	07Feb-17Feb89	10	light		6.1	<125um
	6	07Feb-17Feb89	10			5.1	<125um
Watson's	9	07Feb-17Feb98	10			Lost	
	10	07Feb-17Feb98	10			11.3	<63um
Lagoon	13	07Feb-17Feb98	10			14.7	<63um
	14	07Feb-17Feb98	10			18.4	<63um

Table 5.3. Sediment deposition rates and principal size classes for Lizard Island sites during January and February 1989. All traps were located at approximately 2-3m depth on sand substrate directly adjacent to living corals. Trap apertures were 20-25cm above the substrate.

PERCENTAGE CORAL COVER
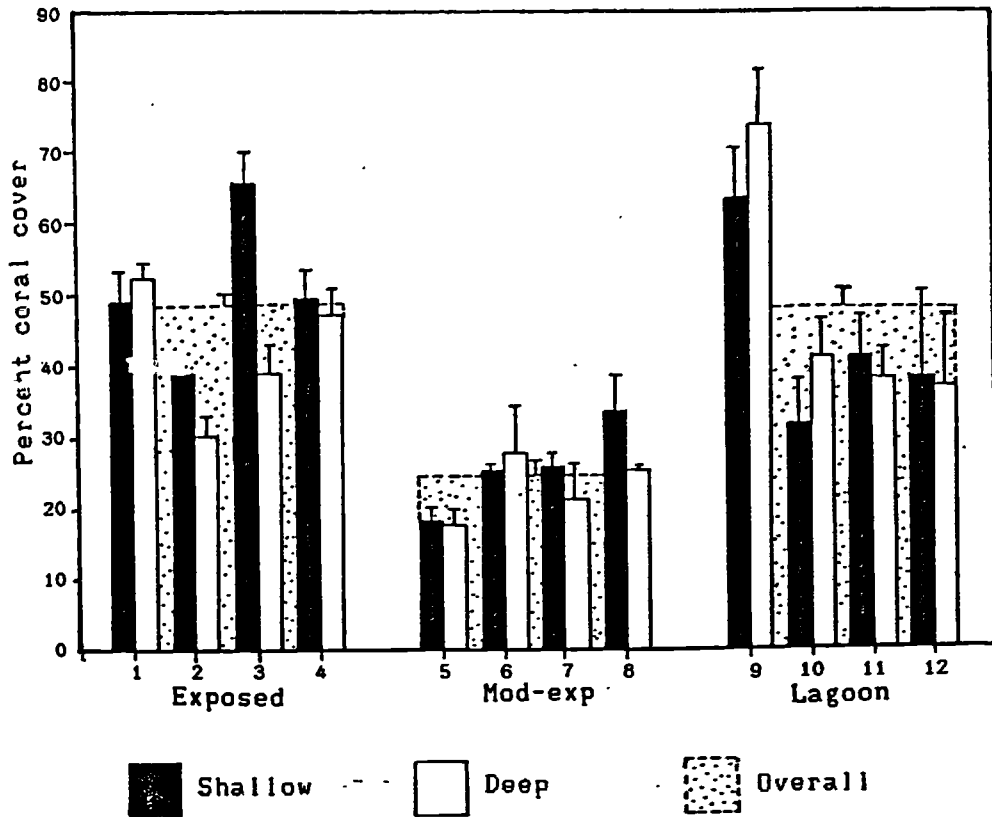
Figure 5.7. Mean percentage coral cover at each site (+SE, n=3 per depth per site). Overall mean (+SE) for each region is shown in light shading behind.

PERCENTAGE CORAL COVER AROUND LIZARD ISLAND

Analysis of variance

Model: Nested 2-way analysis of variance. SITES nested within EXPOSURE, fully crossed with DEPTH

Source		df	Error	Error df
A	Exposure	$(a-1)$	B(A)	$a(b-1)$
B(A)	Sites	$a(b-1)$	Residual	$abc(n-1)$
C	Depth	$(c-1)$	B(A)*C	$a(b-1)(c-1)$
A*C	Exposure*Depth	$(a-1)(c-1)$	B(A)*C	$a(b-1)(c-1)$
B(A)*C	Sites*Depth	$a(b-1)(c-1)$	Residual	$abc(n-1)$
	Residual	$abc(n-1)$		

Where a=the number of exposure categories (3); b=the number of sites within each exposure category (4); c=the number of depth categories (2); and n=the number of transects within each depth at each site (3).

Source	SS	df	MS	F	p	
Exposure	3377.22	2	1688.61	8.65_9^2	0.008	**
Sites	1757.38	9	195.27	6.39_{48}^9	0.000	***
Depth	166.53	1	166.53	2.11_9^1	0.181	ns
Exposure*Depth	35.70	2	17.85	0.23_9^2	0.8	ns
Sites*Depth	711.65	9	79.07	2.59_{48}^9	0.016	*
Residual	1465.83	48	30.54			

Tukey 95%:	Exposed	Lagoon	Moderately exposed

Table 5.4. Analysis of variance to test for differences in coral cover between different exposure regions and depths. Coral cover was significantly lower at Moderately exposed sites than either Exposed or Lagoon sites. Analysis was carried out on arcsin-squareroot transformed data

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The abundance of selected species and species groups at each depth and site is summarised in Table 5.5. The table principally describes the presence and abundance of each species *within the sampled transects*, but where other species were observed immediately adjacent to the transect they have been marked with an asterisk. Some species were locally abundant outside the transects and these have been noted elsewhere in this thesis where relevant. Principal trends in abundance are outlined below, but further details of individual species distributions are given in Appendix A.

Gardineroseris planulata was restricted to Exposed sites. It only occurred on one transect (Site 2, Deep) and was otherwise observed, only very rarely, in shallow water on the reef edge between Pidgin Point and North Point. *Hydnophora microconos* was also only observed at Exposed sites but was fairly common in shallow water at all four sites. It did not occur on any of the deeper transects and was very rare at depths of more than 4m. Of the species selected for study, these two were the only species entirely restricted to Exposed sites. There were, however, a number of species which were much more abundant at Exposed sites than elsewhere, particularly *Acropora hyacinthus, Favia stelligera, Leptoria phrygia* and *Montastrea curta*. In addition to *G. planulata* and *H. microconos*, several other species were not observed in the central lagoon, either within or around the transects (*Acanthastrea echinata, Favia pallida, Leptoria phrygia, Montastrea curta, Plesiastrea versipora*, and *Turbinaria peltata*). Several of these species were present in peripheral areas, for example, between Palfrey Island and Research Point, or between Palfrey and South Islands, where the highly turbid lagoonal conditions were less distinct.

Branching *Porites* species (particularly *P. cylindrica* and *P. nigrescens*, but also *P. rus*) were much more abundant in the lagoon than elsewhere. Site 9 (Palfrey) in particular, was completely dominated by highly branching colonies of these species as well as large colonies of ramose *Pachyseris rugosa, Psammocora contigua, Echinopora mammiformis, Pavona cactus, Millepora* sp., and foliaceous (principally vertical plates) *Echinopora gemmacea*. At this site, there were almost no massive colonies of any species.

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Figure 5.8. Mean abundance of *Leptoria* colonies per 2x20m band transect at each site (n=3 per depth per site).

■ Shallow (1-2m)   □ Deep (4-6m)

LEPTORIA PHRYGIA: PROJECTED SURFACE AREA AS A PERCENTAGE OF TOTAL AREA
FOR EACH SITE AND DEPTH

	EXPOSED SITES			
	Coco1	Coco2	Cryst	NthPnt
Shallow	3.39×10^{-2}	2.88×10^{-2}	1.55×10^{-2}	4.30×10^{-2}%
Deep	4.46×10^{-2}	0.62×10^{-2}	0.41×10^{-2}	1.23×10^{-2}%
	MODERATELY EXPOSED SITES			
	Turtle	China	Osprey	Research
Shallow	0.12×10^{-2}	0.32×10^{-2}	0.08×10^{-2}	0.30×10^{-2}%
Deep	-----	0.02×10^{-2}	0	----- %

Table 5.6. Areal surface area of *Leptoria* as a percentage of total areal coral cover at each site and depth to demonstrate that reduced cover in Moderately-exposed sites in comparison to Exposed sites, cannot be explained by reduced overall coral cover.

'-----'   no colonies were recorded.
'0'   Colonies were recorded. but all were vertical and therefore did
          not contribute to horizontal coral cover.

Site 9 was quite distinct from the three other Lagoon sites in this respect as massive corals were common at Sites 10-12, though not as abundant as in Moderately-exposed and Exposed regions.

Abundance, size distribution and morphology of _Leptoria phrygia_. The distribution of _Leptoria phrygia_ was very different in each of the three Exposure regions (Figure 5.8). It was completely absent from all sites in the Lagoon, present in very low abundance in north-western sites, and relatively common at all Exposed sites. Percentage cover was calculated from the sum of areal dimensions for all colonies occurring within the $40m^2$ transect strip and expressed as a proportion of the recorded coral cover for the site[1]. When the abundance of _L. phrygia_ was expressed in this way it was clear that even accounting for the lower coral cover in Watson's Bay and other north western sites, cover of _L. phrygia_ was an order of magnitude lower in this region than on the exposed reef front (Table 5.6).

There were significantly more colonies per $40m^2$ at 1-2m depth than at 4-6m (see Figure 5.8) for (a) both Exposed and Moderately-exposed sites combined (Wilcoxon pairs, n=24, Z=3.71, p<0.001) and (b) each Exposure region separately (Exposed: n=12, Z=2.86, p<0.001; Moderately-exposed: n=12, Z=2.12, p<0.05). In contrast, there were no distinct trends in colony size with depth (p>0.10). The largest colonies (total surface area 5631 and $13964cm^2$) occurred on deep transects at Site 1, but otherwise large colonies ($>2000cm^2$) were more common on shallow transects. However, colonies of this size were exclusively restricted to Exposed regions, the largest colony on Moderately-exposed transects having a maximum total surface area of $931cm^2$.

There was a very significant difference in the crab and barnacle populations on _L. phrygia_ colonies between Exposure regions: no colony on Moderately-exposed transects was observed to contain any crabs or barnacles at all, but a majority of colonies (57%) from

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1.   Line intersect lengths for _L. phrygia_ along each 20m transect line had been recorded but incidence of the species was too low for statistical confidence and areal cover in the larger band transect was used instead.
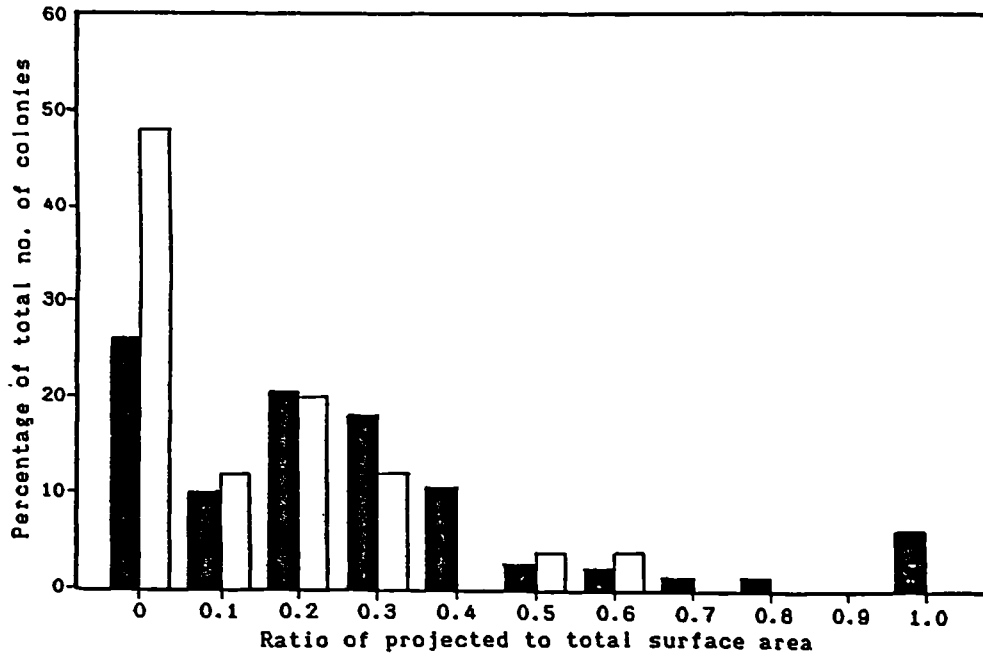
Figure 5.9. Relative proportion of projected to total surface area for *Leptoria* colonies in Exposed (n=292) and Moderately-exposed (n=25) regions. Colonies with a ratio of '0' have no projected surface area and are vertical. Conversely, all tissues of colonies with a ratio of '1' are horizontal.

■ Exposed sites   ☐ Moderately-exposed sites

Exposed regions contained crabs[1], and several contained barnacles.

There was a higher proportion of vertical colonies, and a bias towards greater vertical tissue overall, in Moderately-exposed sites than in Exposed sites (Figure 5.9). To test the significance of differences in orientation of colonies between the two regions, the number of colonies with areal to total surface area ratios of (a) 0 and >0, and (b) 0-0.1 and >0.1 for each region were recorded in two 2x2 contingency tables and tested by chi-square. In each case there were significant differences (for categories 0 and >0:   =5.335, df=1, p=0.0209; and for categories 0-0.1 and >0.1:   =5.306, df=1, p=0.0210) confirming that the number of vertical colonies, as a proportion of the total, was higher in Moderately-exposed sites than Exposed sites.

Sediment-trapping sections of tissue were entirely absent on all colonies from Moderately-exposed sites, whereas they were not uncommon in Exposed sites, occurring on almost 20% of all colonies (Table 5.7c). Nevertheless, they represented only a small proportion of the total tissue surface area (just over 1%, Table 5.7d).

Dead patches surrounded by living tissue were present in both Moderately-exposed (mean percentage of colonies with dead patches per transect: 24.0%; range: 0-50%) and Exposed regions (mean per transect: 39.4%; range: 4.5-59.5%). Colonies containing one to several remnants were present at approximately the same abundance in each region (Moderately-exposed 16.0%, Exposed 19.3%). The minimum size of remnants was 6cm^2.

The general size of colonies of *Leptoria* at the Cod Hole (outer barrier reef) was large (total surface area >1000cm^2 and up to 15,470cm^2), with few or no dead patches and extensive areas of flat or concave (potentially sediment-trapping) surface, often >400cm^2 in area.

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1. Mean density (±SE) on colonies containing crabs was $1.67 \pm 0.123 \times 10^{-2}$ crabs per cm^2 of living tissue surface area.

a) Total number of colonies of *Leptoria* recorded for each site
and at each depth (total sampled reef area)

	Coco1	Coco2	Cryst	NthPnt	All exposed Sites
Overall	89 ($240m^2$)	54 ($240m^2$)	74 ($240m^2$)	75 ($240m^2$)	292 ($960m^2$)
Shallow	56 ($120m^2$)	38 ($120m^2$)	52 ($120m^2$)	42 ($120m^2$)	188 ($480m^2$)
Deep	33 ($120m^2$)	16 ($120m^2$)	22 ($120m^2$)	33 ($120m^2$)	104 ($480m^2$)

b) Total tissue surface area of *Leptoria* (m^2) per $100m^2$ reef at
at each site and depth

	Coco1	Coco2	Cryst	NthPnt	All exposed Sites
Overall	2.78	0.84	1.11	1.93	1.67
Shallow	2.33	1.35	1.97	3.12	2.19
Deep	3.23	0.34	0.26	0.74	1.14

c) Percentage of the total number of *Leptoria* colonies with some
sediment-trapping sections of tissue (%)

	Coco1	Coco2	Cryst	NthPnt	All exposed Sites
Overall	13.48	12.96	22.97	28.00	19.52
Shallow	10.71	10.53	25.00	40.48	21.28
Deep	18.18	18.75	18.18	12.12	16.35

d) Proportion of the total tissue surface area of *Leptoria* which
was sediment-trapping (%) at each site and each depth

	Coco1	Coco2	Cryst	NthPnt	All exposed Sites
Overall	1.07	0.79	1.12	1.18	1.07
Shallow	1.39	0.84	0.99	1.38	1.21
Deep	0.84	0.59	2.11	0.31	0.81

Table 5.7. Sediment-trapping characteristics of *Leptoria phrygia* in
exposed regions. Sediment-trapping tissues were not observed on
colonies from any Moderately-exposed sites.

DISCUSSION

Physical parameters

Although full characterisation of sediment environments around Lizard Island was not an objective of this study, substrate sediment analysis and sediment trap data provided indications of local sediment sizes and some background information on the range of sedimentation rates. At Coconut Bay in particular, but in Exposed sites in general, the range of sediments available for local resuspension was biased towards coarse grain sizes (Figure 5.5a-1). This was reflected in the sediment sizes (1-2mm) predominating in traps over periods of strong south-east winds (Table 5.3) but, as expected, these larger sediments were not lifted to the same extent when winds were milder; under such conditions, settling sediment grain sizes were smaller. Substrate sediment sizes were relatively evenly distributed in Moderately-exposed regions and substantially biased towards finer sediments in the Lagoon. Traps in Watson's Bay during strong north-west winds collected considerably more sediment (22 and 52mg.cm^{-2}.day^{-1}) than during south-east winds of similar wind-speeds (4 and 6.5mg.cm^{-2}.day^{-1}) but in both cases dominant grain sizes were much smaller (63-250um) than in Coconut Bay. Lagoonal sites showed more consistent sedimentation levels for north-west and south-east winds and dominant grain sizes were yet smaller still (<125um). In each case, the size of settling sediments reflected, to some extent, the bias in substrate grain size.

At Coconut Bay and in several lagoon sites, substrate sediments were fairly well sorted. The predominance of large sediment sizes in Exposed sites, and smaller sizes in Lagoon sites, can be related to the difference in wave energy prevailing in each region. Orme *et al* (1974), in a study of the sediments of Lady Musgrove Island (southern Great Barrier Reef), found a similar trend for exposed and lagoonal sediments, as well as changes towards finer sediments with depth.

Marshall and Orr (1931) made a six-month study of sedimentation rates at Low Isles which are inshore islands approximately 180km south of Lizard Island. At most sites their sediment traps were in shallower

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water (0-2m) than those deployed at Lizard Island[1], but one trap (Site E on the north-west side of the island) was at a depth of 3.6m below mean sea level. Sedimentation levels at this site varied from 3.6 to 194mg.cm^{-2}.day^{-1}.[2] The modal rate was 5-10mg.cm^{-2}.day^{-1} (n=24), but rates of >20mg.cm^{-2}.day^{-2} occurred several times. Rates higher than 30mg.cm^{-2}.day^{-1} occurred on three occasions (91, 95, and 194mg.cm^{-2}.day^{-1}) and were all associated with northerly winds (to which this site would be particularly exposed), although northerly winds did not necessarily cause high sedimentation rates at other times. The highest rate, 194mg.cm^{-2}.day^{-1}, was linked to the highest northerly wind speed of approximately 17.5 knots. ·When wind speeds at Lizard Island were predominantly from the north-west, sedimentation rates were considerably lower than those at Low Isles recorded by Marshall and Orr (1931) at a maximum of 52mg.cm^{-2}.day^{-1}. Sedimentation in Watson's Bay during south-east winds was less than 10mg.cm^{-2}.day^{-1}, which is comparable with Site E at Low Isles under similar lee conditions.

It is interesting to note that Marshall and Orr (1931) also record extremely high levels of sedimentation at one southern site (Site B) exposed to south-east winds. Of a total of 25 records for this site, 13 were over 100mg.cm^{-2}.day^{-1}, with six of these over 300mg.cm^{-2}.day^{-1} (max. 900mg.cm^{-2}.day^{-1}, the highest levels occurring during periods of strong south-east winds). Marshall and Orr (1931) attribute the extreme sedimentation rates at this site to the existence of a surge channel, but they also imply that corals existed close by and these must, as in the present case in Coconut Bay, be tolerant of the highly abrasive effects of large suspended sediments.

Long-term sedimentation rate studies have been carried out on the inshore fringing reefs of Magnetic Island, off Townsville, Queensland (Willis, 1987). Willis found very high sedimentation rates of up to

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1. Direct comparison of traps from different depths must be treated with caution, particularly in areas where resuspension is significantly controlled by wave action. Wave energy is attenuated with depth and depth will therefore affect both the particle size and quantity of sediment moved. See, for example, Reineck and Singh (1980) and Leeder (1982) for a discussion of the dynamics of sediment transport.

2. Marshall and Orr (1931), Table II. Rates have been calculated from total amount of sediment in grams (column 3) divided by the product of the number of days deployed (normally 7) and the sediment trap aperture area of 44cm^2.

280mg.cm^{-2}.day^{-1} at 1m sites and just under 100mg.cm^{-2}.day^{-1} at 4m[1]. In view of the fact that these figures represent means over sampling periods of an average of 56 days, it is very probable that influxes over shorter terms were much greater.

Both Low Isles and Magnetic Island are nearshore, and their reefs are subject to much greater terrigenous influence from topsoil erosion than Lizard Island. Magnetic Island is also affected by dredging of the harbour channel and surrounding area, and might be expected to have higher general sedimentation rates than Lizard Island sites as a result.

Secchi disc readings and PAR attenuation coefficients indicated that, at least during summer months, light penetration was lower in Lizard Island lagoon than in other regions. Attenuation coefficients recorded by Barnes and Crossland (1983) across the reef from South to Bird Islands and into the Lagoon encompass the range of coefficients found in the present study (0.092-0.191m^{-1})[2].

To summarise, divisions of Lizard Island sites into three categories of exposure with a correlated gradient of sediment influence (from Lagoon, through Moderately-exposed sites to Exposed sites) is reflected in the physical data reported here. However, these data are insufficient to fully characterise the sedimentation and turbidity regimes of these regions, making it difficult to separate the influence of settling sediment from that of turbidity. Nevertheless it seems probable that the *type* of sediment influence varies from one region to another. A summary of the most important regional characteristics relevant to the present study is given in Table 5.8. Some Exposed sites are clearly subject to very heavy sedimentation loads, but fine sediments are less abundant and resuspension of coarse sediment will tend to occur only during strong winds, when residence times will be low

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1.   Calculated from Figure 14, p.41 in Willis (1987), corrected for 56 day period and trap aperture of 7.07cm^2.

2.   Barnes and Crossland (1983) actually report attenuation coefficients (E$_d$) from log$_{10}$ rather than log$_e$ (=ln) plots. These can be converted by the equation

$$Kd = \frac{Ed}{\log_{10}e} = \frac{Ed}{0.4342945}$$

MAIN CHARACTERISTICS OF THE REGIONS OF LIZARD ISLAND

Exposed

Substrate sediments:	Coarse
Abrasion:	Probably consistently high during winter, less severe during summer.
Turbulence:	High and persistent during winter, occasionally high during summer
Sedimentation rates:	Periodically high, probably particularly during winter, but concurrently high turbulence and therefore high passive sediment loss. Low sedimentation rates of small sediment sizes
Light:	High incident light levels in summer, moderate in winter

Moderately-exposed

Substrate sediments:	Mixed
Abrasion:	Fairly low in winter, occasionally fairly high in summer during strong NW winds
Turbulence:	Moderate in winter, occasionally high in summer during strong NW winds
Sedimentation rates:	Uncertain, probably consistently moderate during winter, fairly high during summer NW winds.
Light:	Probably more consistently moderate year-round than other regions.

Lagoon

Substrate sediments:	Predominantly very fine
Abrasion:	Low all year
Turbulence:	Low all year
Sedimentation rates:	Uncertain, probably consistently moderate all year
Light:	Low all year with the exception of periods of summer calm

Table 5.8. Environmental conditions in each of the three exposure regions of Lizard Island.

due to turbulence. Corals in these regions will be subject to relatively heavy abrasion from the effects of 'sand-blasting'. Sediment resuspension may have a strong influence on coral distribution by restricting species that are intolerant of abrasion to regions remote from sediment patches. There is no experimental information about the tolerance of coral tissues to abrasion although several authors (Johannes, 1975; Loya, 1976; Rogers, 1983) have suggested that it may have an important effect on corals.

In the lagoon, sedimentation rates were much lower, even during strong winds. However, visibility was often very poor, particularly after strong winds, and the present results indicate that light attenuation is greater in this region than elsewhere. Turbidity may be particularly critical in the lagoon, but it is also possible that sedimentation may occur at a higher chronic rate, with longer potential residence times where turbulence is of less assistance in sediment removal. The combination of lowered energy input (due to light attenuation) and increased energy loss (due to sediment removal) may favour species that can photoadapt well and/or reduce energetic costs of sediment removal by strategies such as morphological adaptation-favouring passive sediment removal.

Sedimentation rates in Watson's Bay (Moderately-exposed) were moderately high during north-west winds but, though sometimes strong, these are normally sporadic and far less common or persistent than the south-east winds affecting Exposed sites. Sedimentation rates in this region were considerably lower during south-east winds. It does seem probable, therefore, that this region may be subject to lower overall sedimentation rates than the lagoon.

Species distributions

Reference to species distributions in relation to relevant aspects of sediment rejection and tolerance are given in Chapters 2-4 and draw on information contained within this Chapter. Of those species studied experimentally, the following correlations are some of the most significant.

Three species (*Leptoria phrygia*, *Favia stelligera*, and *Gardineroseris planulata*) were particularly sediment-sensitive in rejection efficiency experiments (Chapter 3). It is notable that *L. phrygia* and *G. planulata* are entirely absent from the Lagoon, and only one colony of *F. stelligera* was observed there. The two faviids are also much less abundant at Moderately-exposed sites than at Exposed sites.

Echinopora lamellosa and *Merulina scabricula* were also sediment-sensitive (Chapter 4) but were present in all habitats. The colonies of both these species were more acutely angled in Lagoon sites, but *E. lamellosa* always had regions of dead skeleton and probably tolerates death of parts of the colony, relying on a growth strategy to overcome sedimentation problems.

Mycedium elephantotus, which also suffered some tissue death during field experiments, was not common in any region and was not observed on Moderately-exposed transects, although it was observed, rarely, on some coral outcrops. It was only abundant in gullies cutting into the north-eastern facing reefs between Pidgin and North Points. The distribution of this species was not clearly related to sediment-related characters of the environment.

Pectinia lactuca was only found in abundance in north-eastern gullies, usually only one colony being observed on transects. This species is a very strong sediment rejector (Chapter 2), normally displays morphologies assisting passive sediment removal (Chapters 2 & 4), and is relatively tolerant of heavy loads of overlying sediment where morphology is less favourable (Chapter 4). These characteristics argue that *P. lactuca* should be relatively well adapted for lagoonal conditions. In fact, only very small colonies were observed in the Lagoon of Lizard Island, but *Pectinia* is known to occur in abundance in highly turbid waters in other regions of the Great Barrier Reef (Veron, 1986).

Diploastrea heliopora is a good sediment rejector (Chapter 2) and sediment-tolerant (Chapter 4). As expected from these characteristics, it was present in all regions, but was less common in the Lagoon than elsewhere. *Porites* is also sediment-tolerant in the medium term

(several days, Chapters 2-4), and thus might be expected to be relatively abundant in areas of high sediment load. At Lizard Island *Porites* was common in all habitats but branching species became progressively more abundant than massive species from Exposed to Lagoon sites.

Fungia repanda was not distinguished from *F. concinna* during field surveys but the species pair was more common in Exposed sites than elsewhere, and rare in the Lagoon. It generally occurred on semi-consolidated coral rubble, several metres away from sand patches. As discussed earlier (Chapter 4), Schuhmacher (1977, 1979) found that several ciliary rejectors amongst the fungiids became exhausted if rejection had to be maintained for long periods of time. It is possible that persistent chronic sediment resuspension of fine sediments has a similar effect on *F. repanda/concinna*, restricting its distribution in the lagoon at Lizard Island.

Morphological variations in *Leptoria phrygia*

There are detectable differences in the abundance, the ratio of projected to total surface area, and the extent of sediment-trapping tissues of *Leptoria phrygia* across the range of habitats studied. *L. phrygia* is most abundant in Exposed sites, where it has a larger mean colony size than in Moderately-exposed sites. It is also completely absent from the Lagoon. The extent of potentially sediment-trapping tissue also shows a definite decrease from the outer barrier reef, through Exposed Lizard Island sites, to Moderately-exposed sites. These changes in abundance and morphology suggest that distributions of *L. phrygia* are strongly related to sediment regime.

The morphological plasticity of corals is a well-documented phenomenon and the huge intraspecific variation has, historically, caused serious problems for coral taxonomists. Many growth forms show a flattening response with depth which is assumed to be an adaptation to maximise interception of light (e.g. Goreau, 1959; Dustan, 1975; Graus & Macintyre, 1976, 1982; Jaubert, 1977; Wallace, 1978; Veron, 1981; Fricke & Schuhmacher, 1983). Some branching species (particularly from the Pocilloporidae and Acroporidae) show characteristic variations in the thickness and spacing of branches in response to degree of hydrodynamic

energy (e.g. Veron & Pichon, 1976; Roberts *et al*, 1977; Oliver *et al*, 1983; Veron & Wallace, 1984). In response to sedimentation, the change in morphology normally decreases the tissue area intercepting downward sediment flux, leading to communities dominated by finely branching, columnar and vertical growth forms (e.g. Marshall & Orr, 1931; Maragos *et a*, 1970; Loya, 1976; Randall & Birkeland, 1978; Veron, 1981; this study).

As coral growth is relatively slow (from millimetres to several centimetres per year), gross growth-form changes in the community will not normally be useful indicators of environmental change on time scales of days or months. However, morphology can reflect the overall environmental conditions prevailing in a community and may be particularly useful in sedimentation studies. There is an interesting conflict between the response to sedimentation and to light: the first tending to force morphology into the vertical plane, and the second, to the horizontal plane. Some species may respond more readily to one than the other, depending perhaps on their dependence on autotrophy, or on suspension feeding. The result is that the morphologies of a small suite of species may have the potential to describe the ambient light and sediment regimes of an environment. A serious problem in impact studies where the possibility of increased sedimentation is involved, is the gathering of turbidity and sedimentation rate data that is meaningful, since these vary tidally, seasonally, in relation to the return time of cyclonic events, or in relation to rainfall. But targeted morphological studies of a few species could be carried out in a short period to provide an integration of these variations.

Based on the fact that *Leptoria phrygia* is not tolerant of overlying sediments, a number of predictions were made for this species across sediment gradients. This study has shown that some morphological characters of *L. phrygia* do behave in predictable ways and suggests that morphological characters of sediment-sensitive species do have real potential. Further studies focussed on morphological characters of sediment-sensitive species which are present in inshore waters (such as *Echinopora lamellosa*) may reveal other species that can integrate effects of both turbidity and sedimentation and be useful environmental descriptors.

SECTION II

CHAPTER 6

(A)

METHODS IN HARD CORAL TISSUE ANALYSIS I.

TISSUE RECOVERY BY THE WATERPIK METHOD

METHODS IN HARD CORAL TISSUE ANALYSIS I.
TISSUE RECOVERY BY THE WATERPIK METHOD

SUMMARY

This study describes a freeze-thaw modification of the WaterPik technique (Johannes & Wiebe. 1970) to improve tissue recovery for biomass analyses in the hard coral *Leptoria phrygia* (Ellis & Solander, 1786).

Isolation of *Leptoria* coral tissue with its endosymbiotic zooxanthellae is hindered by the presence of skeletal algae (*Ostreobium*), and renders unsuitable those methods of tissue recovery that would combine skeletal and tissue components. The standard waterpikking method of Johannes and Wiebe (1970) as applied to *fresh* specimens of *Leptoria* is shown to recover only 49.1% of the zooxanthellae, 44.4% of zooxanthellar chlorophyll *a*, and as little as 16.6% of tissue lipid. The proportions of chlorophyll *a* and zooxanthellae recovered were not significantly different, but that of lipid was very significantly lower ($p < 0.001$) suggesting that this component has a different distribution through the tissues.

In contrast, when the corals were subjected to a period at $-20°C$ (>24 hours) and re-thawed, tissue recovery using the waterpik technique was dramatically improved ($>95\%$) for all components investigated. Contamination from the skeletal algae was negligible. Examination of zooxanthellae following the freeze-thaw indicate that cell counts from tissue slurries waterpikked into seawater reflect true cell abundances but division rates and size determinations should be made with caution. Counts made from deionised water media following the freeze-thaw treatment are inappropriate. Contamination from the skeletal algae was negligible.

A freeze-thaw procedure. by improving tissue recovery from corals, may broaden the spectrum of species for which waterpikking is effective.

INTRODUCTION

The scleractinian coral, *Leptoria phrygia* (Ellis & Solander, 1786), is a massive meandroid faviid, occurring throughout the Indo-West Pacific and present on the reef crest and slopes of most non-turbid habitats on the Great Barrier Reef (Veron. 1986). Like many faviids (Jeffrey, 1968; Halldal, 1968) it contains a green band of Siphonales algae (*Ostreobium*) in the upper regions of its skeleton. This band may lie directly or, more rarely, many millimetres beneath the overlying coral tissue, and is also of variable thickness (approximately 2-10mm).

Any study of biochemical characteristics of coral tissues must necessarily overcome problems resulting from the intimate association of

these organisms with their underlying skeleton. For those species with skeletal algae, the problem is greatly increased as it is also necessary to isolate coral-zooxanthellae tissue from this component. One method that has become widely used since its introduction in 1970 is the use of a fine high-pressure jet of water from a 'WaterPik' or similar instrument, to strip coral tissue from the skeleton (Johannes & Wiebe, 1970).

There are few reported tests of tissue recovery using this method, and those which do exist depend upon the visual absence of tissues rather than a biochemical analysis (e.g. Johannes & Wiebe, 1970; Davies, 1984). Nevertheless, when fresh specimens of a number of coral species are exhaustively waterpikked, the resulting skeletons are visually very clean. This has led to a general consensus that for certain taxa (notably the pocilloporids) the method recovers a sufficiently high proportion of the total living material for quantitative biomass analyses (e.g. Davies, 1984; Porter et al, 1984; Gattuso, 1985; Hoegh-Guldberg & Smith, 1989; and others). For other species. where tissues occur deep within a coral skeleton, or where they are strongly bound, it is clear that the waterpik method recovers an unacceptably low fraction. Johannes and Wiebe (1970) discuss this question for a number of Pacific and Caribbean species and divide corals into three groups on the basis of tissue recovery. Their observations indicated that for only about a third of the species was recovery adequate for quantitative biomass determinations.

Early tests with *Leptoria* in this study suggested that even very extensive waterpikking of fresh colonies resulted in incomplete recovery of tissue. On the other hand, it was observed that the tissues of pre-frozen *Leptoria* colonies had broken down substantially and when waterpikked were very much easier to free from the skeleton. Furthermore, in contrast to the fresh specimens, resulting skeletons were visually tissue-free.

The investigations described below were undertaken to test the tissue recovery from *Leptoria* after a freeze-thaw treatment against tissue recovery when individuals were waterpikked fresh.

MATERIALS AND METHODS

All specimens of *Leptoria phrygia* were collected from 2-5m depth on the exposed fringing reefs of Coconut Bay, Lizard Island[1], a mid-shelf, continental island of the northern Great Barrier Reef, Australia.

Ten independent samples of *Leptoria phrygia* (corals 1-10) were removed from the field 11 weeks following spawning and immediately waterpikked into 300-600ml Whatman GF/F ($\approx$ 0.7um) filtered seawater. Tissue recovery was improved and standardised by a consistent schedule of scrubbing with a non-flexible toothbrush followed by waterpikking. A scrub/pik cycle was carried out until all obvious surface tissue had been removed or until waterpikking resulted in no further recovery. The skeleton was then frozen at -20°C, thawed (2 hours) and re-waterpikked into a similar volume of filtered seawater (no scrubbing with a toothbrush was required). For slurries from both fresh and frozen corals the filtered seawater was divided into four portions. The first portion was continually recycled through the waterpik until the majority of tissue had been removed and then poured into a separate container. Splashing was prevented by enclosing one hand and the coral in a plastic bag which was sealed around the wrist with a rubber band. The coral was re-pikked with the second volume, again recycling the water. The third and fourth volumes were used for final cleaning of the coral, plastic bag, and the waterpik itself.

Each tissue slurry (pre- and post-freezing) was subjected to an identical schedule for the determination of constituents (Figure 6a.1). The tissue slurries were homogenised (2 minutes), their volume measured, and samples taken for chlorophyll, lipid, and zooxanthellae number analyses. Care was taken to keep the slurry thoroughly mixed prior to each sample removal.

Analytical methods

Tissue chlorophyll. Three 5-10ml samples of homogenised tissue slurry were immediately vacuum filtered through 2.5cm Whatman GF/C filters.

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1. For further details of the collection habitat, see General Introduction and Chapter 5.

BIOCHEMICAL ANALYSES
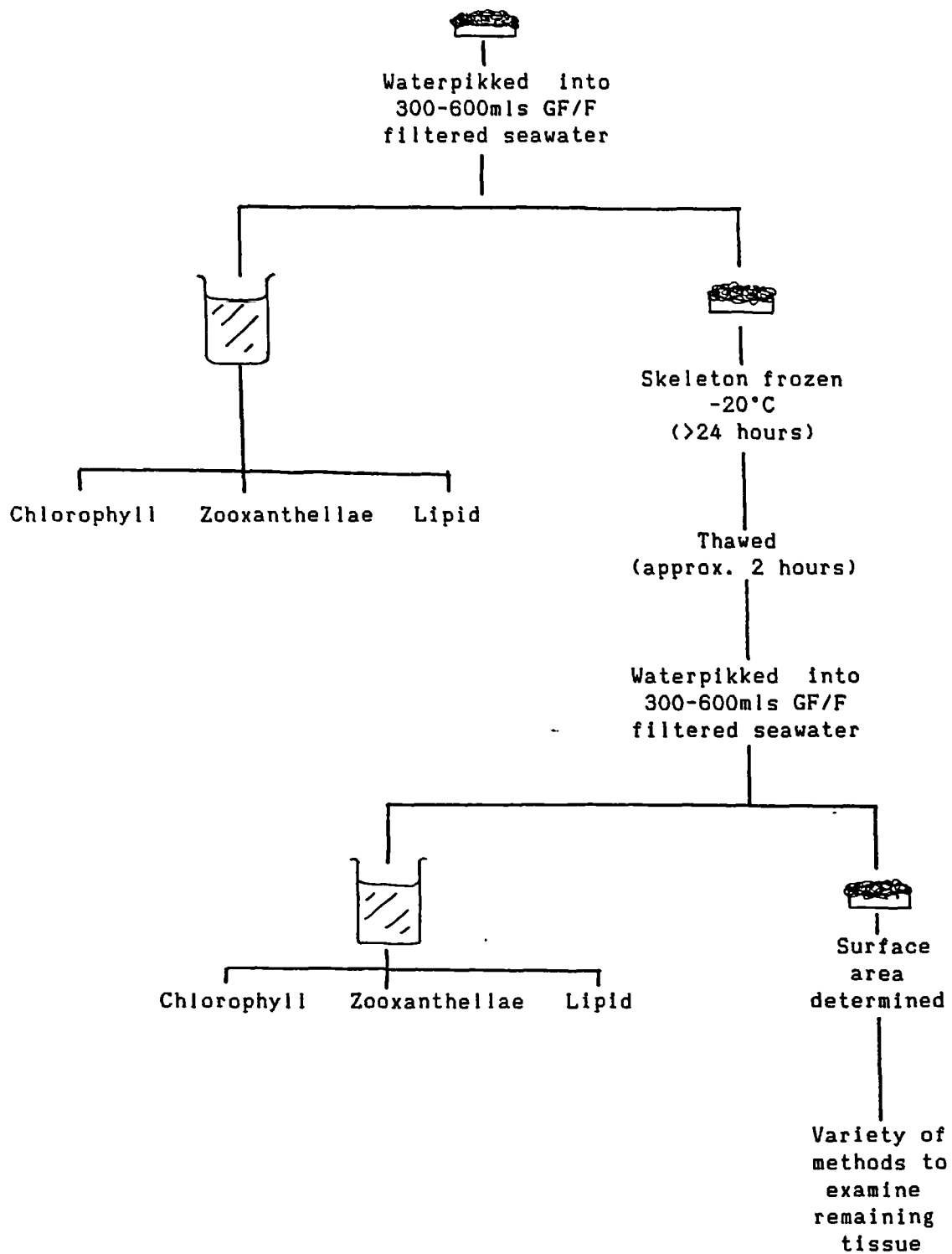
Figure 6a.1. Schedule for biochemical analyses of *Leptoria phrygia*.

Filters with residues were frozen in labelled and capped plastic petri dishes for later analysis. All stages of analysis and storage were carried out in subdued lighting or in the dark.

Filters were crushed and ground into 4ml of 100% AR acetone solvent in a glass pestle and decanted into re-calibrated, graduated test-tubes[1]. Solvent was made up to 4ml, the tubes were capped with parafilm, and the mixture centrifuged at 2,400 x g for 15 minutes. Absorbance was read at 663 and 630nm on a Varian scanning spectrophotometer. Pigment concentrations were estimated by the equations of Jeffrey and Humphrey (1975).

Zooxanthellae. Two 10ml portions of homogenised tissue slurry were each added to 2ml of 5% formalin in seawater. Eight counts of zooxanthellae per portion (16 in total per coral) were made in a Neubauer haemacytometer.

The effect of freeze-thaw on zooxanthellae was examined by counting the numbers of distorted and broken cells as a proportion of the total. The three treatments were a) fresh specimens waterpikked into filtered seawater; b) frozen and thawed specimens waterpikked into filtered seawater; c) frozen and thawed specimens waterpikked into deionised water. An additional 0.35mg NaCl was added without delay to the deionised water samples of the third treatment to improve the osmotic gradient and reduce disruption of zooxanthellae.

Six corals were used for each treatment. For each replicate, a total of 200 cells across both chambers of the haemacytometer were counted and scored as 'normal', 'distorted' or 'broken'.

Lipid. Four 10ml aliquots of tissue homogenate were transferred to tared scintillation vials and frozen at <-20°C within 15 minutes of waterpikking. Each sample was lyophyllised to constant weight

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1. Re-calibration was necessary as the graduated tubes available were found to show errors of almost ±10% on 4ml.

(approximately 60 hours). In each of the freeze-dried samples, the tissue was ground to a powder and lipid extracted in 2:1 chloroform:methanol (v:v) (based on Folch *et al*, 1957). Determination of lipid for the very low concentrations in the freeze-dried tissues (≃400-4000ug) was carried out by the spectrophotometric sulphophosphovanillin method described for marine invertebrates by Barnes and Blackstock (1973). The detail and a discussion of both the extraction and colour determination methods as they were applied to *Leptoria* is described in Chapter 6*b*. Two minor methodological deviations apply here: (a) the solvent/tissue mixture underwent a 5 minute sonication following addition of the initial 15ml chloroform:methanol and again for the 5ml 2:1 wash to ensure that all lipid had been extracted from the zooxanthellae; and (b) additional GF/F-filtered seawater blanks were taken through the whole procedure to control for lipid contamination from this source.

Surface area. Surface area determinations of all coral skeletons were made by the tin-foil method of Marsh (1970).

Tissue remaining in the skeleton following fresh and freeze-thaw treatments (corals 1-10)

After both fresh and freeze-thaw treatments, the tissue remaining in the skeleton was examined in three ways. (a) Slices were made at random through three skeletons (corals 1, 3 & 4) and the sections were assessed under a binocular microscope. (b) Three of the remaining samples (corals 5, 6 & 7) were refrozen (i.e. for a second time), re-thawed and waterpikked exhaustively into 50ml filtered seawater. These tissue slurries were subjected to the full analyses (Figure 6*a*.1) although replicates were reduced to one chlorophyll (20ml), two lipid (10ml), and one zooxanthellae (10ml) aliquot per coral. (c) In contrast to the findings of Jeffrey (1968) for *Favia* sp., it was not possible to slice *Leptoria* samples horizontally and separate skeletal algae from coral/zooxanthellae tissue without contamination. Generally the skeletal algal layer was beneath but almost continuous with the tissues above and in no specimens was it absent. In rare cases where the layers were divided by a few millimetres, the division was sporadic and the hillocky morphology of the skeleton prevented a clean

separation. However, for two skeletons (corals 2 & 8) morphology allowed part of the upper section to be removed. After surface area determination, each was broken up into small pieces and immersed in 15mls of 2:1 chloroform:methanol at 4°C overnight, prior to an otherwise identical schedule for lipid analysis. Chlorophyll and zooxanthellae analyses were not carried out on these samples.

Contamination from skeletal algae

To confirm that, following a freeze-thaw, the waterpik jet would not dislodge skeletal algae in quantities that would cause significant contamination, two colonies (intact tissues and skeleton) were frozen at -20°C and, while still cold, the tissue and entire upper section of skeleton was sliced off (with a sharp blade, as rotary saws caused powdering of the surface). The cut was low enough that animal tissues were not obviously present and in such as way that the lower skeletal algae were exposed. When the skeleton had thawed, the exposed algae were waterpikked into 50ml seawater. 10ml subsamples of the slurry were freeze-dried for lipid and chlorophyll analyses as described previously.

RESULTS

The living tissue surface area of corals used for these analyses varied between 30-50cm^2 with one exception at 76cm^2. Data for all components and all tissue slurries were corrected for slurry volume and normalised to surface area (cm^2).

Efficiency of the freeze-thaw technique for tissue recovery

Tissue remaining in the skeleton following fresh and freeze-thaw treatments. Following a single freeze-thaw treatment, *Leptoria* tissues were much easier to remove, and the resulting skeleton was very clean. White tissue strands of a few millimetres in length were teased from the deep valley centres. These had never been observed when fresh specimens were waterpikked. Although the dark green band of skeletal algae was clearly visible no obvious coral

Coral replicate	Chlorophyll a %	Lipid %	Zooxanthellae %
1	55.07	15.00	41.70
2	47.13	31.90	64.54
3	57.73	16.60	50.07
4	73.80	24.67	52.80
5	47.08	14.23	63.97
6	27.98	14.06	54.78
7	25.17	11.32	33.41
8	35.64	14.14	38.08
9	52.87	23.47	58.54
10	23.89	8.66	33.63
Mean*	44.40	16.62	49.11
Range Max	73.80	31.90	64.54
Min	23.89	8.66	33.41

Table 6a.1. Recovery of tissue components from freshly waterpikked *Leptoria* as a percentage of the total recovered from fresh and frozen combined.

* For all tissue components. means have been calculated on arcsin-squareroot transformed data but are presented back-transformed.

ANALYSIS OF VARIANCE

Source	SS	df	MS	F	p	
Between components	2463.1	2	1231.6	21.88	<0.0001	***
Within components	1519.9	27	56.3			
95% LSD	Zooxanthellae	Chlorophyll		Lipid		

Table 6a.2. One-way ANOVA to test for differences between the proportions of chlorophyll, zooxanthellae and lipid recovered from colonies waterpikked fresh. 95% LSD indicates that there are no significant differences in the proportions of chlorophyll and zooxanthellae. . but that the proportion of lipid recovered is significantly lower.

tissues could be observed. On sectioning of the skeleton and microscopic examination, occasional tiny flecks of tissue could be detected. While these indicated that removal was not absolute, they were estimated to represent very much less than 5% and probably less than 1% of the total.

Lipid levels in the three slurries from the second freeze-thaw (corals 5, 6 & 7) were undetectable (detectable limits were estimated to be $\approx$0.6% of the 'total' component means). Similarly, chlorophyll levels were at the limits of reliable detection (detectable limit approximately 1%). Numbers of zooxanthellae were detectable for all three corals and represented 0.38% (range 0.13-0.54%) of the total.

Direct determinations of lipid remaining in the two sections of skeleton which could be separated with confidence from underlying skeletal algae (corals 2 & 8), gave values of 0.019mg.cm^{-2} and 0.058mg.cm^{-2} which represented 1.03% and 1.88% of the post freeze-thaw totals for each respective coral.

Contamination from skeletal algae. During waterpikking of skeletal algae many small pieces of aragonite were dislodged from the skeleton. These were green and clearly contained skeletal algae bound to skeletal fragments. They quickly sank to the bottom of the collecting container leaving the slurry suspension almost completely colourless. No attempt was made to collect any particles that settled out at the bottom as these would not have been dislodged during waterpikking of the intact coral tissue.

Chlorophyll a determinations for the two corals averaged 0.071±0.024ug.cm^{-2} (mean±SD) or less than 1% of the total from their respective coral tissues. Lipid levels were very low at 0.016±0.009mg.cm^{-2} or a mean of 0.64% of the coral tissue total.

Recovery efficiency from corals waterpikked fresh. In view of the above results, data given below are based on the assumption that tissue removal after the freeze-thaw process is substantially complete and that contamination from skeletal algae is negligible. When referring to a tissue component for a given replicate coral, the

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Treatment	Number of corals	Zooxs per coral	Mean % distorted (range)	p	Mean % broken (range)	p
Fresh (seawater)	6	200	2.42 (1.0-4.5)	\	0.08 (0-0.5)	\
				: p<0.01		: p<0.01
Frozen (seawater)	6	200	21.58 (11.5-27.0)	/ \	1.58[1] (0.5-3.5)	/ \
				: ns		: p<0.01
Frozen (deionised water)	6	200	29.50 (20.5-36.5)	/	31.25[2] (27.5-37.5)	/

Table 6a.3. Condition of zooxanthellae following different waterpikking procedures. Differences in the percentage of broken cells were examined by Mann-Whitney's rank test.

[1] No obvious zooxanthellae fragments in the tissue medium. Broken zooxanthellae had kinks or slight breaks in membranes and were not completely open.

[2] Many broken zooxanthellae have half or more of their membranes lost. Fragments of zooxanthellae were apparent in the tissue medium.

'total' is the sum of the estimate from the fresh tissue slurry plus that following the freeze-thaw.

The percentage of each component recovered by waterpikking tissues fresh was calculated for each of the ten replicate corals (1-10; Table 6a.1). For chlorophyll and lipid, the normality of the percentage data was improved by arcsin-squareroot transformation. These means are therefore calculated on transformed percentages but are presented back-transformed.

For all components, recovery from waterpik slurries of fresh coral specimens was very poor (<50% of the total). Furthermore, for all tissue components there was considerable variation in the recovery between replicates (Table 6a.1). It would therefore be inappropriate to use a correction term for analyses from fresh specimens for this species.

Whilst there was no statistical difference between the proportions of chlorophyll a and zooxanthellae numbers recovered (44.4% chlorophyll a; 49.1% zooxanthellae), lipid recovery was significantly lower at 16.2% (One-way ANOVA on transformed percentage data: Table 6a.2). This provides evidence that chlorophyll and zooxanthellae differ from lipid in their distribution through the coral tissue. There was no statistical difference in the chlorophyll c_2:a or chlorophyll a:zooxanthellae ratios between fresh and total tissue.

Effect of freezing on zooxanthellae

There was a significant and substantial increase in the distortion of zooxanthellae in seawater slurries as a result of the freeze-thaw (Table 6a.3; Mann-Whitney U=36, n1=n2=6, p<0.01). Whilst few of the cells were very severely distorted, it is important to note that when severe distortion did occur these cells were sometimes difficult to distinguish from dividing cells.

There was a significant but small increase in ruptured zooxanthellae of corals frozen prior to waterpikking into seawater (Mann-Whitney

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SUMMARY OF BIOMASS STATISTICS FOR *LEPTORIA PHRYGIA*

Component	n	Mean	SD	CV%
Zooxanthellae ($\times 10^6 . cm^{-2}$)	10	2.91	0.73	25.1
Chlorophyll Total ($ug . cm^{-2}$)	10	13.40	2.76	20.6
a	10	9.46	1.92	20.3
Lipid ($mg . cm^{-2}$)	10	2.99	0.68	22.8
Chl*a*/zoox. (pg/cell)	10	3.40	0.98	28.8
Chlc_2:*a*	10	0.41	0.07	17.0

Table 6a.4. Summary of biomass statistics for *Leptoria* based on 'total' recovery of components (fresh + frozen).

U=35.5, n1=n2=6, p<0.01). However, fragments of zooxanthellae cells
were not obvious in the medium and all but one of the broken cells had
only one small nick in the membrane and no obvious organelles exuding
from the cell. The percentage of cells that had completely
disintegrated appeared to be negligible.

Distortion of zooxanthellae was higher when waterpikking was carried
out into deionised water and almost one third of all zooxanthellae were
broken. Many zooxanthellae fragments were observed in the medium
indicating that the true percentage of broken cells might have been
considerably higher than those counted.

Summary of biomass parameters for *Leptoria*

The total chlorophyll, lipid, and zooxanthellae numbers per cm^2,
chlorophyll *a* per zooxanthella and chlorophyll c_2:*a* ratio for *Leptoria*
based on the means of corals 1-10 are summarised in Table 6*a*.4. In view
of the fact that all corals were collected from the same habitat and
depth, and on the same day, the high coefficients of variation
(CV=SD/mean%) emphasise the high level of natural variation between
individuals even under similar environmental conditions.

DISCUSSION

Data for *Leptoria* presented here show that freeze-thawing has a
profound effect on the recovery of tissue components. Not only was the
recovery of chlorophyll, zooxanthellae and lipid less than 50% of the
estimated total when fresh colonies were waterpikked, but there was also
great variation in recovery from coral to coral.

Although *Leptoria* has tissues grading into skeletal algae which
hinder empirical tests of remaining tissue components, the combined
evidence from the three methods used in this study supports the view
that the freeze-thaw technique recovers more than 95% of all tissue.
The adhesion of skeletal algae and skeleton seems very strong and
therefore is unlikely to present a contamination problem.

In order to be confident that tissue estimates reflect the true levels in the organism, the effect of the freeze-thaw process for each component must be addressed.

Zooxanthellae. The freeze-thaw caused a significant increase in distorted and ruptured zooxanthellar cells. However, the number of ruptured cells was small (1.58%) for tissue taken through the freeze-thaw process once and waterpikked into seawater and even these cells were damaged only very slightly. No zooxanthellar tissue was observed in the medium. and it was therefore concluded that the proportion of cells that had entirely disintegrated was negligible. Nevertheless, distortions caused by the freeze-thaw could cause confusion in identifying dividing cells, indicating that mitotic indices as well as zooxanthellae cell size or volume estimations should be carried out with caution.

Clayton and Lasker (1984) froze zooxanthellae pellets from the anemone *Aiptasia* which had previously been suspended in distilled water. They observed no lysis as a result of this treatment and they report that zooxanthellae from a number of anemones suspended in distilled water showed no lysis for more than 1.5 hours. In contrast, Johannes and Wiebe (1970) suggest that considerable lysis occurs in deionised water although they do not discuss the time course of damage. The present analysis showed that substantial and unacceptably high zooxanthellae cell damage occurred when corals were first frozen and thawed, and subsequently waterpikked into deionised water. This was despite attempts to improve the osmotic concentration as soon as possible. For studies which require cell counts, this procedure would be inappropriate.

Chlorophyll. Provided that the membrane structure of the photosynthetic unit is not disrupted, and the tissues are not exposed to light, the freeze-thaw itself should not affect the integrity of the chlorophyll molecules. Holm-Hansen and Riemann (1978) examined the effect of freezing on chlorophyll of phytoplankton which had been filtered onto Whatman GF/C glass-fibre filters and frozen for up to 3 weeks at -20°C. Their data showed no loss of chlorophyll as a

result of this treatment. Indeed, freezing is a frequent step in the analysis of chlorophyll (e.g. Barnes & Crossland, 1978; Falkowski & Dubinsky, 1981; Chalker et al, 1983; Kinzie et al, 1984; Streamer et al, 1986).

Lipid. Morris (1972), in a study of the effects of different preserving methods, concluded that lipids maintained at temperatures below -30°C do not alter significantly. It has since become generally accepted that rather than being the cause of lipid breakdown or alteration, freezing prevents their oxidation, and that temperatures of -20°C and colder are suitable for lipid storage up to several months (see Hopkins et al, 1984). During the present study, all periods of freezing were at -20°C or below and periods of exposure to air (during waterpikking, homogenisation, etc.) were kept to a minimum. However, in this case it was not the intention to examine lipids qualitatively. For detailed qualitative analyses it may be necessary for all steps (freeze-thaw, waterpikking and homogenisation, etc.) to be carried out in an oxygen-free atmosphere.

Increased yield of biomass components following freeze-thaw can be explained by the breakdown of tissues and cell membranes, and the greater ease with which tissues can subsequently be removed with a waterjet. Tissue breakdown has two primary causes. Firstly, the formation of ice crystals which can damage the membranes and organelles through simple volume changes. Secondly, temperature gradients set up during freeze-thawing create stresses through the tissues. As freezing takes place, the outer epidermis and tissues cool down first, setting up thermal gradients from the outer to the inner tissues of the polyps and from the outside to the interior of the skeleton. The mechanical stresses resulting from these gradients are heavily influenced by the type of freezing method used. A slower freezing rate would result in a smaller temperature difference from outside to inside, smaller thermal stresses, and would theoretically cause less mechanical damage. In the present study, ambient coral temperatures prior to freezing were approximately 27°C. The corals, which each had a volume of 70-110cm^3, were transferred to -22°C, and packed with other frozen materials. Under these conditions, the zooxanthellae were clearly protected from

breakdown stresses to a greater extent than the surrounding coral tissues. This is probably due to their spherical shape, their small size (about 10um), and the strength of their cell membranes. In theory, there should be a freezing rate for a coral tissue which optimises animal tissue breakdown with minimal damage to zooxanthellae. Freezing conditions during this study were probably close to optimum as only a very small increase in broken zooxanthellar cells was detected (see Table 6a.3).

An investigation by Streamer *et al* (1986) appears to be the only coral study that specifically refers to the recovery advantage of a freeze-thaw procedure. Snap freezing in liquid nitrogen was used to ensure instantaneous termination of metabolism or carbon exchange in *Acropora formosa*. Although freezing was not used as a forerunner to the waterpik technique, in the course of a number of tests to ensure that freezing would not affect later analyses the authors demonstrated an improvement in tissue recovery using Fluorinert and centrifugation. There are also a number of studies in which the purpose of freezing may have been to assist breakdown, *although this was not* actually discussed. For example, prior to extraction of chlorophyll from tissues of *Acropora acuminata*, Barnes and Crossland (1978) subjected each coral sample to two freeze-thaw treatments. Similarly, Falkowski and Dubinsky (1981) froze specimens in liquid nitrogen prior to direct chlorophyll extraction from the pocilloporid coral *Stylophora pistillata*. In both cases the freezing process would almost certainly have increased the breakdown of zooxanthellae and tissues and assisted the release of chlorophyll.

During the course of the present study there was some incidental evidence that even from the pocilloporid *Seriatopora pistillata*, the recovery of tissue could be improved by a little over 10% using a freeze-thaw procedure. There is some support for this view in the literature. Glynn and Krupp (1986) used waterpikking as an index of the ease with which the cushionstar coral predator *Culcita novaeguineae* could feed on coral tissues. From waterpikking fresh specimens, they recovered 0% (*Montipora verrucosa*) to 67.5% (*Pocillopora verrucosa*) of

the total organic matter[1]. Whilst their purpose may not have been to be exhaustive, it is of concern that such a high percentage (>30%) remained in *Pocillopora* after the waterpik treatment. In another study, Davies (1984) considered it necessary to narcotise *Pocillopora eydouxi* prior to waterpikking in order to achieve effective tissue removal.

For any coral, the proportion of tissue recovered will depend upon such factors as the depth and binding strength of tissues and the intimacy of the tissues with the skeleton. These may well vary substantially even within a species and, with additional differences in water jet quality between waterpik models, may account for some of the variability of tissue recovery described above. Nevertheless, as the pocilloporids are used extensively in physiological studies of corals, it would be advantageous to confirm the level of quantitative recovery of tissues by the waterpik technique prior to extensive work with these species.

On the other hand, where the effect of different experimental treatments on tissue component levels is examined and if the percent recovery is high (better than 90-95%), minor variation in the recovery is likely to be obscured by the wide natural variation between individuals. In the present study, the range is illustrated in Table 6a.4 where the coefficients of variation for chlorophyll, zooxanthellae numbers and lipid in *Leptoria* are more than 20% even for individuals collected from the same habitats at the same time of year. Data for tissue components for other coral species indicate that *Leptoria* is by no means atypical. Indeed, in many studies the variation is much greater. For example, *Stylophora pistillata* had a lower absolute level of chlorophyll *a* per cm^2 ($3.11\pm1.14ug.cm^{-2}$)[2] but a higher coefficient of variation (36.8%; Porter *et al*, 1984). In the same study, zooxanthellae numbers were also lower at $1.04\pm0.67 \times 10^6$ $cells.cm^{-2}$[3] but the CV is yet higher at 64.8%. This is not simply due to the low number of replicates

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1. These figures are deduced from calculations of (1 minus medians) from their Table VIII as a percentage of the (median) in their Table IV.

2. Porter *et al* (1984). Table 1: chlorophyll *a* per unit area for light-adapted corals $3.11\pm0.66ug.cm^{-2}$ (mean$\pm$SE, n=3) has been converted to mean$\pm$SD by multiplying SE by $\sqrt{3}$. CV=SD/mean%

3. Again SE has been converted to SD by the factor $\sqrt{3}$.

as the data from Falkowski and Dubinsky (1981) for this coral shows even higher variation with as many as 10 replicates (Chl $a.cm^{-2}$: CV=101%; Zooxs.cm^{-2} CV=62%)[1].

In summary, the improvement in recovery of the tissue components of *Leptoria* studied here as a result of freezing is highly significant. It is very probable that adaptations of this freeze-thaw technique could be usefully applied for a number of other tissue components such as protein, and to a wide range of other coral species.

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1. Table 1, light-adapted *Stylophora*, SE converted by $\sqrt{11}$.

CHAPTER 6

(B)

METHODS IN HARD CORAL TISSUE ANALYSIS II.

GRAVIMETRIC AND SPECTROPHOTOMETRIC DETERMINATIONS

OF TOTAL LIPID

METHODS IN HARD CORAL TISSUE ANALYSIS. II. GRAVIMETRIC AND SPECTROPHOTOMETRIC DETERMINATIONS OF TOTAL LIPID

SUMMARY

Gravimetric and spectrophotometric methods for the determination of total lipids are examined for the scleractinian coral *Leptoria phrygia* (Ellis & Solander. 1786). Specifically, this study describes the application of the sulphophosphovanillin assay (Chabrol & Charonnat, 1937), and uses this lipid-specific colour reaction to compare three chloroform:methanol lipid extraction methods.

The sulphophosphovanillin assay was found to be a useful alternative to gravimetric methods where total lipid values are expected to be low (<5mg). Where expected lipid levels are high enough for sufficient precision to be achieved through simple weighing techniques, gravimetric methods are recommended. Of the three solvent extraction combinations compared, the 2:1 unpurified chloroform:methanol (v:v) of Stimson (1987) was found to result in lipid estimates almost three times higher than purified chloroform:methanol extractions following procedures of Folch *et al* (1957) or of Bligh and Dyer (1959). Estimates from the two purified extractions showed no significant differences.

INTRODUCTION

Lipid is a dominant biochemical constituent that has both a structural and a storage role in the physiology and maintenance of the individual in a wide range of marine organisms (Lawrence, 1976). Lipids are known to be important both in structural and storage roles for coelenterates group (Bergmann *et al*, 1956; Patton *et al*, 1977; Zamer & Shick, 1989) and, in the hard corals, occur in both the tissues and skeletal matrix (Young *et al*, 1971).

A number of studies suggest that lipids constitute 25% or more of the dry weight of anemones (Bergmann *et al*, 1956; Blanquet *et al*, 1979; Kellogg & Patton, 1983). Although the majority of hard corals generally have somewhat lower lipid levels (Meyers, 1977; Szmant-Froelich & Pilson, 1980; Glynn *et al*, 1985; Chapter 6b) similar values have been recorded (Patton *et al*, 1977). Significantly, Patton and his colleagues have estimated that 75% of the lipid in *Pocillopora capitata* is storage lipid.

This study is concerned with methods for determination of total lipids. It was prompted by the need to quantify total lipids in an appraisal of the effect of sediment on the reef coral *Leptoria phrygia* (Chapter 7) which had previously been identified as a sediment-sensitive coral (Chapters 3 & 4). Although detailed qualitative analyses of lipid classes may be of subsequent importance in understanding the mechanisms of such stresses, estimates of total lipids still have an important role in studies of the gross effects of environmental parameters such as sedimentation.

Investigations of lipid content have been made using histological staining (Cook & Kelty, 1982; Kellogg & Patton, 1983; Wigglesworth, 1988) and CHN techniques (Gnaiger & Bitterlich, 1984; Zamer & Shick, 1989), but by far the most common techniques involve the extraction of lipid from tissue using various organic solvents and solvent combinations, followed by gravimetric, spectrophotometric, or chromatographic *analyses of the extract.*

A variety of extraction solvents have been used in the determination of lipids from coelenterate tissues (ethanol:ethyl ether: Patton *et al*, 1977; Patton & Burris, 1983; Patton *et al*, 1983; benzene methanolic KOH followed by petroleum ether: Meyers, 1977; chloroform-methanol: Blanquet *et al*, 1979; Szmant-Froelich & Pilson, 1980; Kellogg & Patton, 1983; Stimson, 1987). In recent years there has been some agreement that combinations of chloroform and methanol result in a more complete lipid extraction from animal tissues than other previously popular solvent mixtures (Sperry, 1955; Schmid, 1973; Christie, 1982) although even these solvents have some drawbacks (Schmid *et al*, 1973a&b). Two principal chloroform:methanol combinations have been used in coelenterate studies, namely 2:1 (v:v) chloroform:methanol based on the techniques of Folch *et al* (1957) and 1:2 (v:v) chloroform:methanol based on those of Bligh and Dyer (1959). In addition, Stimson (1987) used a curtailed version of the former method in which the methanol portion was not removed.

Stimson's work addressed a number of important questions including the changes in lipid levels over time, with planulation, and in relation to light. He used an unusual protocol for the estimation of total lipids: first fixing coral pieces in formalin, followed by extraction

using chloroform:methanol 2:1 (v:v) after which the entire extract was dried to constant weight. There are reasons to believe that formalin may not be an entirely satisfactory precursor for lipid analyses (Morris, 1972). But chloroform:methanol extracts contain numerous salts and non-lipid contaminants and these are normally removed by the addition of water or a salt solution before the solvent is dried and weighed. With suitable water volumes, the chloroform:methanol:water solution becomes biphasic, the methanol and water in the upper phase and the chloroform in the lower phase. Since the methanol:water phase has a higher affinity for the salts and non-lipid contaminants than chloroform, suitable ratios of these three liquids results in an essentially pure chloroform lower layer with almost all of the lipid, leaving methanol, water and non-lipid materials in the discarded upper phase.

At least two workers known to the author have followed Stimson's methodology in somewhat similar studies of lipid level changes under experimental conditions of stress (unpubl., *pers. comm.*). Furthermore, the results reported in Stimson's paper have great relevance to the sedimentation study for which these investigations of lipid methodologies were precursors. For these reasons, it was desirable to evaluate the method in relation to the more commonly used purified chloroform:methanol techniques. If the values were found to be *consistently* higher with low coefficient of variation (CV=SD/mean, as a percentage), a correction term could be applied to results reported using the method of Stimson, allowing direct comparison with other studies.

A second purpose of this work was to investigate methods for the total lipid determination of the hard coral *Leptoria phrygia*. A number of considerations in the study of this species demanded a method that could accurately quantify lipid levels as low as 0.1-5mg per sample. These included the necessarily small size of coral individuals (a constraint of the experimental set-up); the need to separate tissue from skeleton without skeletal contamination (discussed in Chapter 6a); constraints on time and space imposed by availability of equipment; and, in a situation where a number of assays (chlorophyll, protein, lipid, zooxanthellae numbers, etc.) were to be carried out on the same tissue,

the desire to avoid sequential assays on the same sub-sample (Hopkins *et al*, 1984).

At this level of sensitivity, accurate gravimetric determinations require sophisticated microbalances and there can be serious problems resulting from fluctuating water content. The sulphophosphovanillin assay of Chabrol and Charronat (1937) is a spectrophotometric technique and depends upon the reaction of lipid with sulphuric acid, orthophosphoric acid and vanillin to form a pink complex. It was developed for the medical determination of total blood serum lipids (Zollner & Kirsch, 1962; Drevon & Schmit, 1964) and can accurately detect microgram quantities of lipid. The method was used in a comparison of techniques for determining total lipids of marine invertebrates including two anemones and a sea pen (Barnes & Blackstock, 1973). Only one reference has been found to its employment in the determination of coral lipids (Glynn *et al*, 1985) and these authors do *not discuss the deta*ils of the method for corals.

As a lipid-specific colour reaction, the sulphophosphovanillin technique was used as a baseline against which to compare the solvent extraction methods. It is therefore discussed first in the following account.

METHODS

Samples of *Leptoria phrygia* were collected from 2-5m depth on exposed fringing reefs of Coconut Bay, Lizard Island[1], on the northern Great Barrier Reef, Australia. These colonies were maintained for up to several months in flow-through aquaria at Lizard Island Research Station prior to analysis.

Small coral colonies were briefly washed with distilled water and immediately frozen at -20°C for transport to the Australian Institute of Marine Science in Townsville, where subsequent analyses were undertaken.

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1. Further description of the collection habitat is given in the General Introduction and Chapter 5.

The sulphophosphovanillin technique

Corals were completely thawed, waterpikked (Johannes & Wiebe, 1970, as modified in Chapter 6a) into 300-500ml of recycled deionised water and homogenised for 2 minutes. The slurry volume was measured, thoroughly remixed, and 10ml subsamples transferred to tared scintillation vials. The vials were immediately frozen to -80°C and later lyophyllised to constant dry weight (approximately 60 hours). Empty vials and deionised water blanks were frozen and lyophyllised in identical fashion.

For the early investigations of the sulphophosphovanillin assay in this study, the 2:1 chloroform:methanol solvent recommended by Folch *et al*, (1957) was employed. The extraction of lipid from freeze-dried tissue followed the '2:1Purified' method detailed in Table 6b.1.

The spectrophotometric method used here follows that of Barnes and Blackstock (1973) modified for coral tissue (see below).

Reagents. Initial work was carried out using the Total Lipid Test. Combination (TLTC) kit of Boehringer Mannheim. However, after early testing both standards and reagents were made up in the laboratory.

Sulphuric acid (AR) (Specific gravity 1.84g)

Phosphovanillin reagent. 1600ml Orthophosphoric acid (AR 83%) was combined with 400ml distilled water. 4g vanillin crystals were added and the resulting reagent thoroughly mixed. The reagent was made up several hours prior to use.

Cholesterol standard. To provide the basic stock solution of 2mg.ml^{-1}, 0.2g crystallised cholesterol (Boehringer Mannheim) was dissolved in 100ml AR ethanol in a volumetric flask at 20°C. (Barnes & Blackstock, 1973, recommend dissolving cholesterol in chloroform/methanol solvent to avoid the necessity of an extra blank. However, ethanol was preferred in this study because there is less danger of concentration changes in the standards due to solvent evaporation.) All standards were kept tightly capped.

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Standard curve. Further dilutions of the stock solution to 1.75, 1.5, 1.25, 1, 0.75, 0.5, 0.25, 0.1 and 0.05mg.ml^{-1} ethanol formed the basis of the standard curve. Three 1ml aliquots of each concentration were transferred to clean, dry screw-cap test-tubes and the ethanol evaporated to dryness in a vacuum desiccator over silica gel at room temperature.

Tissue analyses. Lipid was extracted from freeze-dried tissue using 2:1 chloroform:methanol solvent based on the method of Folch *et al* (1957) (Table 6b.1). The resulting salt-purified lipid-chloroform mixture was vacuum-dried over silica gel at room temperature. During these studies, samples were flushed with nitrogen only if they were stored frozen or for any period without vacuum.

Cholesterol equivalent for lipid extracted from *Leptoria phrygia*. In contrast to Barnes and Blackstock (1973)[1], no prior assumptions were made about the cholesterol equivalent for *L. phrygia* tissue lipid. The standards were made up assuming a 1:1 relationship and the cholesterol equivalent was evaluated experimentally, by determining the ratio of spectrophotometric weight (normalised to cholesterol) to gravimetric weight for a range of tissue lipid concentrations.

Two independent *Leptoria phrygia* colonies were waterpikked exhaustively into deionised water, the slurries frozen and freeze-dried, and each entire tissue extracted into 15ml 2:1 chloroform:methanol (purified as above). The resulting two chloroform samples were vacuum-dried over silica gel to constant weight (67.20mg and 31.59mg). Each extract was then resuspended in 10ml chloroform and replicate samples of a range of volumes transferred to tared screw-top tubes. These were again vacuum dried to constant weight (the sum of gravimetric weights for the tubes corresponded closely with the earlier estimates at 67.02mg and 32.07 respectively). The residue in each tube was resuspended in 10ml chloroform, divided to give expected lipid values which would fall within the absorbance range 0.2-1.0, dried and analysed as below.

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1. Barnes and Blackstock (1973) made up cholesterol standards assuming a relationship of 0.8:1, cholesterol to tissue lipid.

Extraction efficiency of chloroform:methanol solvent when applied to
coral tissue. The extraction efficiencies of 2:1Purified solvent
were examined for 5 low (<100mg) and 2 high (≈ 1g) tissue loadings.
The extraction efficiency depends upon the partitioning of lipid
between solvent and tissue and can be modelled by the exponential
equation $X=e^{(aN+b)}$ (where X=lipid recovery determined by
spectrophotometric analysis, and N=number of extractions) as
described by Chalker and Dunlap (1981) for chlorophyll determina-
tions.

To each dry lipid extract was added 2ml concentrated sulphuric acid
(AR), the tops were lightly screwed down and the test-tubes placed in a
boiling water-bath for a total of 10 minutes. The tubes were not mixed
prior to heating as this resulted in lipid deposits on the sides.
Instead each tube was vortexed for 10 seconds after 5 minutes and
returned to the water bath. The tubes were removed and cooled rapidly
in an ice bath. The resulting lipid-sulphuric acid solution was again
vortexed for 10 seconds, and 0.5ml transferred to a clean dry test-tube
to which 12.5ml phosphovanillin reagent was added. The reagents were
well mixed (10 seconds) and the time noted. The absorbance was read
against a 0.5ml sulphuric acid/12.5ml phosphovanillin standard. Ethanol
and appropriate chloroform:methanol blanks, in addition to the empty
vial and deionised water blanks, were taken through the same procedure.
All glassware was cleaned thoroughly with solvent prior to use.

Comparison of solvent extraction procedures

One sample of *Leptoria phrygia* with a tissue surface area of 76cm^2
(Marsh, 1970) was gently washed with fresh water and frozen at -20°C.
The coral was thawed and waterpikked exhaustively into approximately
350ml deionised water (Johannes & Wiebe, 1970, as modified in Chapter
6a). Following homogenisation for two minutes the total volume was
recorded, the slurry was thoroughly remixed, and 10ml portions were
transferred to tared scintillation vials. Vials were capped, frozen to
-80°C and lyophyllised (approximately 60 hours) to constant weight ("dry
weight"). Ten vials were randomly allocated to each of three treatments
which are summarised below. The detailed steps involved in each method,
as undertaken here, are given in Table 6b.1.

LIPID EXTRACTION PROCEDURES

A) Chloroform:methanol 1:2 (v:v) (Bligh & Dyer, 1959) with purification

a) 15ml of chloroform:methanol 1:2 was added to the scintillation vial in 2 stages. First the tissue was ground into approximately 2ml with a glass rod. When completely mixed the remaining solvent was added.

b) 4ml deionised water was added, the resulting mixture shaken vigorously (100 shakes), and left overnight in the dark at 4°C.

c) The solvent tissue mixture was transferred to 30ml screwtop centrifuge tubes and spun at 1,800xg for 20 minutes.

d) The supernatant was removed to a second centrifuge tube.

e) A further 5ml pure chloroform was used to rinse the scintillation vial and then wash the pellet in the first centrifuge tube.

f) The tube was resealed, shaken vigorously (100 shakes) and left for 30 minutes prior to centrifugation as before.

g) The supernatant was pooled with that in the second tube and, if not being used for extraction efficiency testing, the pellet was discarded.

h) 5ml 0.9% NaCl in deionised water was added to the combined supernatant, shaken vigorously, left to stand for 30 minutes, and centrifuged at 1,800xg for 20 minutes, resulting in a cleanly biphasic solution.

i) The upper phase was discarded, and the lower chloroform layer was transferred to a clean, dry, tared, screw-top test-tube, evaporated to dryness in a vacuum desiccator, and reweighed.

j) Residues were resuspended in 10ml chloroform and, based on expected lipid values, divided into volumes suitable for colour analysis. All tubes were then re-evaporated to dryness prior to the sulphophosphovanillin assay.

B) Chloroform:methanol 2:1 (v:v) (Folch et al, 1957) with purification

a) 15ml of chloroform:methanol 2:1 was added to the scintillation vial in 2 stages as for method (1) above.

b) The resulting mixture (no additional water) was shaken vigorously (100 shakes), and left overnight in the dark at 4°C.

c-j) As above

C) Chloroform:methanol 2:1 (v:v) (Stimson, 1987) without purification

a-g) As for 2:1 purified (B), above

h) The supernatant was filtered through 2.5cm Whatman No.1 filters into tared, screwtop test tubes. Filters were washed with a further 3ml of chloroform:methanol 2:1 and the entire filtrate dried to constant weight in a vacuum desiccator.

i) Residues were resuspended in 10ml chloroform and, based on expected lipid values, divided into volumes suitable for colour analysis. All tubes were then re-evaporated to dryness prior to the sulphophosphovanillin assay.

Table 6b.1.   Descriptions of extraction methods for total lipids.

A) Chloroform:methanol 1:2 (v:v) (Bligh & Dyer, 1959)
       with purification

B) Chloroform:methanol 2:1 (v:v) (Folch et al, 1957)
       with purification

C) Chloroform:methanol 2:1 (v:v) (Stimson, 1987)
       without purification

'1:2Purified' (based on Bligh & Dyer, 1959). Bligh and Dyer's extraction assumes that the tissue sample contains water, and it requires an initial ratio of 1:2:0.8 (v:v:v) chlorofo....ethanol:water. As this was clearly not the case with freeze-dried coral tissue, water was added in the desired proportion as recommended by them. The pellet was re-extracted with a further volume of chloroform, and the resulting combined solvent was purified with one volume of 0.9% salt in deionised water (a final ratio of 2:2:1.8).

'2:1Purified' (based on Folch et al, 1957). Tissues were extracted with 2:1 chloroform:methanol and the pellet washed with one third of the same volume of 2:1. The combined solvent was purified with 0.2 of its volume of 0.9% salt in deionised water (a final ratio of 2:1:0.6 chloroform:methanol:water).

'2:1Unpurified' (based on Stimson, 1987). In the present study, 2:1 chloroform:methanol extraction was carried out on freeze-dried tissue (formalin-preservation was not part of the evaluation), and the solvent was filtered through Whatman No.1 filters which were then re-washed with fresh 2:1. No further purification was undertaken and the filtrates were vacuum dried over silica gel.

Solvent extractions from dried materials containing algae or bacteria can result in substantially less than 100% recovery of certain biochemical constituents. Dubinsky and Aaronson (1979) suggest the addition of 3N HCl to chloroform:methanol solvent to improve the recovery of lipid from algal cells. An alternative, used to check extraction efficiency in this case, is the use of sonication.

CHOLESTEROL STANDARD CURVE
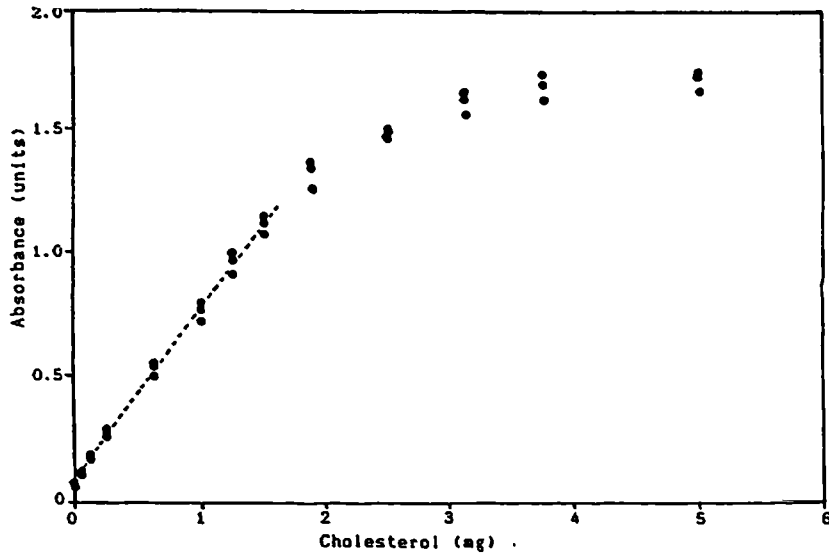
Figure 6b.1. Plot of cholesterol standard against absorbance to demonstrate that linearity is restricted to absorbances less than approximately 1.2 units.

ABSORBANCE CHARACTERISTICS (CHOLESTEROL)

—■—Absorbance at 540nm   —♦—Absorbance at 535nm   —▲— Absorbance at 530nm
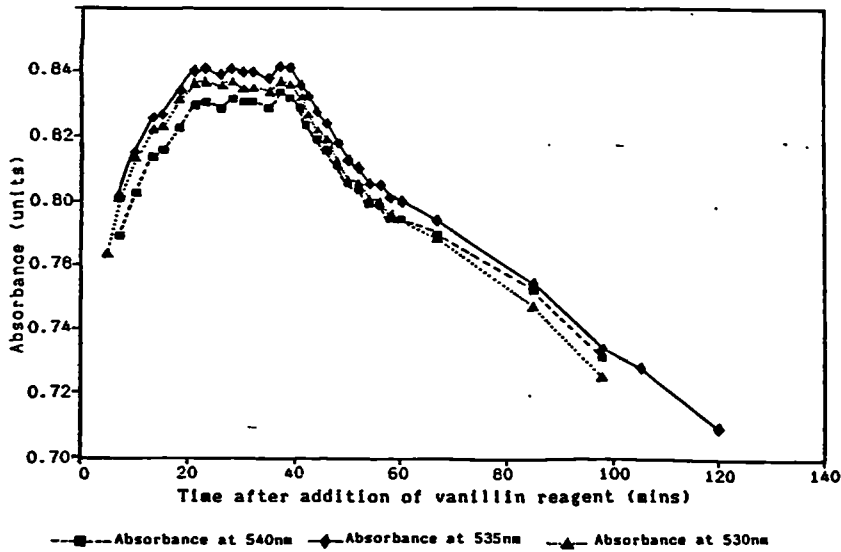
Figure 6b.2. Typical plot of absorbance against time for cholesterol standard (1.25mg). Highest absorbance was at 535nm for cholesterol (see above) and at 525nm for coral lipid; all later readings were made at 530nm for both cholesterol and tissue lipid (see text). Although absorbance appears stable from approximately 20-40 mins after addition of reagent. occasionally (and particularly for absorbance values near the upper limits of linearity) readings were stable for less than 10 minutes. For this reason. all readings were restricted to 20-25 minutes after addition of reagent. Stability was similar for coral lipid.

Immediately following solvent addition, five random vials from each treatment were sonicated for 5 minutes to ensure that zooxanthellae had been fully broken down for lipid release.

In each case gravimetric weights (measured to 0.01mg) of chloroform extract were obtained. The residues were then resuspended in chloroform (10ml), thoroughly mixed, and 5ml removed to a second tube. All 5ml samples were then re-dried under vacuum and their lipid content estimated spectrophotometrically against cholesterol standards.

RESULTS

Characteristics of the sulphophosphovanillin technique

Linearity. The relationship between colour development and lipid content of the standard/sample was curvilinear (see Figure 6b.1). Absorbances in excess of approximately 1.2 absorbance units lay outside the linear range. At absorbances of 0.1-1.2 the fitted line was highly significant (r^2=0.9979, df=31, p<0.0001).

Wavelength of maximum absorption, and temporal stability of the colour complex. Figure 6b.2 shows a typical example of the temporal stability for the three wavelengths 540nm, 535nm and 530nm, for the cholesterol standard. Multiple testing of both cholesterol and tissue samples indicated that while maxima occurred at 535nm for cholesterol, they occurred at 525nm for the *Leptoria* tissue lipid. As the difference between readings at 530nm and the relevant lipid maximum was less than 1%, all subsequent readings for both tissue lipids and lipid standards were standardised to 530nm.

After addition and mixing of phosphovanillin reagent, the time at which absorbance was read was critical (Figure 6b.2). For both cholesterol standard and coral tissue lipid, colour development was fairly stable at 0-1.0 absorbance units between 20 and 40 minutes. However, occasionally, and seemingly arbitrarily, colour development maximised at 17 or 18 minutes and was stable for less than 10 minutes. Also, the intense colour near or at the upper limits of linearity was significantly less stable than that at lower
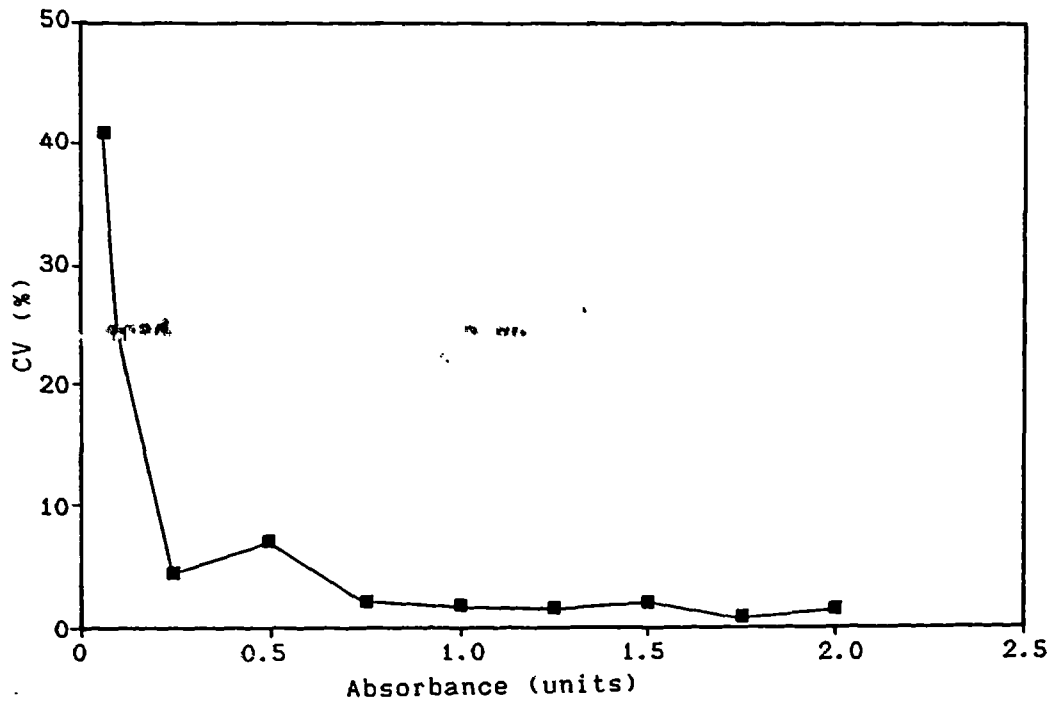
COEFFICIENT OF VARIATION

Figure **6b.3.** The coefficient of variation (CV=SD/mean) for spectrophotometric determinations against absorbance (n=3) showing the dramatic reduction from >20% at absorbances of less than 0.12 units to less than 7% at absorbances of greater than 0.2.

concentrations. Absorbances higher than 1.0/1.1 were occasionally observed to fall 0.1 units in less than a minute only 25 minutes after mixing. Subsequent absorbances were therefore read at no less than 20 and no more than 25 minutes after addition and mixing of reagent.

Coefficient of variation (CV). Figure 6b.3 shows a plot of the coefficient of variation (mean/SD expressed as a percentage) for a variety of absorbance values based on the cholesterol standards used in this study. At each absorbance the CV is calculated on three replicates. The variability is unacceptably high at absorbances of less than 0.2 but is consistently less than 7% at absorbances above this level.

Comments on the technique. Barnes and Blackstock (1973) offer a number of practical hints to which the following may be added.

In order to achieve absorbances in the range 0-1.2 for the expected lipid concentrations of the extracts, the volume of sulphuric acid used for digestion can be altered (without, however, changing the final mixing ratio of 25:1 vanillin reagent to sulphuric acid). In the present study, results from assays using a digestion volume of at least 2ml were more consistent than those using smaller volumes. It is probable that the larger volume of acid assisted digestion of lipid that may have been left on the sides of the tube during drying. Larger volumes of 12.5ml of reagent and 0.5ml sulphuric acid (as compared to 2.5ml and 0.1ml respectively used by Barnes & Blackstock, 1973) in the final mixing concentration of 25:1 helped to reduce pipetting errors.

Readings from disposable cuvettes were found to be unreliable and even with glass cuvettes there was a danger of contamination between samples because the viscous fluid loosely adhered to the glass sides. To minimise such problems all tubes to be read in one batch were ordered from low to high concentration *prior* to the addition of the phosphovanillin reagent (the intensity of the brown colour after acid digestion usually correlated with lipid content unless considerable amounts of other carbon materials were present).

CHOLESTEROL EQUIVALENT FOR *LEPTORIA* TISSUE LIPID
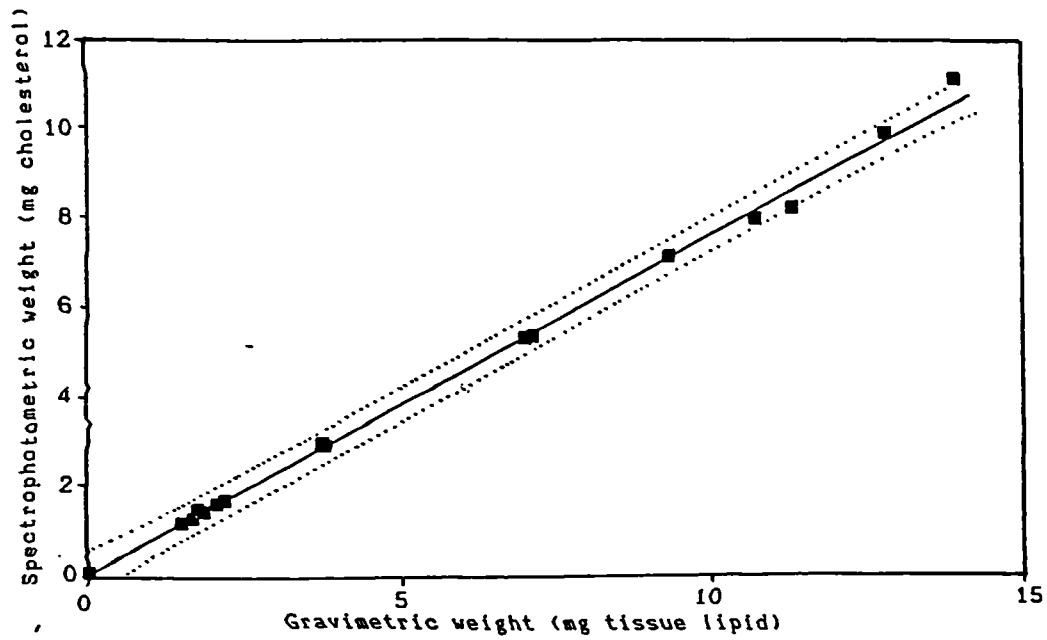
Figure 6b.4. Spectrophotometric weight of lipid (in mg cholesterol) against gravimetric weight of tissue lipid to evaluate the cholesterol equivalent for *Leptoria* tissue. The regression line ($y=0.76x$) is plotted $\pm95\%$ confidence interval for the y estimate.

Between batches, the addition of a 10% HCl solution to a washed cuvette was found to erase all trace of pink colour in readiness for further analyses.

Cholesterol equivalent for lipid extracted from *Leptoria*. The regression coefficient for the cholesterol equivalent (Figure 6*b*.4) was close to, but significantly different from 0.8 (p<<0.001), the regression line being given by the equation y=0.76x ($\pm$0.01, 95%CI). For this tissue, at least, the cholesterol equivalent of 0.76:1 is a little lower than the 0.8:1 determined for serum lipids.

Extraction efficiency of chloroform:methanol solvent for *Leptoria* tissue. Following spectrophotometric lipid determinations for multiple extractions from each tissue sample, the parameters 'a' and 'b' in the equation $X=e^{(aN+b)}$ were, for each sample, estimated by a plot of lnX against N. These parameters were then used to quantify the extraction efficiency $E=1-e^{a}$ (the fraction of remaining lipid removed during each extract).

The extraction efficiency for the five low tissue loadings (<100mg) always exceeded 0.95 (i.e. 95% of the total lipid was extracted in the first extraction; n=5, mean=0.975). For the higher tissue loading, however, the efficiency dropped to 0.88 and 0.93 (mean=0.91). In these cases two extractions were required for better than 95% extraction of total lipid[1].

Comparison of solvent extraction procedures

Dry weights of tissue samples immediately after freeze-drying averaged 62.49mg (n=30, SD=0.84, range=60.58-64.06mg). All subsequent gravimetric and spectrophotometric determinations of total lipid have been normalised to sample weight to avoid any variation due to sample size variation. In all cases, analysis of blanks indicated that contamination of chloroform, methanol, tubes, deionised water, etc., was negligible.

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1. Means are calculated on arcsin-squareroot transformed data and back-transformed.

(a) Lipid per unit dry weight

ug lipid/mg dry weight

	1:2P	2:1P	2:1UP
Sonicated	53.30	57.34	168.04
	53.28	50.27	202.22
	79.09	48.65	157.01
	51.99	51.34	144.39
	52.72	55.07	172.64
Not sonicated	53.40	49.94	191.85
	58.65	52.62	115.12
	61.13	52.26	119.82
	53.02	61.31	118.58
	54.36	57.88	148.18
n	10	10	10
$\bar{x}$	57.09	53.67	153.78

(b) Analysis of variance (1:2P and 2:1P extractions only)

Source	SS	DF	MS	F	p
Method	58.653	1	58.653	1.624	0.277 ns
Sonication	0.116	1	0.116	0.003	0.961 ns
Method* Sonication	22.363	1	22.363	0.482	0.498 ns
Error	742.465	16	46.404		

Table 6b.2. Comparisons of gravimetric determination of lipid for different extraction and purification methods. 2(a) total lipid per unit dry weight (ug lipid/mg dry weight). 2(b) Analysis of variance table for comparison between the two purified methods. At replication of n=10. there was no difference between the two methods, and sonication did not significantly affect the weight of lipid extracted.

2:1P   Chloroform:methanol 2:1, Purified
1:2P   Chloroform:methanol 1:2, Purified
1:2UP Chloroform:methanol 1:2, Unpurified

Gravimetric lipid estimates. Estimates of lipid content determined by each method are presented in Table 6b.2a. Between treatment variances were significantly heterogeneous (Cochran=0.92, p<0.01: Winer, 1971 p. 208). Inspection indicated that the variance of estimates for the unpurified, filtered extraction was substantially higher than for either purified extract. When this treatment was removed the assumption of homogeneity of variance was no longer rejected.

The two purified solvent treatments were re-analysed using a Model I, 2-way analysis of variance (Factors: Extraction method, Sonication), to test the null hypothesis that there was no difference between extraction methods. The ANOVA (Table 6b.2b) indicates that there was no detectable difference between the two remaining purified solvent treatments, nor was there any significant effect of sonication.

As there was no difference between purified estimates at the given level of replication, the data for both purified extraction treatments were combined and compared against the estimates for the unpurified extraction treatment. The difference was highly significant (Mann-Whitney U=200, n_1=10, n_2=20, p<0.001), indicating that gravimetric lipid estimates using this unpurified extraction technique are 2.78 times that using conventional, purified methods[1].

Spectrophotometric lipid estimates. Estimates of lipid content determined spectrophotometrically are presented in Table 6b.3a. The assumption of homogeneity of variance was violated (Cochran=0.95, p<0.01), and was again principally attributed to the unpurified treatment. The data for 2:1UP were dropped prior to analysis of variance of the remaining purified treatments (Table 6b.3b). There was again no difference between purified treatments, and no effect of sonication.

In contrast to the gravimetric determinations, the mean lipid estimate for the unpurified extraction (2:1UP) was lower (33.418ug.mgdryweight^{-1}) than for the purified solvent methods

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1. Calculated on the *pooled* mean (55.38ug) of the purified extractions.

(a)   Lipid per unit dry weight

ug lipid/mg dry weight

	1:2P	2:1P	2:1UP
Sonicated	37.77	41.47	32.10
	40.70	37.07	45.90
	67.11	38.15	30.85
	39.46	41.31	18.33
	39.46	40.69	
Not sonicated	38.64	38.21	41.51
	43.11	41.73	25.26
	41.16	36.16	34.03
	40.08	48.49	55.66
	35.26	38.53	17.13
n	10	10	9
$\bar{x}$	42.28	40.18	33.42

(b)   Analysis of variance (1:2P and 2:1P extractions only)

Source	SS	DF	MS	F	p
Method	21.923	1	21.923	0.458	0.508 ns
Sonication	23.788	1	23.788	0.497	0.491 ns
Method* Sonication	47.045	1	47.045	0.984	0.336 ns
Error	765.103	16	47.819		

Table   6b.3.   Comparisons of spectrophotometric   determination   of
lipid   for   different extraction and purification   methods.   2(a)
total   lipid per unit dry weight (ug lipid/mg dry   weight).   2(b)
Analysis of variance table for comparison between the two purified
methods.   At replication of n=10, there was no difference   between
the   two methods, and sonication did not significantly affect   the
weight of lipid extracted.

2:1P   Chloroform:methanol 2:1, Purified
1:2P   Chloroform:methanol 1:2, Purified
1:2UP   Chloroform:methanol 1:2, Unpurified

(pooled mean: 41.228ug.mgdryweight^{-1}). However, when estimates from the unpurified treatment were tested against the pooled purified treatments, the difference was not statistically significant (Mann-Whitney U=127, n_1=9, n_2=20, 0.10>p>0.05).

The ratio of absorbance weight to gravimetric weight is summarised in Table 6b.4. There is close agreement between those of the two purified extraction methods. Furthermore, these correspond favourably with the earlier ratio determined for 2:1Purified (Figure 6b.4) of 0.76.

The foregoing analyses have been carried out on all replicates of the data. However, the exceptionally high gravimetric value of one sample (79.09ug.mgdryweight^{-1}) and its spectrophotometric equivalent (67.11ug.mgdryweight^{-1}), for 1:2P (Tables 6b.2a & 6b.3a), can be described statistically as an outlier (Dixon's critical value = 0.681 (grav.) and 0.818 (spectr.), n=10, p<0.01, see Sokal & Rohlf, 1981, p.413). It is probable that this replicate represents a genuine variation in lipid per unit dry weight rather than a difference between extraction techniques. Removal of the outlier strengthens the conclusions drawn above.

On the assumption that the outlier does not reflect extraction differences, there is little difference between the purified methods for the estimation of total lipid for this coral. The adjusted gravimetric means becoming 54.65±3.1 compared to 53.67±4.1ug.mgdryweight^{-1} for 1:2P to 2:1P respectively (±SD). The minimum detectable difference (MDD) for this level of replication is 3.34ug or 6.2% of the pooled mean[1], but the experimental difference (0.98ug) between the extraction methods is only 1.8% of the pooled mean. Similarly, the adjusted spectrophotometric means excluding the outlier are 39.52 compared to 40.18ug.mgdryweight^{-1} for 1:2P and 2:1P respectively. In this case the MDD is 2.71ug (or 6.8% of the pooled mean[2]) but the actual experimental difference (0.66ug) was again much lower, representing only 1.7% of the pooled mean. Thus, estimates from the two purified extraction methods agree within a few percent.

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1. Calculated on pooled statistics: gravimetric mean=54.13ug, n=9.47, s=3.59, a=0.05, ß=0.10 (see Zar, 1984: pp.135-6)

2. Spectrophotometric mean=39.87ug, n=9.47, s=2.91, a=0.05, ß=0.10

```
        ****    Treatments    ****

        1:2P       2:1P

        0.709      0.723
        0.764      0.737
        0.849      0.784
        0.759      0.805
        0.748      0.739
        0.724      0.765
        0.735      0.793
        0.673      0.692
        0.756      0.791
        0.649      0.666

Mean¹   0.738      0.751

        ----- ns -----
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Table **6b.4.** Ratio of spectrophotometric to gravimetric lipid estimates for the two purified solvents. The two ratios were compared by a t-test on arcsin-transformed data. For the level of replication in this analysis (n=10) there was no difference between means (p>0.10).

[1] Means are calculated on arcsin-squareroot transformed data and presented backtransformed.

GRAVIMETRIC AND SPECTROPHOTOMETRIC METHODS COMPARED

	Advantages	Disadvantages
Spectrophotometric determinations -	o Can determine ug amounts of lipid o Is lipid-specific so contaminants are not as critical	o Represents an extra step - takes longer o Expensive o Timing critical o Some foreknowledge of lipid content required for suitable subsampling
Gravimetric determinations	o Fast o No subsampling required o Cheap o Little equipment necessary	o Requires sophisticated balances and conditions for ug determinations o Impurities measured as lipid

Table **6b.5.** Advantages and disadvantages of the gravimetric and spectrophotometric methods for determination of total lipids

DISCUSSION

The sulphophosphovanillin technique

Technically, the sulphophosphovanillin assay adequately fulfilled the requirements for estimation of lipid with precision at levels of <5mg. Bayne (1973) reported a coefficient of variation of 20% for repeated assays (n=14) on tripalmitin standards using the sulphophosphovanillin technique, and on this basis rejected the method as too inaccurate to be useful. The CV's for cholesterol standards did not approach his unsatisfactory level except at absorbance values of <0.2. While such low absorbances should be avoided, this study is in agreement with that of Barnes and Blackstock (1973) that the method should not be rejected on the grounds of lack of precision.

Nevertheless, for many ecological studies, where resources and facilities are limited, this spectrophotometric method would only be a useful alternative where gravimetric methods are impractical. There are procedural problems such as the strict timing requirements for colour formation, the highly corrosive reagents, the relatively high cost of reagents, the extra equipment (glassware, waterbath, accurate micropipettes, spectrophotometer), and substantially increased time required for analysis. Table 6b.5 compares the gravimetric and spectrophotometric assays with a summary of the advantages and disadvantages of each. In the present study, spectrophotometric analyses for *Leptoria* were successful, and the method was found to be useful. However, if freeze-drying techniques are to be employed for this or other corals, it is recommended that, where possible, the tissue slurry is concentrated so that small volumes can be freeze-dried efficiently, yielding dry-weights of sufficient magnitude for gravimetric analyses.

The sulphophosphovanillin 'cholesterol equivalent' for *Leptoria* was found to be close to, but significantly less than the 0.8 standard used in the Boehringer Mannheim TLTC test kit. If ratios for other anthozoans (*Tealia*, *Metridium* and *Pennatula phosphorea*) are calculated from Table IX of Barnes and Blackstock (1973) (allowing for the 0.8:1

equivalent used in their standard curves), they become 0.80, 0.70 and 0.49 respectively. The value of 0.76 for *Leptoria* is compatible with these values, but there is a considerable range within the coelenterate groups so far investigated.

Lipid extraction

Extraction efficiency. The efficiency of 2:1 chloroform:methanol in extracting lipid from tissue samples of <100mg was very high (97% of total lipid recovered in the first extraction). This decreased to around 90% for higher tissue loadings of up to 1g. The extraction volume was not altered for the higher tissue load (15ml) and it is probable that both the smaller ratio of solvent to tissue, and greater problems of diffusion and mixing through the thicker tissue layer, were responsible. Nevertheless, in their detailed studies of lipid and protein methodology, Hopkins *et al* (1984) reported a significant effect of tissue loading on lipid recovery which appears to be independent of variation in extraction efficiency. In their study, even after a number of extractions, the total lipid recovered as a percentage of dry weight decreased with increasing tissue loading. In order to avoid variations in lipid estimates resulting from these problems, the weight of freeze-dried tissue for lipid extraction should be constant within practical limits.

The use of sonication did not significantly improve lipid extraction and it is therefore concluded that the combination of freeze-thaw, followed by waterpikking and homogenisation in deionised water is sufficient to allow extraction of all lipid from tissue and zooxanthellae.

Comparison of extraction procedures. There were two *a priori* reasons to suppose that the unpurified extraction procedure would lead to higher estimates of lipid than either of the purified solvent procedures. Firstly, failure to remove the methanol portion would leave salt and other non-lipid contaminants in the extract. Secondly, even where methanol is removed by the addition of water, several authors highlight the added advantages of replacing water

with a mild salt solution (e.g. Folch *et al*, 1957; Bligh & Dyer, 1959; Barnes & Blackstock, 1973). Barnes and Blackstock (1973) actually test the difference between extracts treated with water or with a 0.9% salt solution, and for the three coelenterates they examined the salt-treated extracts could be as little as half the gravimetric weight of those treated with water only.

As predicted, the present study found that the unpurified procedure (2:1UP) led to much higher gravimetric estimates (x2.87) than its purified equivalent (2:1P). It was disappointing, however, that the coefficient of variation for the unpurified procedure was also much higher (19.8%) than the 2:1 purified equivalent (7.6%). In contrast, the lipid estimate by spectrophotometric analysis for unpurified extracts, although lower, was not significantly different from the purified equivalents. Again, however, the variability of the estimates was significantly higher, possibly because some lipid was lost during the filtration stage, despite the subsequent chloroform:methanol wash of the filters. Alternatively, impurities may have interfered with the colour reaction. Nevertheless, the similarity between the estimates for unpurified and purified extracts by the colour method indicates that extra gravimetric weight was indeed a result of non-lipid contamination, rather than a more efficient extraction of lipid material.

Following from this study, and in combination with some concerns relating to the adverse effect of formalin on total lipid analyses (Morris, 1972), it is recommended that (a) further examination of the effect of formalin preservation be carried out prior to the use of this method as a precursor for lipid studies in corals, and (b) results using unpurified solvent extraction be viewed with some caution. Removal of the methanol phase is desirable in lipid studies.

In the parallel comparison between the two purified solvent combinations, 2:1P and 1:2P, there was no significant difference in lipid recovery at the level of replication of this study (n=10). Kopecky (1969), in a study of lipid recovery using a range of chloroform:methanol combinations concluded that maximum lipid extraction occurred with ratios in the range of 1:2 through 1:1 to

2:1. Bligh and Dyer (1959) based their final recommendations on the observation that 1:2 resulted in a higher gravimetric recovery than any other chloroform:methanol combination that they tested, but their study specifically related to tissues with substantial water content.

For many ecological purposes, the two purified methods as defined here can probably be considered analogous for the determination of total lipids. In practice, variation at ecologically significant levels is likely to outweigh the small differences between these methods. For example, the coefficient of variation for lipid analyses between ten *Leptoria* individuals from the same habitat, at the same time of year, using the same methods, was >20% (Chapter 6a, Table 6a.4), and considerably higher than the coefficient of variation for the combined purified data (6.6%)[1] for replicate tissue samples of the one individual used here. However, Schmid (1973) discusses the significance of solubility coefficients of solvents (which change with chloroform:methanol ratio and tissue water content) in the recovery of the different lipid classes and warns that polar lipids can be lost to the discarded methanol layer under certain circumstances. For more qualitative lipid analyses, therefore, some further consideration of chloroform:methanol:water ratios may be required.

The lipid content determined by purified extraction for the 5 *Leptoria* individuals used here, was 6.8±1.7% dry weight (mean ±SD). Although this falls well short of the values of around 30% quoted for anemones (Bergmann *et al*, 1956; Kellogg & Patton, 1983; Blanquet *et al*, 1979), values reported for scleractinia are variable and many are much lower. *Pocillopora capitata* was found to comprise >30% lipid on the basis of dry weight (Patton *et al*, 1977), but of 25 Caribbean corals investigated by Meyers (1977) only 5 had mean lipid levels of >5% dry weight. Lipid levels for *Pocillopora damicornis* from Panama reported by Glynn *et al* (1985) were less than 1% dry weight. On the other hand, values for the symbiotic/aposymbiotic coral *Astrangia danae*, were approximately 17%[2] (Szmant-Froelich & Pilson, 1980). The method used to

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1. With the outlier excluded.

2. Calculated as 'lipid' divided by 'total' for 'field corals' from Table 1 in Szmant-Froelich and Pilson (1980).

determine 'dry weight' may very well account for some of these differences. Almost certainly, time of year in relation to gametogenesis and spawning or planulation is another influence. Richmond (1983) and Stimson (1987) have both shown that planulae are rich in lipid. The *Leptoria* used for this study were collected approximately 2 months after spawning and the lipid values may well, therefore, be lower than in the months immediately preceding their November/December spawning period.

CHAPTER 7

LETHAL AND SUB-LETHAL EFFECTS OF PERSISTENT DAILY
SEDIMENT INFLUXES ON *LEPTORIA PHRYGIA*

LETHAL AND SUB-LETHAL EFFECTS OF PERSISTENT SEDIMENT INFLUXES ON *LEPTORIA PHRYGIA*

SUMMARY

Colonies of the massive faviid. *Leptoria phrygia* (Ellis & Solander. 1876). were subjected to increasing daily sediment loads in the laboratory to evaluate the effects on mortality and lipid levels. Nine replicate flat colonies were assigned to one of 13 treatments (5 controls and 8 sediment loads ranging from 1-1000mg.cm^{-2}.day^{-1}). Daily sediment doses of a clean, calcium carbonate/quartz sand of size range 63-250um. were divided into five equal portions and applied five times per day for a total of 23 days.

No mortality or overt tissue damage was observed for any control coral or fr> sediment doses of 1 or 10mg. $^{-2}$.day^{-1}. From 25mg.cm^{-2}.day^{-1} both the number of colonies and the severity of tissue damage increased until, at the maximum dose of 1000mg.cm^{-2}.day^{-1}, 7 of the 9 replicates suffered total mortality and the remaining two were seriously affected. Depths of fine sediment causing tissue damage were estimated to be 1-1.5mm provided they remained on the tissue for at least 3 days.

Between 25 and 1000mg.cm^{-2}.day^{-1} the degree of mortality was most strongly correlated with the weight of overlying sediment. This in turn was significantly correlated with fine-scale differences in colony convexity and with increasing daily sediment load. *Leptoria* showed intra-species variation in both sediment tolerance and rejection capability unrelated to sediment load or convexity. There was no relationship between the_ complexity or length of meanders and the effects of sediment. Unfortunately, freezing failures during storage forced lipid analyses to be abandoned.

The sediment tolerance of *Leptoria* is discussed in relation to the species distribution and recorded sedimentation rates around Lizard Island. It is concluded that sediment may be an important controlling factor for this species. However, comparison with previous experiments suggests that this laboratory experiment may underestimate field mortality for equivalent sedimentation rates.

INTRODUCTION

During the course of previous field and laboratory experiments and observations, the faviid coral *Leptoria phrygia* (Ellis & Solander, 1789) was found to be a moderately efficient sediment rejector but intolerant of unrejected sediments overlying its tissues (Chapters 2-4). In order to investigate the tolerance in more detail. a laboratory experiment was designed to examine the lethal and sublethal effects of increasing daily sediment influxes on this coral. The experiment had two principal aims:

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(a) to examine the daily sedimentation rates required to cause stress and mortality; and (b) to evaluate total lipids as a potential indicator of sublethal stress. Unfortunately total loss of samples for lipid analyses occurred through freezing failures during storage and the second aim had to be abandoned[1].

Bleaching, mesenterial extrusion, mucus production and unusual behavioural activity have all been cited as indicators of stress to corals (see review by Brown & Howard, 1985), and of various forms of sediment stress in particular (e.g. Kolehmainen, 1974; Rogers, 1983; Peters & Pilson, 1985; Yamasu & Mizofuchi, 1989). All of these responses have been observed for Australian corals in response to sediment (Chapter 2), and were the focus for overt signs of sublethal stress.

METHODS

Collection of specimens

Specimens of *Leptoria phrygia* were collected from 3-6m depth on the exposed reef front of Coconut Bay, Lizard Island, on the northern Great Barrier Reef, Australia[2].

The morphology and size of colonies were standardised by taking cores with a 7cm-diameter corer attached to an air drill (Done, *pers. comm.*). Each core sample was taken from a separate individual and selected for uniform near-flat morphology. Samples were drilled to a depth of approximately 3cm and removed with a hammer and chisel[3].

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1. In view of the loss of lipid samples, the rationale for total lipids as a potential indicator of sublethal stress has been deferred to Appendix 7.1.

.2. For a further description of Lizard Island and the collection site, see the General Introduction and Chapter 5.

3. During initial testing of the drilling technique a 2cm-thick plastic guide for the drill bit was first secured to the reef to prevent the drill bit from slipping. In this way the cut was clean and damage was limited to 1-2mm of the edge tissue of the core. With experience the guide was rarely necessary, but the drill bit must be very accurately machined so that its rotation is circular. If its rotation is slightly off-centre and forms an ellipse, damage to surface tissues can occur.

Samples were immediately transferred to flow-through aquaria at Lizard Island Research Station (Plate 7.1). The irregular base of each cored sample was cut to a flat horizontal surface with a diamond saw, leaving experimental colonies approximately 2-3cm thick (Plate 7.2). During this process the corals were out of salt water for approximately 30 seconds.

Once techniques had been refined, mortality during collection and preparation of cored samples was <4%, and all mortality, if it occurred, took place within the first 8-10 days. Microscopic examinations showed that tissues on the circumference of the cored sample had healed after 4 wee___. but experimental colonies were maintained for 5-7 weeks prior to experiments to allow for complete recovery. No mortality occurred to any experimental control corals and, during the course of various experiments, cored individuals were maintained successfully in aquarium conditions on Lizard Island for more than six months with no mortality or tissue damage[1].

Experimental treatments

The experimental design involved 13 treatments (5 controls and 8 sediment levels) with nine replicates per treatment. The treatments are illustrated diagrammatically in Figure 7.1. The first control group ('CG') comprised nine colonies at the collection site which were marked but left undisturbed (CG1). The second group (CG2) were cored and removed, their bases were cut and they were then returned to the

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1.   An examination of the effect of coring on lipid levels was an integral part of this experiment (see treatment controls, Figure 7.1). The loss of lipid samples prevented evaluation of this aspect. Further support of the contention that cored samples of *Leptoria phrygia* recover completely and are not significantly stressed by laboratory conditions comes from a parallel study of spawning. Of 108 cored samples which were collected, allowed to recover and maintained in laboratory conditions as described above. only 7 did not spawn. All other individuals spawned at the same time of night over the same two days as field colonies (28 and 29 November 1988). Furthermore, there was no difference in the number of eggs spawned by these experimental colonies (which had been maintained in laboratory conditions for four months prior to spawning) and eggs collected from 20 samples taken from the field (broken off parent colonies, rather than cored) two days before the spawning period (p>0.4).

Plate 7.1.   Outdoor   flow-through   aquaria   at
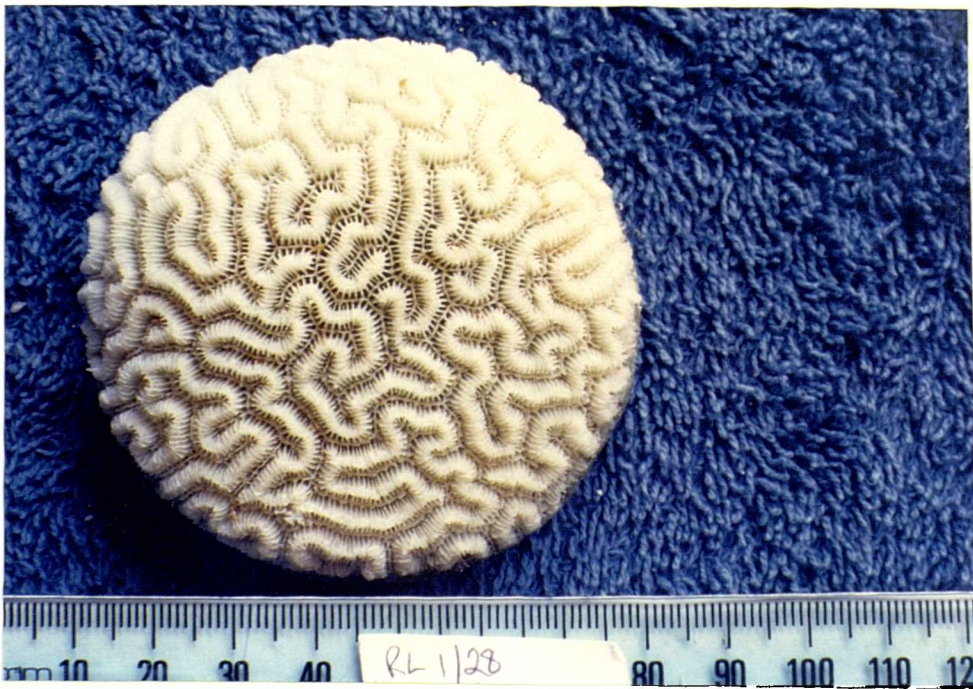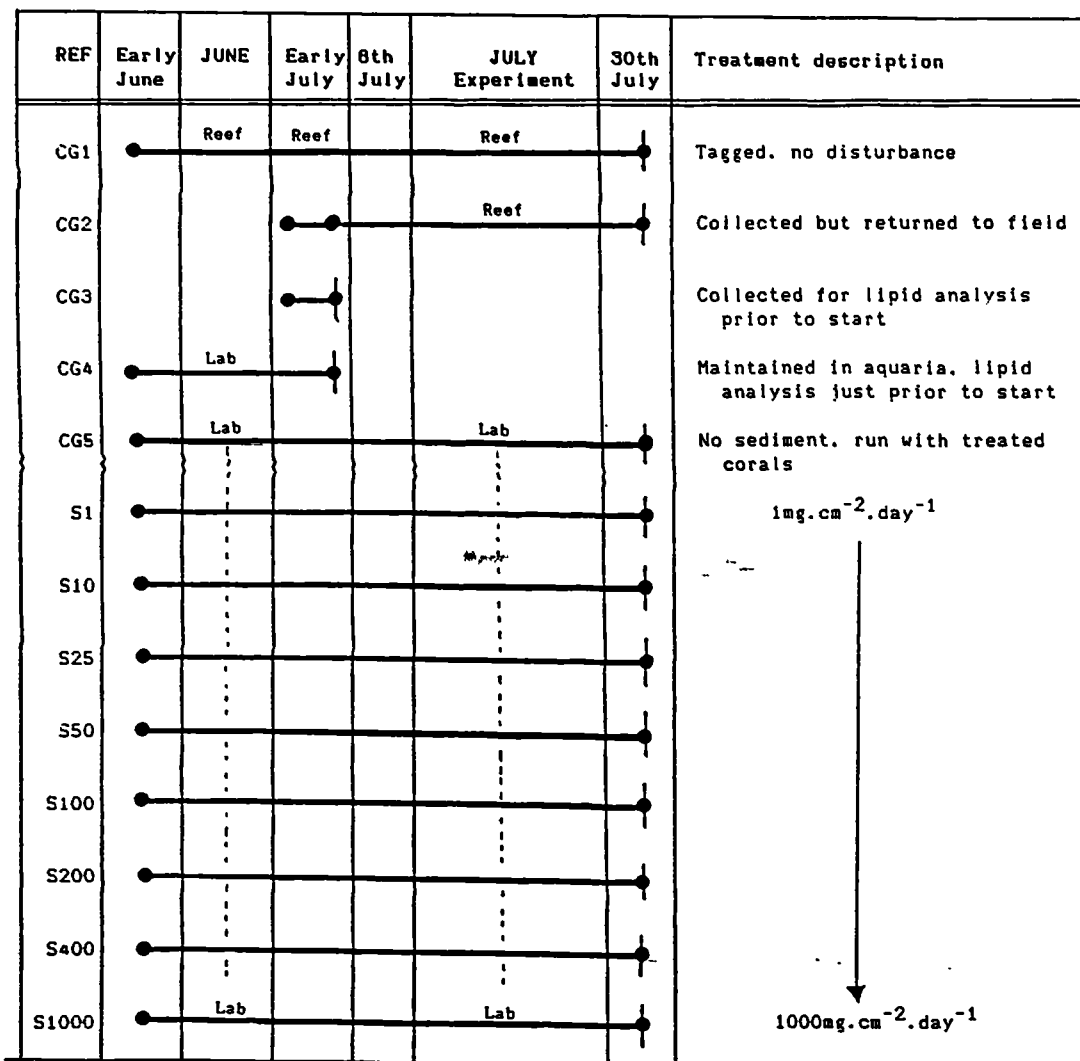Lizard Island Research Station.

Plate 7.2.   A typical   cored colony of *Leptoria
phrygia (x 1)*.

collection site and carefully wedged in concrete blocks such that all living tissue was exposed to light and water circulation. The third control group (CG3) were cored just before the start of the experiment and immediately prepared for lipid analysis. All remaining experimental colonies were prepared within the same period of a few days and allowed to recover for 5-7 weeks in outdoor, flow-through aquaria at Lizard Island Research Station. Just prior to the start of the experiment, a fourth control group (CG4) was prepared for lipid analysis.

Eighty-one remaining experimental colonies were grouped according to fine-scale variations in convexity. Although all had been chosen for near-horizontal morphology during coring, there were still small variations that might influence sediment rejection (see chapter 4). For each experimental colony, an estimate of convexity was made and colonies were grouped into convex (+ve convexity), flat (0 convexity), and concave (-ve convexity) categories. Allocations were made according to a stratified randomisation schedule which ensured that variations in convexity were evenly distributed between the treatments. Three colonies were isolated in each of 27 glass aquaria. Laboratory treatments were: no sediment (the fifth control, CG5), and 1, 10, 25, 50, 100, 200, 400, 1000mg-fine $sediment.cm^{-2}.day^{-1}$ (eight sediment treatments).

The experiment was started on July 8, 1988 and ran for 23 days. For every experimental colony, its daily sediment application was divided into five equal parts and applied evenly over the coral surface in five separate doses at approximately equal intervals across 24 hours. The sediment was a quartz/calcareous sand (approximately 30%/70%) characteristic of the local region, which had been washed, oven-dried for 4-8 hours, and run through a series of stainless steel Endicott sieves to give standard grain sizes. Only sediments of the 'fine sand' size range, 63-250um, were used for this experiment. For this grai size, 1mm depth of sediment is equivalent to $156\pm5mg.cm^{-2}$ (mean$\pm$SD).

Control groups 1-3 (CG1-3) were incorporated so that lipid levels of laboratory corals could be directly related to the levels existing in field corals during the same period. CG2 and CG4 had the additional purpose of determining the effect of the coring and collection method on lipid levels. CG4 and CG5 served as the baselines against which changes in lipid levels in the sediment treatment groups could be determined.

REF	Early June	JUNE	Early July	8th July	JULY Experiment	30th July	Treatment description
CG1	●	Reef	Reef		Reef	↓	Tagged. no disturbance
CG2			●—●		Reef	↓	Collected but returned to field
CG3			●—↓				Collected for lipid analysis prior to start
CG4	●	Lab	↓				Maintained in aquaria. lipid analysis just prior to start
CG5	●	Lab			Lab	↓	No sediment. run with treated corals
S1	●					↓	$1 mg.cm^{-2}.day^{-1}$
S10	●					↓	
S25	●					↓	
S50	●					↓	
S100	●					↓	
S200	●					↓	
S400	●					↓	
S1000	●	Lab			Lab	↓	$1000 mg.cm^{-2}.day^{-1}$

● Significant change in treatment

↓ Corals prepared for lipid analysis

Figure 7.1. Experimental treatments: CG are control treatments; S1-1000 represent sediment treatments 1mg-1000mg.cm^{-2}.day^{-1}. For explanation of controls, see text.

CG1, CG2 and CG5 also served as controls for mortality and tissue damage caused by the sediment treatments.

Aquarium conditions

Aquaria were located outdoors beneath a single layer of shade cloth. Light levels were measured with a LI-COR quantum sensor (Li 1935A) and were equivalent to 5-6m depth in Coconut Bay (i.e. towards the lower end of the collection depth range, see earlier).

Water depth in aquaria was standardised to 14cm with a mean total volume of approximately 9 litres. The input flow was monitored daily and maintained at approximately $750ml.minute^{-1}$ for all tanks. Turbulence petri dishes (Chapter 3) were introduced into the tanks in the positions of experimental corals and varying sediment loads spread evenly across their surface. At this flow rate no disturbance of the grains was detected.

Salinity, measured daily with a refractometer, varied between 33-34°/... Temperature fluctuated on a daily cycle, with a maximum range of 1.6°C. The mean aquarium temperature changed from 25.5°C to 24.1°C during the course of the experiment, with a peak of 26.7°C between midday and 1630 hours (early July) and a low of 23.2°C in the early hours of the morning (late July).

Measured parameters

Sediment accumulation. Sediment accumulations on experimental colonies were estimated during the course of the experiment, and were collected and weighed on completion.

(a) Temporal changes. Prior to re-application, sediment remaining at the end of the previous 4-5 hour period was estimated according to a predetermined semi-quantitative scale, and an estimate of the surface area covered by the sediment was recorded. The mean of the five estimates was calculated to give an estimate of sediment accumulation for each day and to examine temporal trends.

CALIBRATION OF VISUAL SEMI-QUANTITATIVE ESTIMATES OF
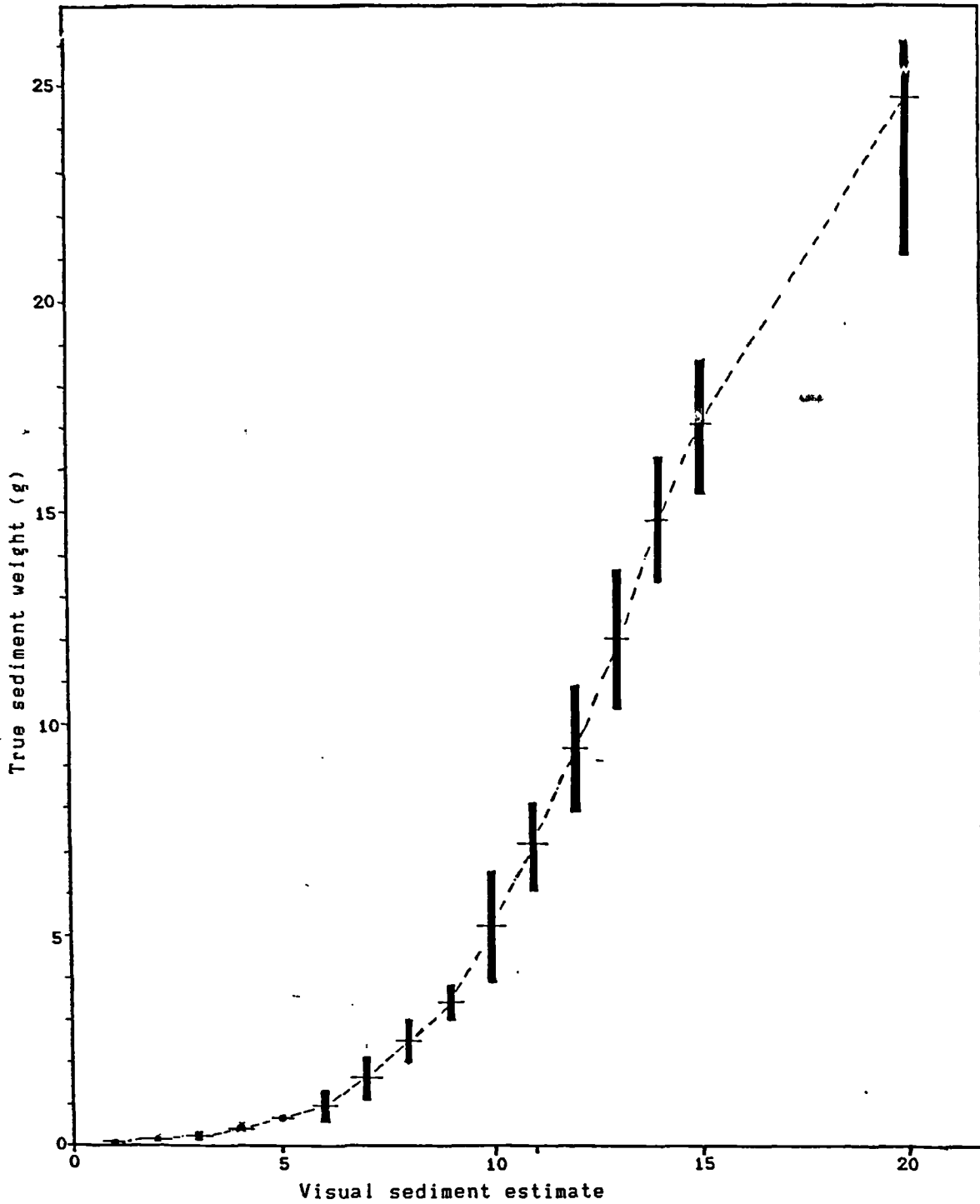## OVERLYING SEDIMENT

Figure **7.2.** Calibration of visual estimates of overlying sediment against measured weight. Shown are means and 95% confidence intervals.

The semi-quantitative scaling method used during this experiment was comprehensively calibrated against weight of sediment using three methods: (a) sediment was spread on an uneven surface of similar area as the experimental colonies and estimates made visually; (b) estimates were made of sediment on cores not used for experiments; and (c) estimates were made of sediment remaining on experimental colonies at the end of the experiment. In all cases, the sediment was removed, dried, and weighed.

The results of the calibrations are indicated in Figure 7.2 ($\pm$95% CI) and show that visual estimates were sufficiently consistent +^ make general statements about the accumulation of sediment over time. However, estimates were more consistent for the same coral than between corals (i.e. an estimate of 6 was ·greater than 5 for the same coral, but the weight of an estimate of 6 for one coral could be different from the same estimate for another coral, particularly if the area covered was also very different). For this reason, graphs of sediment accumulation over time (Figure 7.6) have been plotted against the estimate, and not converted to absolute weights.

(b) Localised sediment accumulation. Sediment was almost always localised, to some degree, in pockets or other distinct regions ´of the coral. At the end of the experiment, the area covered by sediment and the weight of remaining sediment (from direct measurements), were combined to give an estimate of weight per unit area. Sediment depth was calculated on the basis that 1mm depth over 1cm^2 weighs 156mg. Weight per unit area and depth of sediment -- are interpreted with caution as further localisation of sediment within the area covered by sediment occurred in most cases but was extremely difficult to quantify.

Tissue mortality. At weekly intervals the overlying sediment was gently disturbed with a cotton bud or fine paint brush in order to evaluate the degree of tissue damage or mortality beneath. At the end of the three week period a more detailed evaluation of damage was possible, following removal of all remaining sediment. Seven categories of damage were identified as follows:

0	None, all tissues appeared normal
1	No overt mortality but bleaching present
2	Minor tissue death ($<5cm^2$) but sometimes accompanied by bleaching over a wider area
3	Moderate tissue death ($5-15cm^2$), usually with extensive bleaching elsewhere
4	Fairly extensive tissue death ($15-25cm^2$)
5	Very extensive tissue death ($>25cm^2$)
6	Complete death of colony

In fact, recorded mortality always fell into categories 0-2 or 6, with the exception of one coral in category 3 and two corals in category 4. For this reason, categories 3-5 are combined in graphical analyses.

[Lipid analysis. Immediately following termination of the experiment, all laboratory corals were waterpikked into Whatman GF/F filtered seawater and stored at -20°C in preparation for lipid analysis using 2:1 chloroform:methanol solvent (Folch *et al*, 1957) according to the methods described in Chapter 6*b*.

At the end of the laboratory experiment, Control Groups 1 and 2 (in the field) were examined for tissue damage or mortality and all 18 corals were collected and prepared for lipid analysis under the same schedule as laboratory colonies.]

Morphological characters. The surface area of coral skeletons was measured by the tin-foil method of Marsh (1970) and ranged from 40-55cm^2. The degree of complexity of the meanders was estimated on a scale of 0 (completely straight and parallel) to 10 (very highly convoluted), and the number of 'dead ends' to meanders was counted.

During the course of the experiment no field or laboratory control coral showed any signs of damage or mortality from any cause. Estimates of sediment on control corals in the laboratory aquaria were not zero but the nature of such sediment (a medium-brown, light-weight faecal or mucal material of negligible weight) was very different from the introduced sand grains.

Due to the loss of samples for lipid analyses, the following results and discussion are based solely on the influence of sediment on mortality and tissue damage.

General observations

Sediment loads modified the behaviour of *Leptoria phrygia*. A description of sediment rejection mechanisms of *L. phrygia* is provided in Chapter 2 and Appendix A: rejection behaviour in the present experiment was typical for this sediment size (63-250um). In the absence of sediment influxes, *L. phrygia* tentacles were seldom seen to be fully expanded during the day, although tentacle tips often protruded from the valleys. Normally polyps opened out during dusk and remained expanded until dawn, with only occasional retractions. The rare exceptions were when storm cloud cover reduced light to early dusk levels. When sediment was applied during the day, tentacle tips generally disappeared completely and might or might not reappear as rejection commenced. At night most polyps retracted immediately and would only re-expand as sediment was removed from the region. Polyps were unable to expand fully with more than a scatter of sediment grains on the surface, thus sediment influxes or accumulated sediment would have a major influence on heterotrophic feeding at night for vulnerable tissues. Once sediment had been removed from a particular region of the colony, polyps expanded normally. Tissues immediately beneath, or adjacent to, accumulations of sediment often became swollen, but sediment accumulations in one region did not cause unusual behaviours in the rest of the colony.
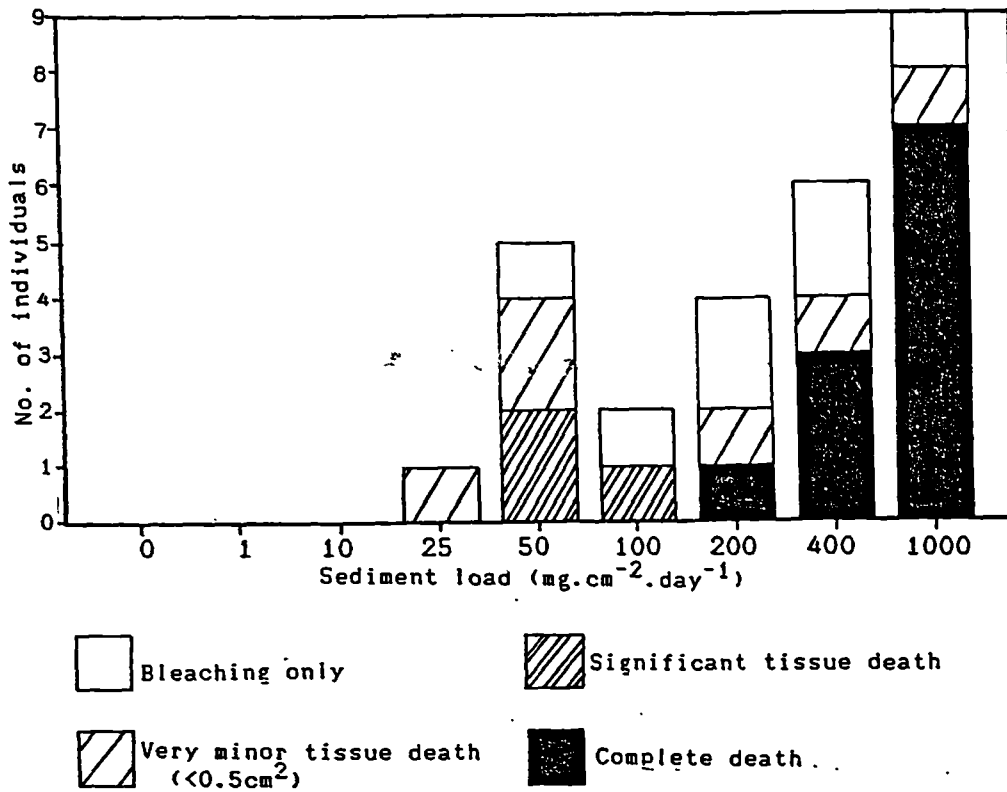
EFFECT OF SEDIMENT LOAD ON TISSUE DAMAGE

Figure 7.3. Effect of increasing daily sediment load on mortality and tissue damage. The maximum number of individuals per treatment is nine.

Extrusion of mesenterial filaments is a normal initial response of *L. phrygia* to sediment influxes (see Plate 2.8 and Appendix A) but this became much less common after two or three days of regular sediment applications. The filaments were not easy to see as they protruded from the tissues of the wall or oral disc only around a millimetre at most. During the later part of this experiment, mesenteries extending 2-3mm were occasionally visible around accumulations of sediment that had caused at least some tissue damage beneath. They were never observed on controls, nor on areas of a treated coral where sediment had been removed. It is probable that these observations represent the two types of mesenterial response discussed in Chapter 2, the first being an exploratory examination of the grains as a potential food source, and the second being a response to physiological stress.

Mucus was involved in sediment rejection but became more obvious as sediment accumulations persisted on the tissues. The highly agglutinated nature of heavy sediment accumulations suggested that mucus may play an important role in the development of diffusion barriers created by the sediment layer. A number of corals were seen to ingest sediment particles, but this ceased altogether after the two to three days.

Thick sediment layers (several millimetres) that had been overlying an experimental colony for some time (several days) gradually turned black (characteristic of anoxic sediments and muds) and became very agglutinated. This darker-hued sediment was present on all corals that suffered total death or extensive damage although only the sediment closest to the coral surface was strongly affected. No experimental colony was seen to reject sediment once this condition prevailed, although living tissues on the peripheries could still do so.

Treatment effects

The degree of mortality within treatments after 23 days showed an increase with increasing sediment loads at levels of greater than 25mg sediment.$cm^{-2}.day^{-1}$ (Figure 7.3). No overt tissue damage was observed for any colony subjected to less than 25mg sediment.$cm^{-2}.day^{-1}$. All corals that received 1000mg sediment.$cm^{-2}.day^{-1}$ were affected and 7 of the 9 replicates completely died.

	Mortality	Input Sediment	Minimum Convexity	Overlying Sediment	Meander complexity
Mortality	1.0000 (1.0000)				
Input Sediment	0.5564 (0.0001) **	1.0000 (1.0000)			
Minimum Convexity	-0.4926 (0.0003) **	0.0091 (0.9473) ns	1.0000 (1.0000)		
Overlying Sediment	0.8170 (0.0000) ***	0.5316 (0.0001) **	-0.5156 (0.0002) **	1.0000 (1.0000)	
Meander Complexity	-0.0114 (0.9339) ns	NR	NR	-0.0108 (0.9374) ns	1.0000 (1.0000)

Table 7.1. Spearman rank correlation matrix for independent and dependent variables. Treatments of less than 25mg/cm^2.day excluded (n=54). Correlation coefficient is given with probability in parentheses. Significance is adjusted to allow for multiple comparisons using the Dunn-Sidak equation $\alpha'=1-(1-\alpha)^{\frac{1}{k}}$ where k=number of comparisons=8. On this basis, a true significance level of α=0.05 requires a probability of α'=0.0064, for α=0.01 α'=0.0013, and for α=0.001 α'=0.0001. Significant correlations are indicated on this basis. 'NR'= not relevant.

MEAN CONVEXITY OF COLONIES IN EACH TREATMENT
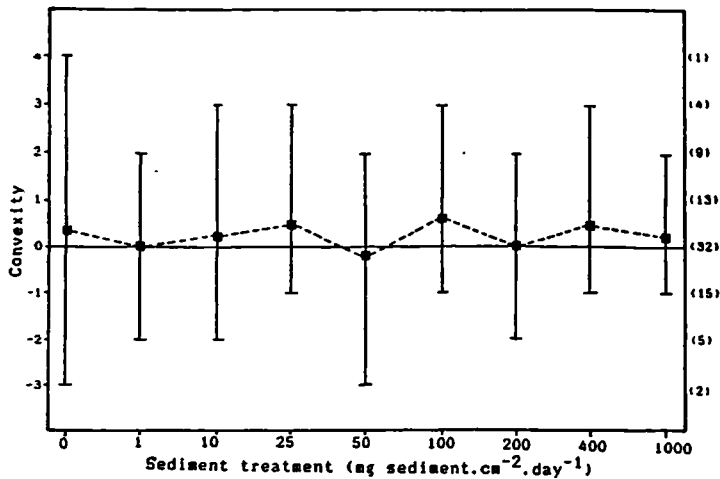
Figure 7.4. Mean convexity (solid square) and range (vertical bars) for colonies in each sediment treatment. Convexity on the y axis is given on the left (with the total number of colonies for each convexity category on the right in brackets). and varied between -3 (mildly concave) and +3 (mildly convex) for treated colonies. However, most colonies were very close to flat (60 of the total 81 colonies were within ±1). By chance, the 50mg.cm^{-2}.day^{-1} had slightly lower mean convexity than other treatments.

Correlation between degree of mortality, input sediment load, individual colony convexity, and meander complexity, was tested by Spearman's rank correlation coefficient for the six affected sediment treatments ($25-1000mg.cm^{-2}.day^{-1}$; Table 7.1). There were several significant correlations. Mortality was most strongly correlated with overlying sediment load ($p<0.001$), but was also significantly correlated with input sediment load and minimum colony convexity ($p<0.01$). Variations presumably reflect other factors such as differences in rejection capability of individual colonies. Meander complexity had no effect either on overlying sediment or on mortality ($p>0.9$).

As these results suggest~~ that convexity and input sediment load interacted to promote tissue mortality, the stratified random allocation of convexity to treatments was again reviewed to determine whether it could account for any of the variability across treatments. Table 7.1 confirms that there was no correlation overall between convexity and input sediment load but, by chance, there was a slightly lower average convexity for the 50mg treatment than others (Figure 7.4). This may have contributed to the greater susceptibility of this treatment group, but the differences in mean and absolute convexities were very slight and it is unlikely to account for all of the mortality shown.

Temporal patterns

Mortality. Only two replicates in the highest sediment treatment showed any tissue mortality before the sixth day. Three further replicates at $1000mg.cm^{-2}.day^{-1}$ and one each at 400 and $200mg.cm^{-2}.day^{-1}$ showed damage on the sixth day. Figure 7.5a-f illustrates the time-course of mortality for each sediment load based on mortality levels after 1, 2 and 3 weeks. As would be expected, with the exception of the 50mg sediment.$cm^{-2}.day^{-1}$ treatment, there is a clear trend, with damage to the colony becoming apparent earlier with increasing sediment load. No damage occurred to the only affected colony treated with $25mg.cm^{-2}.day^{-1}$ for over two weeks.

Sediment accumulation. Means of the five daily estimates of sediment accumulation are plotted against time for each colony in Figures 7.6a-i. The pattern of accumulation indicates that a level of
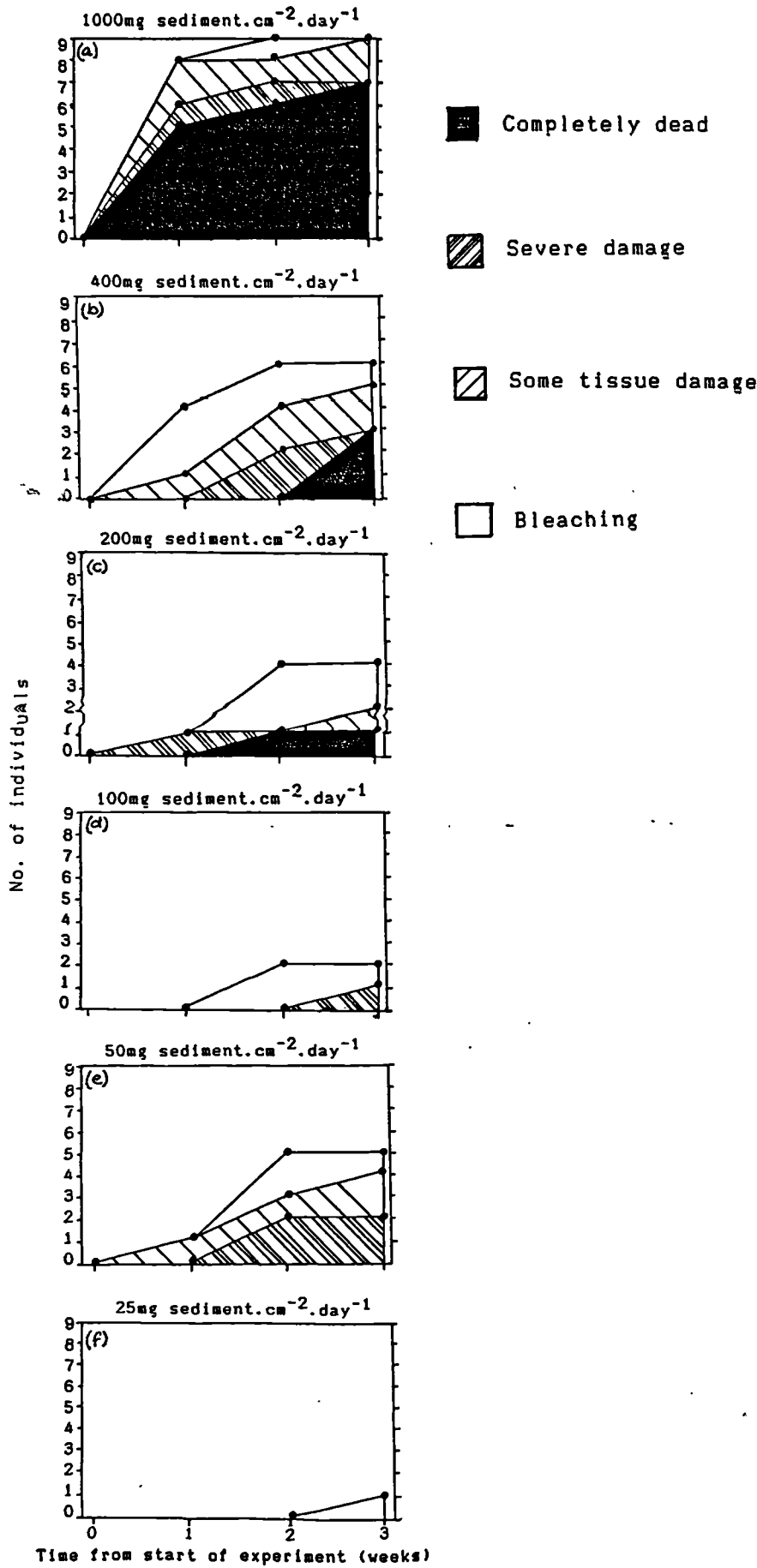
Figure **7.5.** Number of colonies showing damage at weekly intervals for sediment treatments 25-1000mg.cm^{-2}.day^{-1}.

around '5' (approximately 500-600mg) is critical. Unless this load was evenly distributed across more than half of the experimental colony (i.e. at less than 20mg.cm^{-2}) which was rare, individuals continued to accumulate further sediment and many of those in the high input treatments died rapidly. Provided that overlying sediment did not reach levels of around '5', experimental colonies corals seemed to become more efficient rejectors during the first few days of exposure to the treatments (sediment accumulation reduced).
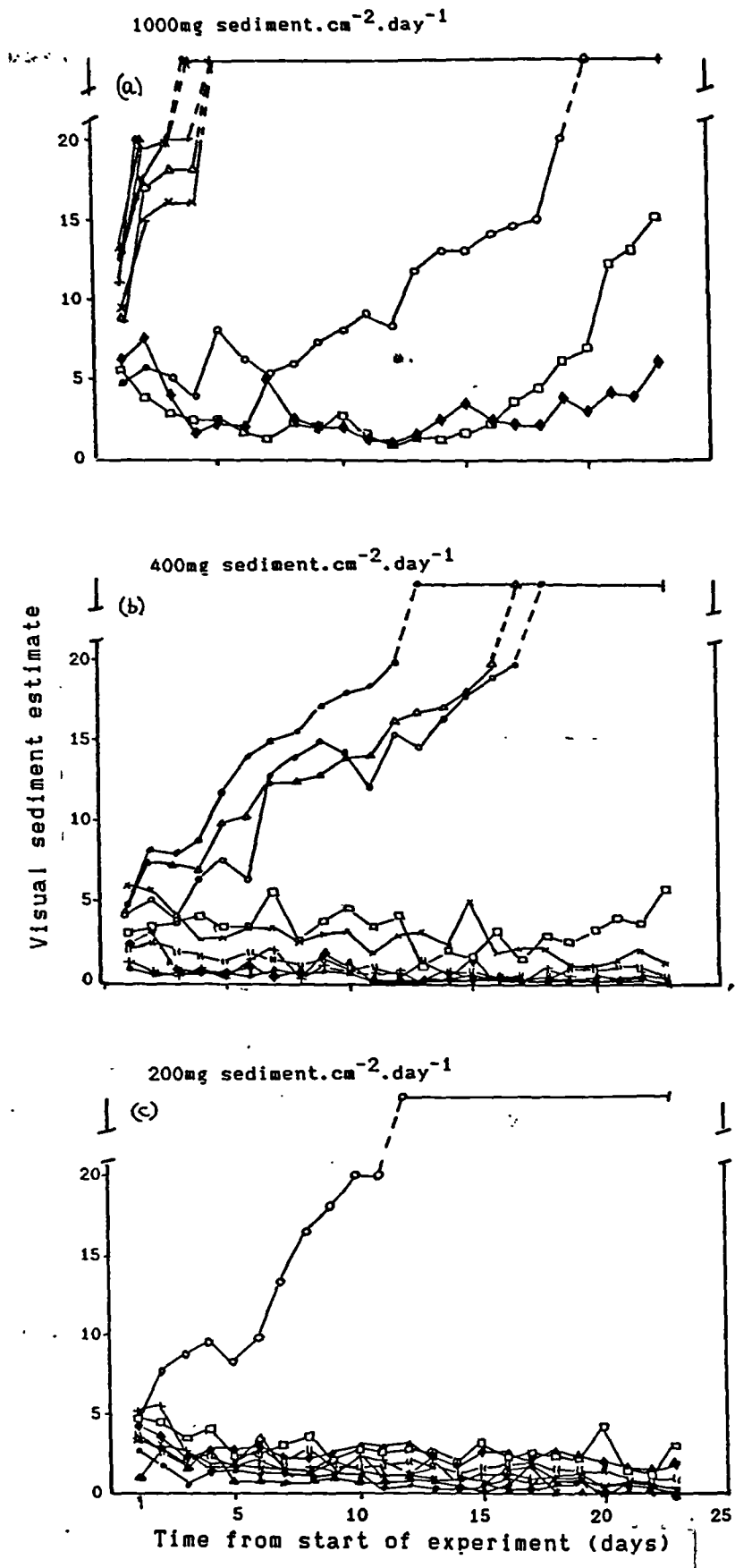
To test whether there was a significant reduction in sediment accumulation over time, estimates of sediment accumulation for all treated corals (excluding controls but including all treatments 1-1000mg sediment.cm^{-2}.day^{-1}) were averaged over three time periods: days 1-3, days 11-13 and days 21-23. Two Sign tests were performed on paired data for each coral (e.g. Sokal & Rohlf, 1981: p.449), the first comparing differences between the first three days and days 11-13, and the second comparing days 11-13 with the last three days.

In both cases there was a definite trend: less sediment remained on experimental colonies as time progressed. Differences were very highly significant during the first 10 day period (n=72, C=16, p<0.001), but less significant for the second period (n=66[1], C=23, p<0.05). In the first comparison, 13 of the 16 corals that showed increased sediment after 10 days had either died or were showing severe damage and all 16 were in treatment categories of 50-1000mg sediment.cm^{-2}.day^{-1}. The rejection capability of these individuals was probably overwhelmed by sediment influx.

There were no changes in turbulence level in the aquaria which could explain the reductions in sediment accumulation from passive influences. The decrease in accumulation of sediment for such a majority of corals suggests that they can acclimate to higher

1. 6 corals had died and are not considered

SEDIMENT ACCUMULATION PATTERNS OVER TIME

1000mg sediment.cm^{-2}.day^{-1}

(a)

400mg sediment.cm^{-2}.day^{-1}

(b)

Visual sediment estimate

200mg sediment.cm^{-2}.day^{-1}
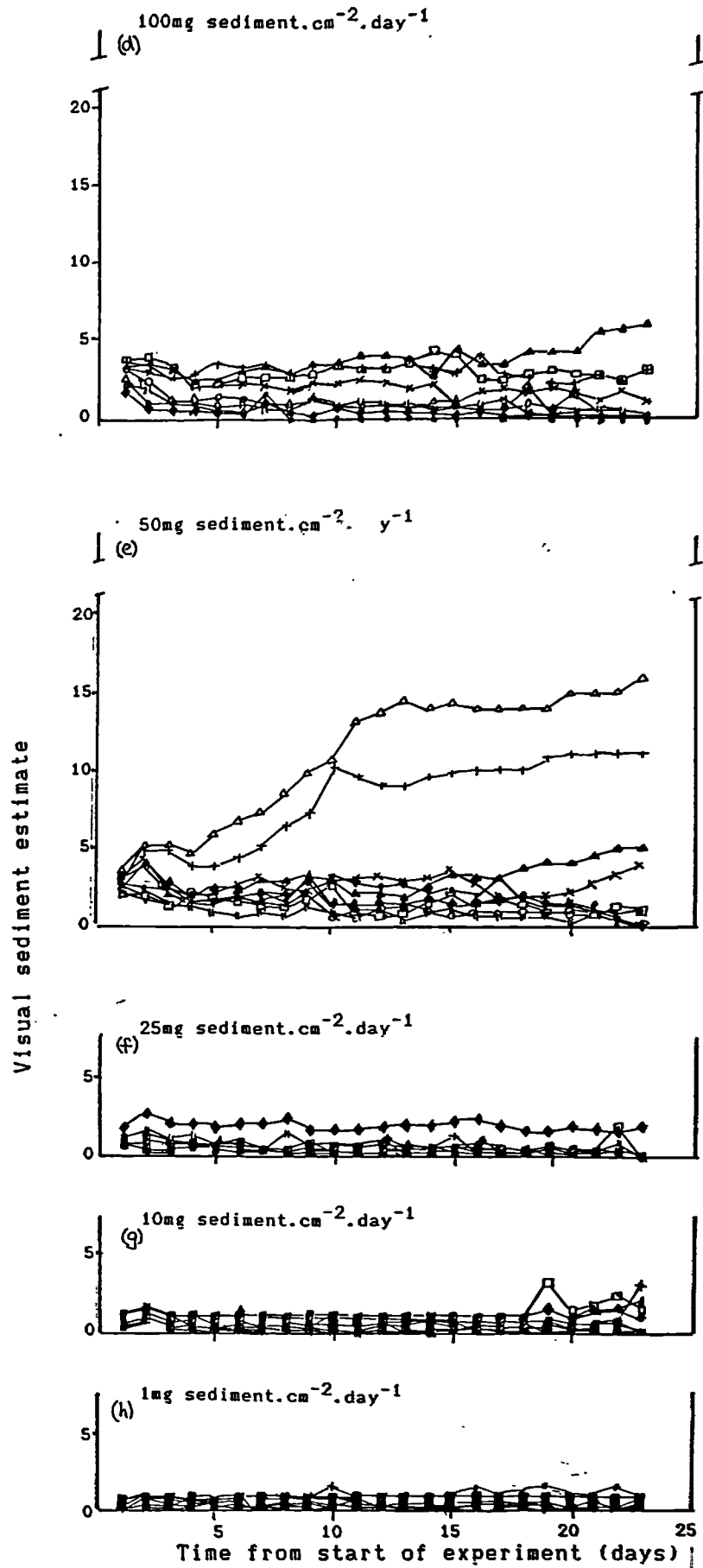
(c)

Time from start of experiment (days)

Figure 7.6 Daily accumulation of sediment for each of the nine replicates in each sediment treatment. The data points are the mean of five daily visual estimates.

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	Ref	Input Sediment Total Weight (mg/cm^2)	Mort	Min Convex	Overlying[1] Sediment Total Weight (mg)	Local Weight (mg/cm^2)	Equivalent Sediment Depth (mm)
					****		
(a)	1	1000	6	-1	41701.8	932.70	5.98
	2	1000	6	-1	43111.6	748.32	4.80
	3	1000	6	0	37431.9	734.09	4.71
	4	1000	6	0	29534.2	672.14	4.31
	5	1000	6	0	30196.4	614.99	3.94
	6	400	6	0	26161.5	606.05	3.88
	7	1000	6	1	27587.6	573.42	3.68
	8	400	6	-1	29710.9	546.84	3.51
	9	200	6	-2	28115.0	537.16	3.44
	10	400	6	-1	22411.2	527.84	3.38
	11	1000	6	2	23544.7	455.84	2.92
(b)	12	50	4	-3	14139.6	387.39	2.48
	13	1000	2	0	13072.1	310.68	1.99
	14	50	3	-2	606.8	296.01	1.90
	15	100	4	-1	876.9	237.01	1.52
	16	50	2	-1	7125.6	220.95	1.42
(c)	17	1000	1	1	570.0	57.05	0.37
	18	50	2	0	42.2	42.15	0.27
	19	400	1	1	555.2	35.63	0.23
	20	50	1	1	285.1	22.07	0.14
	21	200	2	-1	30.3	20.23	0.13
	22	400	2	0	45.3	18.11	0.12
	23	100	1	-1	184.8	16.68	0.11
	24	25	2	-1	37.6	12.32	0.08
	25	200	1	-1	117.2	11.64	0.07
	26	100	0	0	184.8	11.26	0.07
	27	400	1	0	104.1	9.77	0.06
	28	25	0	-1	117.2	8.18	0.05
	29	200	1	1	19.0	6.32	0.04
(d)	30	100	0	2	24.6	6.08	0.04
	31	200	0	0	129.6	5.50	0.04
	32	50	0	0	59.3	4.42	0.03
	33	200	0	0	51.6	4.07	0.03
	34	25	0	0	28.0	3.32	0.02
	35	200	0	2	30.0	3.02	0.02
	36	400	0	3	20.1	3.01	0.02
	37	25	0	3	18.2	2.99	0.02
	38	50	0	0	38.1	2.91	0.02
	39	50	0	1	37.4	2.51	0.02
	40	50	0	2	52.3	2.42	0.02
	41	100	0	0	68.7	2.24	0.01
	42	200	0	1	27.2	1.99	0.01
	43	100	0	0	16.1	1.81	0.01
	44	100	0	3	11.9	1.24	0.01
	45	400	0	2	24.8	1.07	0.01
	46	25	0	0	24.3	1.05	0.01
	47	25	0	0	24.6	1.04	0.01
	48	200	0	0	33.5	1.00	0.01
	49	100	0	2	13.2	0.85	0.01
	50	100	0	0	20.7	0.85	0.01
	51	25	0	0	15.1	0.72	0.00
	52	25	0	2	12.2	0.70	0.00
	53	25	0	1	22.9	0.67	0.00
	54	400	0	0	13.1	0.40	0.00

Table 7.2. Sediment input load, mortality, convexity and overlying sediment accumulation, sorted on weight per unit surface area in local regions of the colony (****). Dotted lines distinguish groups of colonies according to mortality: (a) all colonies died; (b) all colonies showed permanent damage; (c) colonies showed distinct effects; and (d) no colony showed any damage.

[1] Total Weight was measured at the end of the experiment. Local Weight and Sediment Depth are based on estimates of area of tissue covered by sediment. These should be treated cautiously as even more localised sediment accumulations probably occurred beneath but could not be accurately measured. Measurements suggest that depth of sediment later found to cause death were in the region of 1-1.5mm.

sediment load and that rejection effort increases in response[1].
Figures 7.6a-i indicate that the major part of this improvement may
take place in the first 3-5 days although further improvement was
often maintained.

Localised sediment accumulation

Careful measurements with a blunt-ended pointer (causing minimal
disturbance to experimental colonies) suggested that local sediment
accumulations, which were later found to have caused severe damage, were
in the order of 1.0-1.5mm thick provided that this depth remained for at
least 3 days. Tissues were generally very expanded (often 3-4mm)
beneath accumulations of sediment and accurate measurements were not
always possible. As tissues died, sediment accumulation could 'reach
depths of 3mm or more and spread out to neighbouring living tissues.

Surface area covered by sediment was used to convert total sediment
remaining at the end of 23 days to sediment weight per unit area, and to
provide estimates of sediment depth (Table 7.2). Reported values
represent means across the whole area covered. In reality, sediment
often accumulated in slight dips with only a thin layer of sediment
towards the outer edge; values shown in Table 7.2 should therefore be
treated with caution but are shown for general guidance. Of particular
interest from this Table is that some flat corals can effectively reject
high sediment loads of 100 and 400mg.cm^{-2}.day^{-1} for over three weeks
with minimal sediment accumulation (Refs. 41, 43, 48, 50 and 54) while
some flat or even convex corals cannot reject substantially lower loads
of 50mg.cm^{-2}.day^{-1} (Refs. 18 & 20). Thus, *Leptoria phrygia* shows a wide
range of intraspecies variability.

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1. An alternative hypothesis, that the differences in apparent
overlying sediment load were due to a change in observer estimation, was
considered. There are a number of reasons why it seems very unlikely.
Firstly, estimation did not start at the beginning of the experiment as
this method had been used in previous field and laboratory experiments
and in pre-experiment calibrations. Secondly, there was no evidence of
significant changes from the pre- and post-experiment calibration
estimates. Thirdly, independent evidence comes from an earlier
experiment with *Pocillopora damicornis* for which sediment remaining was
estimated from photographs using a grid of points (see Appendix A).
These corals also showed a net improvement in sediment rejection over
weekly time periods.

DISCUSSION

Few medium- or long-term experiments have been carried out with daily influxes of sediment to corals. Rogers applied fine to coarse calcareous sand sediments to the Caribbean corals *Acropora cervicornis* (Rogers, 1979) and *A. cervicornis, A. palmata, Montastrea annularis, Diploria strigosa* and *D. clivosa* (Rogers, 1983) in single doses of 200, 400 and 800mg.cm^{-2} and in doses of 200mg.cm^{-2}.day^{-1} for approximately six weeks. Descriptions of the sediments suggest that they are not dissimilar to those used in the present experiment. *Diploria strigosa* and *Diploria clivosa* are both faviids with meandroid skeletons similar in structure to *Leptoria phrygia*. These experiments were carried out on whole colonies in the field. Little or no damage occurred to the branching *Acropora cervicornis* whereas the wider flat branches of *A. palmata* suffered considerable mortality from only one application of 200mg.cm^{-2}. *Montastrea annularis* showed some bleaching with a single dose of 400mg.cm^{-2} and sediment accumulated in crevices. *Diploria strigosa* did not show any significant damage although the single colony of *D. clivosa* studied, suddenly developed an abnormal colour after 38 daily applications and thereafter rejected sediment less readily, and some mortality occurred.

Hodgson (1990) reported high tissue damage in *Oxypora glabra, Porites lobata,* and *Pocillopora meandrina* after 10 days at daily influxes of approximately 30mg.cm^{-2}.day^{-1} in the laboratory. Unfortunately it is difficult to compare these results because there is no information about convexities, or about sediment type beyond the description 'fine marine sediment'. However, it is possible that the sediments were of a different qualitative type than those used in the present experiment.

The present study demonstrates that mortality of *Leptoria phrygia* is strongly correlated with the weight of sediment overlying the coral tissues. This is principally determined by input levels and the local convexity of the colony, but is modified by individual colony variability in rejection capability and sediment tolerance. However, there was no evidence that either meander complexity or the number of meander ends had any effect on mortality (see Chapter 2) but subtle

influences may have been obscured by overwhelming effects of other factors.

In the laboratory conditions of this experiment, the threshold for mortality of this species was $25mg.cm^{-2}.day^{-1}$ over a three week period. In Chapter 5 it was demonstrated that sedimentation rates around Lizard Island can reach levels of this order. The results from the present experiment would argue that many horizontal or sediment-trapping tissues will die under these conditions, unless other factors reduce adverse effects. Population studies, described in Chapter 5, show that the ratio of projected to total surface area, and the area of sediment-trapping tissues of *L. phrygia* do show changes ross sediment gradients. Although sedimentation rates could be exceptionally high in Exposed sites, the predominant grain size was large (coarse to granule) and turbulence was also high. As discussed in Chapter 3, overlying sediments of fine sediment grain sizes may be a more serious threat than coarser sizes by having a greater effect both on the diffusion barrier and on light attenuation, but also, the residence times of sediments on the tissues in Exposed sites is likely to be short.

Leptoria was not one of the species which showed major differences in rejection behaviour in the laboratory and the field (Chapter 3), and it remained healthy and apparently thrived under laboratory conditions. In fact, all available evidence suggests that mortality in the laboratory may *underestimate* that in the field. All colonies that showed mortality (from the same same sediment type and size) during the field tolerance experiment (Chapter 4) had been affected by the fourth day, whatever the level of input sediment (50mg, 200mg or $400mg.cm^{-2}.day^{-1}$), and in other experiments (Chapter 3), field mortality occurred within 48 hours at $200mg.cm^{-2}.day^{-1}$. In the present experiment, only corals from the highest treatment showed tissue mortality after four days; mortality of the remainder was not observed until the sixth day. This difference may be due to different responses to the frequency of influxes, but this could not explain why mortality in the field at a single dose of $50mg.cm^{-2}.day^{-1}$ would be faster than five doses per day of $80mg.cm^{-2}$ in the laboratory ($400mg.cm^{-2}.day^{-1}$ in total). An alternative is that differences are due to diffusion gradients, as ambient oxygen levels in the aquaria were at saturation. Or it may be that there is a difference in bacterial contamination of

sediments: in Hodgson's recent laboratory work on the sediment tolerance of Hawaiian species (Hodgson, 1990), he demonstrated that bacteria could play an important role in tissue mortality of corals.

In summary, this study suggests that morphologically sensitive tissues of *Leptoria phrygia* are vulnerable to environmental sedimentation rates of $25mg.cm^{-2}.day^{-1}$. It is very likely that chronic loads considerably lower than this level will cause mortality of strongly convex to flat tissue surfaces and that these morphological shifts will be detectable in the community in the ratio of projected to total surface area as shown in Chapter 5. Furthermore, sediment loads of $50mg.cm^{-2}.day^{-1}$ (and more) for periods of only a few days, will cause mortality of vulnerable tissues.

Lipid is a dominant biochemical constituent that has both a structural and a storage role in the physiology and maintenance of a wide range of marine organisms (Lawrence, 1976). If lipid can be regarded as an energy store for an organism, and assuming that other compensating adaptations are not available, it is reasonable to suppose that lipid levels would decline under conditions that either reduce the organism's ability to feed, or increase the cost of maintenance. Changes in overall lipid levels may therefore be an indicator of certain forms of stress which require mobilisation of food reserves.

Some support for this hypothesis is available in the literature: it has been demonstrated for many marine phyla (annelids, echinoderms, crustacea and molluscs, among others), that lipid levels may be high in well-fed individuals, but become depleted as a result of starvation (see discussions in Lawrence, 1976). There is also some evidence that lipid levels may vary with certain other environmental parameters such as temperature (Mauchline & Fisher, 1969).

Symbiotic coelenterates have at least two sources of organic nutrients: heterotrophic, principally from tentacular feeding; and autotrophic, by translocation of nutrients from endosymbiotic zooxanthellae. As with other marine phyla, lipids are known to be important in both structural and storage roles (Bergmann et al, 1956; Patton et al, 1977; Zamer & Shick, 1989) and, in corals, occur in both the tissues and the skeletal matrix (Young et al, 1971). Lipids have, in fact, been suggested as a principal medium for energy transfer between zooxanthellae and host (Kellogg & Patton, 1983; Patton & Burris, 1983).

A number of studies suggest that lipids constitute 25% or more of the dry weight of anemones (Bergmann et al, 1956; Blanquet et al, 1979; Kellogg & Patton, 1983). Although the majority of hard corals generally have somewhat lower lipid levels (Meyers, 1977; Szmant-Froelich & Pilson, 1980; Glynn et al, 1985; Chapter 6b) similar values have been recorded (Patton et al, 1977). Significantly, Patton and his colleagues have estimated that 75% of the lipid in Pocillopora capitata is storage lipid.

There is evidence in the coelenterates that lipid levels are affected by food availability. When compared against controls, Cook and Kelty (1982) detected a decline in lipid in starved hydra. The symbiotic/aposymbiotic coral species *Astrangia danae* showed a similar response (Szmant-Froelich & Pilson, 1980), although in some symbiotic coelenterates, the time-course of lipid depletion appears to be modified in the light due to translocation of biochemical materials from the photosynthetic zooxanthellae (Fitt & Pardy, 1981). There is also some evidence that differences in lipid levels and composition in coelenterates can result from variations in temperature (Hill-Manning & Blanquet, 1980), and Glynn *et al* (1985) attributed the decline in lipid levels oi .ocillopora damicornis and their crustacean symbionts to ocean warming from El Nino.

Interest in lipid levels as a potential indicator of general stress in reef corals has increased in recent years because of the possibility that it may provide an early warning of reef degradation. The evidence above indicates that environmental conditions which hinder heterotrophic nutrition and autotrophic nutrition simultaneously, should affect ambient lipid levels in symbiotic - coelenterates. Increased sedimentation is one such condition. Many researchers have speculated on the inhibiting effect of precipitating sediments on heterotrophic nutrition in corals (e.g. Szmant-Froelich *et al*, 1981; and see Pastorok & Bilyard, 1985), and increased suspended sediment in seawater reduces light available for photosynthesis (e.g. Jerlov, 1970; Kirk, 1983). Although detailed qualitative analyses of lipid classes may be of subsequent importance in the understanding of such stresses, estimates of total lipids to establish gross effects may have an important role in studies of stress in corals.

CHAPTER 8

LIGHT ATTENUATION DUE TO OVERLYING SEDIMENT, AND ITS POTENTIAL EFFECT ON THE PHOTOSYNTHESIS TO RESPIRATION RATIO IN *LEPTORIA PHRYGIA*

LIGHT ATTENUATION DUE TO OVERLYING SEDIMENTS, AND ITS POTENTIAL EFFECT ON THE PHOTOSYNTHESIS TO RESPIRATION RATIO IN *LEPTORIA PHRYGIA*

SUMMARY

Attenuation of light caused by increasing densities of mixed reefal and terrigenous sediments of a range of particle sizes was measured in the laboratory and *in situ* at 3m depth. Sediment-related light attenuation is ecologically substantial and overlying sediments could reduce incident light to less than 20% of ambient at densities commonly found on a range of corals under natural field conditions. For a given weight of sediment per unit area, light attenuation increased as particle size decrease. For a given particle size and weight per unit area, terrigenous sediments caused greater light attenuation than reefal sediments.

Oxygen flux during photosynthesis and respiration were measured using respirometry techniques and used to construct photosynthesis versus irradiance curves for the reef coral *Leptoria phrygia*. Mean daily whole-colony photosynthesis to respiration (P/R) ratios for *L. phrygia* under idealised light conditions, were 1.36 at 3m and 1.18 at 6m depth. An examination of the effect of sediment-related light attenuation on these P/R values predicts that substantially less than 1mm, and generally less than a layer one particle thick, of overlying sediment is required to cause P/R ratios to fall below 1. Ecological and physiological consequences of sediment loading for reef corals are discussed.

INTRODUCTION AND GENERAL METHODS

Sediment may change the energy budget of reef corals by decreasing symbiont photosynthesis through light attenuation, by decreasing heterotrophic feeding, or by increasing energy expenditure through active sediment removal and damage repair. The present study quantitatively examines the potential effect of sediment-related light attenuation on the energy budget of *Leptoria phrygia* which has been shown to be intolerant of overlying sediments (Chapters 3, 4 and 7).

The symbiotic zooxanthellae of reef-building corals maintain the ability to photosynthesise while in the tissue of their host, and have been shown to translocate a significant proportion of their

photosynthetic production to the coral host (Muscatine, 1967; Trench, 1979; Battey & Patton, 1987). The amount of photosynthate translocated can be sufficient to cater for the respiratory and growth organic carbon requirements of corals (Muscatine *et al*, 1981; McCloskey & Muscatine, 1984; Porter *et al*, 1984), thereby suggesting that the symbioses of reef-building corals and their zooxanthellae are potentially autotrophic. However, most corals are well-equipped to feed heterotrophically, and do so, perhaps to supplement their endogenous sources of organic carbon, and perhaps as a way of obtaining organic nitrogen and phosphorus.

The ratio of total colony photosynthesis (P_c) to total respiration (R_c) over 24 hours can provide a measure of the extent to which the colony can be maintained by autotrophy[1]. Total photosynthesis is dependent upon the quantity and quality of incident light, and any impediment such as sediment which reduces these levels, must alter the photosynthesis to respiration (P_c/R_c) ratio. At the point at which the ratio falls below 1, the colony can no longer be sustained by autotrophy and reductions in growth rate, impaired development of gametes, or mobilisation of energy reserves may ensue unless some other compensatory adaptations can occur. One of the -most direct means of energy compensation would be to increase heterotrophic feeding activity. However, overlying sediments can hinder or inhibit active feeding behaviours (Chapter 2), rendering this option ineffective.

The aim of this study is to determine the minimum level of overlying sediment required to reduce the P_c/R_c ratio of *Leptoria phrygia* to less than 1. Firstly, the normal relationships between net photosynthesis and natural light levels for this species were determined over a 24 hour period using respirometry techniques. From these data, a maximum mean P_c/R_c ratio was calculated for idealised light conditions and assuming that all excess photosynthate is successfully translocated from symbiont to host. The light attenuation properties of the four principal sediments used during earlier work, as well as two grain sizes of a

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1.   Muscatine. *et al* (1981) rigorously define P/R as the ratio of zooxanthellar photosynthesis to animal respiration modified by a carbon-translocation factor. For the present purpose, P/R is defined in terms of the whole colony and the effect of translocation is considered in the Discussion.

mainland terrigenous sediment, were examined in both the laboratory and at 3m depth in the field. These attenuation data were combined with the light saturation data to examine P_c/R_c ratio responses to differences in overlying sediment sizes and loads. Analyses are restricted to effects of sediment-related *light attenuation* alone, but the results are discussed in relation to other potential effects of sediment on the coral's energy budget.

TECHNIQUES

Net photosynthesis of *Leptoria phrygia*

Collection and maintenance of corals. Cores of *Leptoria phrygia* were collected from 3-6m depth on the exposed reef front of Coconut Bay, at Lizard Island[1] as described in Chapter 7. Each sample was taken from a different colony and was maintained in flow-through aquaria at Lizard Island Research Station for 6 weeks prior to the start of experiments. Light levels in these aquaria were equivalent to 40-45% of just-subsurface- light at the collection site, which is equivalent to light levels towards the lower end of the collection depth range (see Figure 5.4a). Experimental colonies had a mean surface area of 50cm^2 with almost flat tissues, and were of an even, light brown colour.

Measurement techniques and equipment. Measurements of net photosynthesis were carried out under natural light. Sealable plastic chambers (approximately 1 litre capacity, Plate 8.1) were submerged in a large outdoor glass aquarium. Light was measured with a LI-COR quantum sensor (Li 1935A) placed next to the chambers. Maximum light levels at solar noon in the aquarium were reduced to levels equivalent to approximately 3m depth at the collection site by layers of shade cloth. Water within the chambers was mixed by magnetic stirrers, and the corals were placed on top of a perforated stand to allow free circulation. Oxygen was measured using Clark-

1. For a further description of Lizard Island and the collection site, see the General Introduction and Chapter 5.
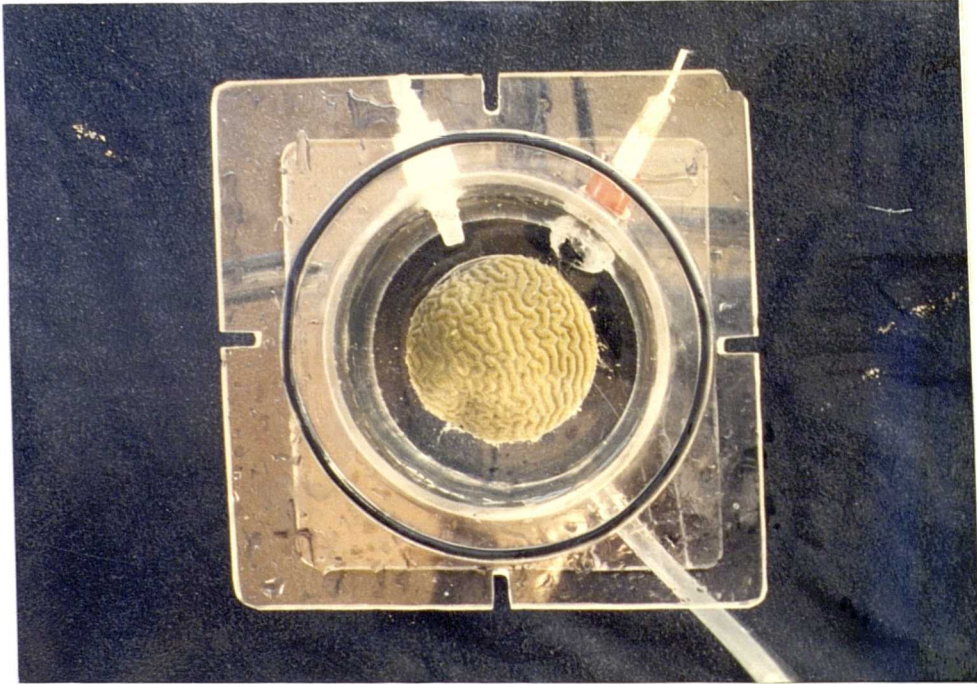
Plate 8.1.   Respirometry   chamber with   *Leptoria phrygia* on a central stand.

type polarographic oxygen electrodes constructed according to the method of Mickel *et al* (1983) positioned close to the stirrer. The chambers were flushed with fresh seawater from the surrounding medium for 5 minutes every hour. Temperature was measured using a small waterproof thermocouple within the experimental aquarium.

Oxygen, temperature and light were recorded once every 6 seconds via the portable data acquisition and analysis system DATACAN (Sable Systems, Los Angeles) on a 640K laptop computer.

Two or (on one occasion) three corals were run simultaneously for a minimum of 24 hours on each of three occasions in September 1988, giving a total of seven colonies. Oxygen concentrations in each chamber were converted to ug weight (accounting for chamber volume and displacement volume of the colony) and differentiated by hour to provide instantaneous rates of change. The mean and standard deviation of each 50 consecutive points (i.e. 5-minute segments) were calculated and normalised to coral surface area (cm^2) and to chlorophyll *a* (ug). Light (I) was averaged across the same time periods and net photosynthesis to light (P/I) curves constructed from 5-minute means using the hyperbolic tangent equation (Jassby & Platt, 1976; Chalker, 1981)

$$P_c^n = P_{c.max}^g \cdot tanh(I/I_k) + R_c$$

or $$P_c^n = P_{c.max}^g \cdot tanh(\alpha I/P_{c.max}^g) + R_c$$

Eqn. 1

where P_c^n is the net photosynthesis of the coral colony for irradiance (I). $P_{c.max}^g$ is the maximum gross photosynthesis at saturating irradiance, alpha (α) is the initial slope of the curve of photosynthesis to light, I_k is the light intensity at which the initial slope (α) meets the horizontal asymptote ($I_k = P_{c.max}^g/\alpha$). The compensation light intensity (I_c) at which respiration is exactly balanced by photosynthesis was calculated from the hyperbolic tangent equation by setting $P_c^n = 0$.

Using light attenuation characteristics for Exposed regions (Chapter 5) and a noon maximum just-subsurface light of

approximately 1600umol(photons).m^{-2}.s^{-1} (this study[1]), maximum noon light levels of 1123 and 788 umol(photons).m^{-2}.s^{-1} at 3 and 6m depth respectively were estimated for the collection site. Idealised light curves for the region were generated from the equation

$$I_t = I_{max} \cdot \sin(t/d \cdot) \qquad\qquad \text{Eqn. 2}$$

where I_t = irradiance at time t, I_{max} = maximum irradiance at the relevant depth, t = time from first light (hours) and d = day length (hours). This equation, when compared empirically with maximum diurnal light levels during experiments, provided a good simulation of the light regime.

For the idealised light curve, daylength (d) was assumed to be 12 hours. Mean 24 hour P_c^g/R_c ratios were calculated by integrating beneath the 24 hour net photosynthesis curve generated from the ideal light curve (Eqn. 2) and light saturation curve (Eqn. 1) for individual colonies. These idealised maximum P/R values were used in predictions based on sediment attenuation.

Biomass parameters. At the end of each experiment, corals were taken through a freeze-thaw procedure (Chapter 6a) and waterpikked into Whatman GF/C filtered seawater. Samples were taken for chlorophyll analysis as described in Chapter 6a. Surface area was measured by the tinfoil method of Marsh (1970).

Attenuation of photosynthetically active radiation (PAR) by sediment

Attenuation of PAR resulting from layers of reefal and terrigenous sediments was examined both in the laboratory and next to *Leptoria* colonies at 3m depth in Coconut Bay.

Downward irradiance. PAR was measured with a Stipe Underwater Lightmeter (a cosine collector using a selenium photocell, with approximately level response between 400 and 700nm, Drew, *pers.*

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1. Chisholm (1989) gives slightly higher values of 1629-1689 umol(photons).m^{-2}.s^{-1} for same region and month (September).

comm.). This meter has a flat, circular aperture responding to downward irradiance[1].

Sediments. Locally-derived sediments were identical to those used in previous experiments and collected from the same source. The composition was approximately 70% calcium carbonate and 30% quartz sand and was sieved into four size ranges, *silt* (<63um), *fine sand* (63-250um), *coarse sand* (500um-1mm) and *granules* (1-3mm). In addition, *fine* (63-250um) and *coarse* (500um-1mm) terrigenous sediments collected from a mainland beach just north of Cairns were . also tested. The terrigenous sediment was darker and more angular, with a substantially higher mineral and detrital content.

Experimental procedure. In order to measure light attenuation for each sediment, a clear perspex petri dish was placed on top of the lightmeter and known weights and volumes of sediments were spread evenly across the surface at increasing densities from 0 to 1000mg.cm^{-2}. The petri dish had no detectable effect on meter readings. Two sets of tests were carried out.

(a) **15cm depth of water in laboratory aquaria.** Each sediment type was tested three times at each density. The light meter was placed at the bottom of a large aquarium with 15cm depth of water above the petri dish (conditions more or less identical to the laboratory experiment, Chapter 7). . All tests took place on cloudless days within one hour of solar noon.

(b) **3m depth *in situ* in Coconut Bay.** Three replicate runs were carried out with all reef sediments but silt (which went too readily into suspension). Terrigenous sediments were not tested. The light meter was placed close to a *Leptoria* colony. Readings were made during cloudless periods within one hour of solar noon. Data were slightly more variable than those in the laboratory because of the effects of ripples at the water surface.

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1.   The cross-calibration of LI-COR globe and Stipe Underwater Lightmeter was very close, with regression statistics of r^2=0.996 (n=48).
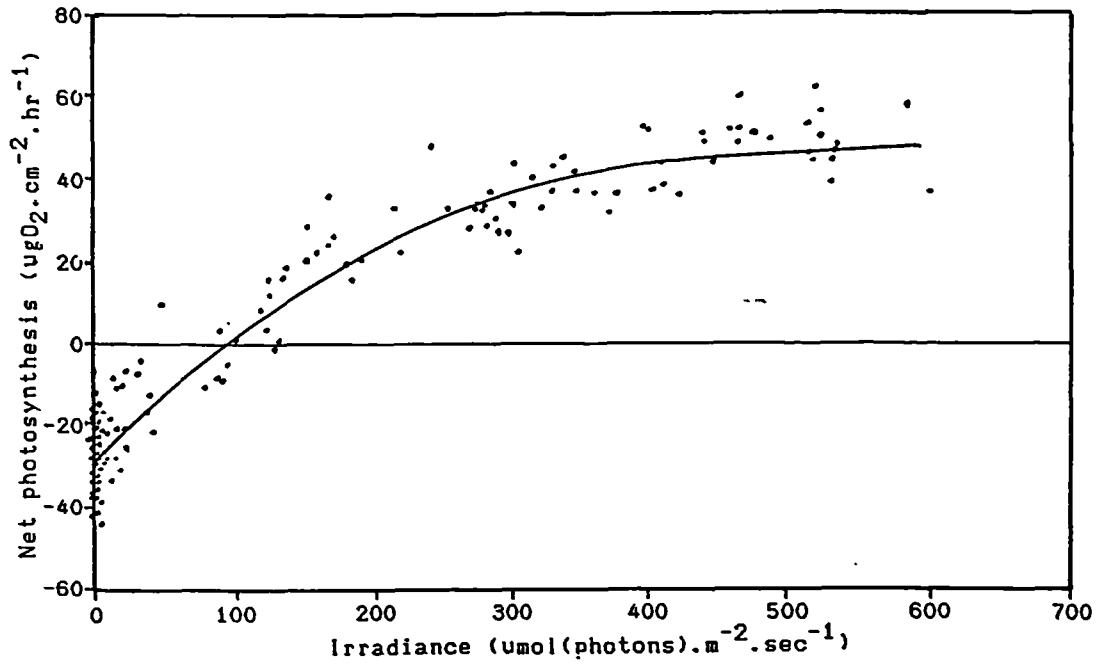
NET PHOTOSYNTHESIS TO IRRADIANCE CURVE

Figure 8.1. Typical light saturation curve for *Leptoria phrygia* showing fitted curve.

RESULTS

Photosynthesis and respiration of *Leptoria phrygia*

A typical net photosynthesis to irradiance curve for *Leptoria phrygia* is shown in Figure 8.1. Colonies had acclimated to light levels of 40-45% of ambient just-subsurface light, equivalent to conditions at approximately 6m at the collection site. Parameters describing the light saturation curve for these conditions are summarised in Table 8.1 for the seven replicate colonies normalised both to surface area (cm^2), and to zooxanthellar chlorophyll *a* (ug).

The idealised P_c^g/R_c (24 hours) ratio for 6m depth was calculated for each coral giving a mean of 1.18 ± 0.07 ($\pm$SE, n=7; Table 8.2). A P_c^g/R_c ratio was calculated for 3m from the same saturation curve characteristics (i.e. without allowing for changes due to photoadaptation, but see Discussion).

By progressively reducing the 24-hour *idealised irradiance values* by an attenuation factor (i.e. reducing I_{max} to 90%, 80%, 70%, 60%, etc., of its original value and generating daylight irradiance values for the new maximum irradiance) and integrating to calculate P/R ratios, the percentage of normal ambient light resulting in a mean P/R ratio of 1 was estimated to be 52% of $I_{max(3m)}$ and 73% of $I_{max(6m)}$ (Table 8.2). A similar procedure was adopted to evaluate the light level at which the minimum P/R ratio would be reduced to 1.

Sediment-related light attenuation

For a given sediment weight per unit area, light attenuation caused by overlying sediments increased as particle size decreased (Figures 8.2 & 8.3). Furthermore, for the same particle size and weight per unit area, the terrigenous sediment caused higher light attenuation than its reefal equivalent.

For the same sediment size, light attenuation was generally slightly higher when measured *in situ* than at 15cm depth in the laboratory. This may be a result of spectral changes in ambient light with depth.

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Parameter	Area (cm^2) (Mean$\pm$SE)	Chlorophyll a (ug) (Mean$\pm$SE)
R_c	-19.72 ± 1.65 $(ugO_2 \cdot cm^{-2} \cdot hr^{-1})$	-2.12 ± 0.21 $(ugO_2 \cdot (ugChla)^{-1} \cdot hr^{-1})$
Alpha	0.290 ± 0.052 $(ugO_2 \cdot cm^2 \cdot hr^{-1} \cdot uE^{-1} \cdot m^2 \cdot s)$	0.0339 ± 0.010 $(ugO_2 \cdot (ugchla)^{-1} \cdot hr^{-1} \cdot uE^{-1} \cdot m^2 \cdot s)$
I_c	69.73 $(uE \cdot m^{-2} \cdot s^{-1})$	64.09 $(uE \cdot m^{-2} \cdot s^{-1})$
I_k	251.93 $(uE \cdot m^{-2} \cdot s^{-1})$	234.22 $(uE \cdot m^{-2} \cdot s^{-1})$
P_c^n max	53.35 ± 7.19 $(ugO_2 \cdot cm^{-2} \cdot hr^{-1})$	5.82 ± 0.84 $(ugO_2 \cdot (ugChla)^{-1} \cdot hr^{-1})$
P_c^g max	73.06 ± 8.49 $(ugO_2 \cdot cm^{-2} \cdot hr^{-1})$	7.94 ± 1.02 $(ugO_2 \cdot (ugChla)^{-1} \cdot hr^{-1})$

Table 8.1. Summary of photosynthesis/light parameters for *Leptoria phrygia*. Mean$\pm$SE for n=7.

	3m	6m
Maximum solar irradiance ($uE.m^{-2}.s^{-1}$)	1123	788
$P^g_{C\ max}/R_C$ (24hr) (n=7) Range: max min	1.36 ± 0.06 1.60 1.15	1.18 ± 0.07 1.53 1.01
Percentage of ambient light which would lower mean P/R ratio to 1 (n=7)	51.65% (i.e. I_{max} attenuated to 580 $uE.m^{-2}.s^{-1}$)	73.60%
Percentage of ambient light which would lower *minimum* P/R ratio (above) to 1	69.28% (i.e. I_{max} attenuated to 778 $uE.m^{-2}.s^{-1}$).	98.73%

Table **8.2.** Idealised P^g_C/R_C (24hr) ratios for *Leptoria phrygia* at 3 and 6m based on maximum irradiance (I_{max}) values for each depth calculated from light attenuation curves for Exposed areas (see Chapter 5). P^g_C/R_C (24hr) is expressed as the mean$\pm$SE of 7 replicates. followed by the range.
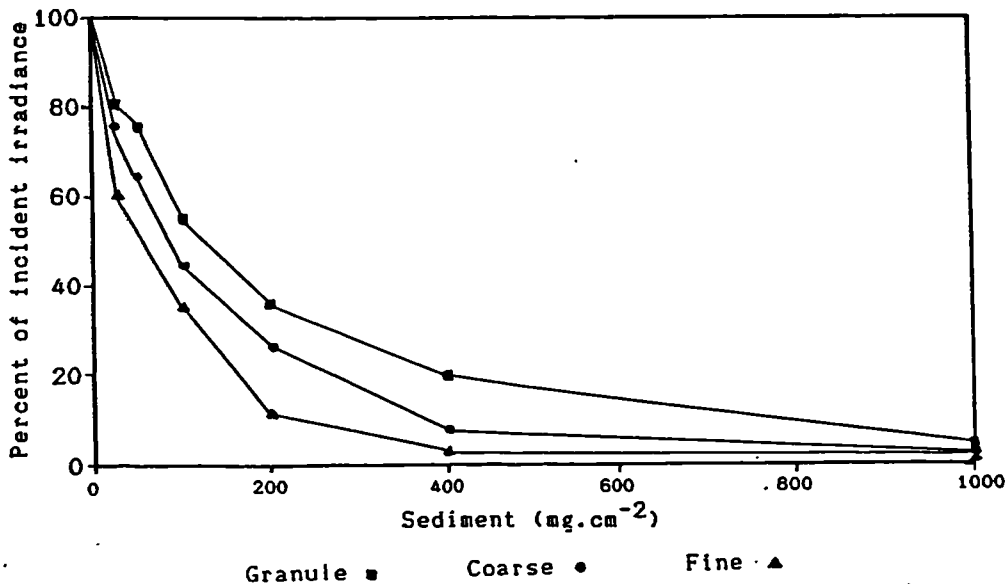
SEDIMENT-RELATED LIGHT ATTENUATION AT 15cm DEPTH
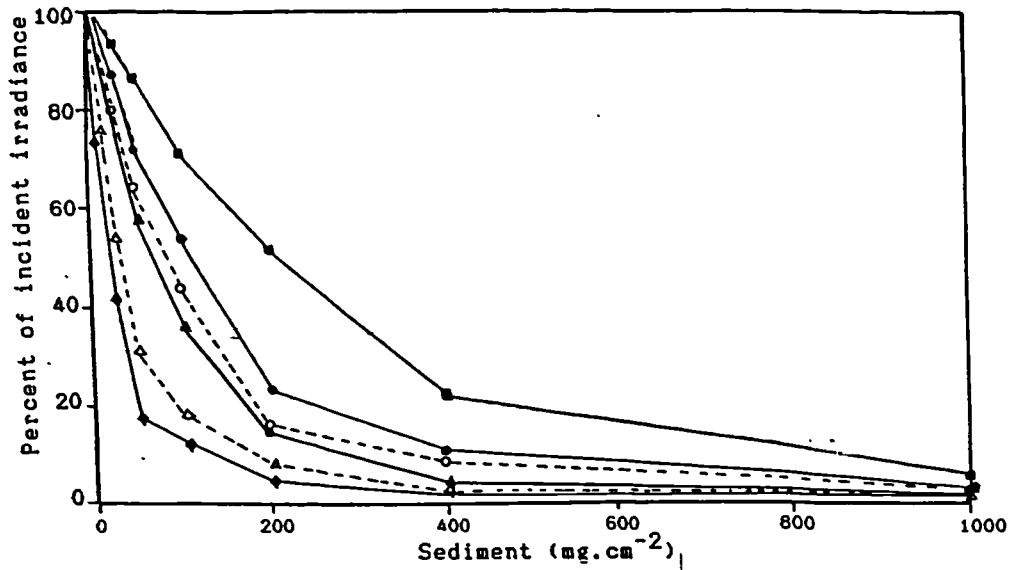
Granule ■   Coarse ●   Fine ▲   Silt ◆

Figure 8.2. Attenuation of light (PAR) by
increasing densities of reefal (solid symbols
and lines) and terrigenous (open symbols and
dashed lines) sediments at 15cm depth laboratory
aquaria.

SEDIMENT-RELATED LIGHT ATTENUATION AT 3m DEPTH

Granule ■   Coarse ●   Fine ▲

Figure 8.3. Attenuation of light (PAR) by
increasing densities of reefal sediments at 3m
depth in Coconut Bay.

Synthesising the effects of sediment-related light attenuation with P/I characteristics for _Leptoria phrygia_

By reference to the sediment-light attenuation curves for 3m in Coconut Bay (Figure 8.3), the approximate density of sediments required to cause light attenuation to critical levels of 52% (3m) and 73% (6m) of ambient light (Table 8.2) were estimated and are shown in Table 8.3. The approximate equivalent depth of sediment is also indicated and shows that for 6m depth, a layer of less than 1 particle thickness is sufficient to reduce overall light to levels insufficient to sustain P/R ratios of greater than unity.

As an alternative approach, sediment densities of $150mg.cm^{-2}$ and $300mg.cm^{-2}$ were chosen to approximate 1 and 2mm depth of sediment respectively. The light attenuation caused by these sediment depths was simulated for an increasing number of daylight hours until mean P/R ratios fell to unity (Table 8.4). At 6m, overlying sediments at densities of $300mg.cm^{-2}$ (approximately 2mm depth) reduce P/R ratios to 1 after only 1-3 hours.

DISCUSSION

This study shows that both sediment size and sediment quality have a very significant effect on light attenuation, and that relatively low levels of overlying sediment can cause appreciable reductions in the P/R ratio of _Leptoria phrygia_. As an initial estimate, substantially less than one millimetre of sediment on the tissue surface could prevent a coral from being fully autotrophic. Furthermore, there are several reasons why the results and interpretations reported here would be conservative and would _underestimate_ the effects of acute sediment influxes on coral energetics.

(a) P/R ratios have been calculated on the basis that all excess photosynthate is successfully translocated to the animal. This may not be so.

(b) P/R ratios have been generated from idealised light conditions. Maximum irradiances over the daylight period at Lizard Island during the

Sediment size		Approximate weight causing attenuation of light to the indicated percentage of ambient	
	Weight per 1mm depth.cm^{-2}	51%	73%
Granule (1-3mm)	139mg	120mg.cm^{-2} (0.9mm)	50mg.cm^{-2} (0.4mm)
Coarse (500um-1mm)	114mg	80mg.cm^{-2} (0.7mm)	25mg.cm^{-2} (0.3mm)
Fine (63-250um)	156mg	50mg.cm^{-2} (0.3mm)	<25mg.cm^{-2} (0.2mm)

Table 8.3. Weight of reefal sediments required to reduce ambient light at 3m and 6m to levels at which the P_c^g/R_c (24hr) ratio for *Leptoria phrygia* would fall below 1. Numbers in parentheses give the (approximate) equivalent depths of sediment based on weight of sediment occupying 1mm depth over an area of 1cm^2. At a water depth of 6m, these correspond to less than one layer of sediment.

NUMBER OF DAYLIGHT HOURS OF OVERLYING SEDIMENT REQUIRED TO CAUSE P/R RATIOS TO FALL TO LESS THAN 1

Depth	3m		6m	
Weight of sediment	$150mg.cm^{-2}$	$300mg.cm^{-2}$	$150mg.cm^{-2}$	$300mg.cm^{-2}$
	Daylight	hours	Daylight	hours
Sediment size				
Granule	10	5-6	4	2-3
Coarse	7	4-5	.3	2
Fine	4-5	3	2	1-2

Table 8.4. Number of daylight hours of overlying sediment at levels of $150mg.cm^{-2}$ or $300mg.cm^{-2}$ required to reduce overall daily irradiance to levels at which the P_c^g/R_c (24hr) ratio for *Leptoria phrygia* would fall to less than 1. Equivalent depths of sediment are as follows: *Granule* 150mg: 1.1mm, 300mg: 2.2mm; *Coarse* 150mg: 1.3mm, 300mg: 2.6mm; and *Fine* 150mg: 1mm; 300mg: 1.9mm. .

three full days of the experiment were closely simulated by the idealised sine curve, but intermittent cloud cover often reduced light levels below saturation levels and would lead to less than maximum P/R ratios in reality.

(c) P/R ratios for 3m have been calculated from light saturation parameters estimated from corals acclimated to lower light levels. Several authors have shown that corals growing in shade or low-light show metabolic photoadaptation including increases in (a), and decreases in R, I_k and I_c (Kawaguti, 1937; Redalje, 1976; Wethey & Porter, 1976a,b; Davies, 1977, 1980; Zvalinski et al, 1980; Falkowski & Dubinsky, 1981; Chalker et al, 1983; McCloskey & Muscatine, 1984; Porter et al, 1984; Gattuso, 1985). With increasing depth, corals also tend to become darker, principally as a result of increasing concentrations of chlorophyll and accessory pigments (Falkowski & Dubinsky, 1981; Titlyanov et al, 1981). These changes generally lead to increased efficiency in the utilisation of incident light such that shade-adapted corals, when placed in conditions of higher than normal ambient light, have higher P/R ratios than corals living naturally under the higher light levels. It is probable, therefore, that the calculated P/R ratio for 3m of 1.36 is higher than would be shown by corals maintained at ambient light levels equivalent to 3m depth.

(d) P/R ratios have been calculated assuming a constant respiration rate across the 24-hour cycle. Edmunds and Davies (1988) have shown that illumination can stimulate respiration rates by 40% or more in comparison to those pre-illumination. The measurement of daytime respiration rates is hindered by lack of suitable techniques, and accurate estimates of 24-hour respiration rates are therefore difficult to quantify at the present time. However, in combination with respiratory increases from sediment rejection (discussed further below), 24-hour respiratory rates may be substantially underestimated.

All of the above factors would lead to overestimates of P/R ratios in the present study, and therefore the sediment load required to reduce P/R ratios to unity at Lizard Island would also be overestimated. In different seasons or geographical regions, different light regimes can have some reverse effects: (a) ambient subsurface light levels in excess of 1600umol(photons).m^{-2}.s^{-1} would only increase P/R ratios by a

small amount (as light levels are already saturating for much of the daylight period), but absolute light levels remaining after sediment attenuation could reach saturation for significantly longer periods; (b) longer daylight periods during summer will increase P/R ratios. In both cases, higher sediment loads, or longer periods of a given sediment load, will be required to reduce ratios to the same extent. A further point is that no allowance has been made in these calculations for the skeletal algae *Ostreobium*, although their contribution to the P/R ratio is likely to be negligible in comparison to that of the zooxanthellae/coral association.

An examination of the number of hours ror which 1-2mm of sediment can remain on tissues before P/R ratios fall to below 1 is illuminating (Table 8.4). For a 1-2mm layer of fine sediment, only 3-5 hours at 3m or 2 hours at 6m is necessary for this to occur. Granules of the same depth could be tolerated for several hours longer. It has already been shown that most corals reject coarse sediments more slowly than fine sediments (Chapters 2 and 3), presumably a function of mechanical strength. The present study shows that the injurious influences of fine sediment would be greater (for a given weight per unit area) *because of* its greater effect on light attenuation. The relatively greater abundance of fine sediment in most natural situations makes this all the more important.

Given that sediments cause light attenuation, underlying tissues might be expected to show photoadaptations to low light such as increase in chlorophyll per unit area causing darkening of the tissues (see earlier). However, rather than darkening, tissues beneath heavy sediment accumulations bleach. Mechanical damage, disease or other factors resulting from the presence of sediments presumably cause loss of zooxanthellae or pigment, or both, which prevents normal photoadaptive compensation.

In reality, light attenuation effects due to overlying sediments cannot be considered in isolation from the energetic cost of sediment rejection which can be a very active process (Chapter 2). Dallmeyer *et al* (1982) showed that suspended peat resulted in increases in respiration for the Caribbean coral *Montastrea annularis*, and Yamasu and Mizofuchi (1989) have shown similar increases in *Fungia repanda* in

response to suspensions of red clay. Increases in respiration resulting from active rejection of larger sediments have been demonstrated in the Caribbean species *Montastrea annularis*, *Acropora palmata* and *Diploria strigosa* (Abdel-Salam & Porter, 1988).

Any increase in respiratory demand will decrease the 24-hour P/R ratio and thus, where rejection activity is less successful such as in concave regions of the colony surface, the point at which the ratio falls below 1 will be reached earlier. Abdel-Salam and Porter (1988) found that respiration rates of sediment-treated corals increased over a 4-hour period following initial influx. This may reflect a general increase in polyp activity across the colony during active rejection, but what is not clear is how long the increased activity is maintained, and whether it is sustained only by the parts of the colony underlying the sediment. If the whole colony remains affected, the overall energy drain would be greatly magnified. With *Leptoria phrygia*, it is possible that behavioural adaptation to restrict strong rejection activity to specific routes across the colony, or to reduce the extent of unnecessary activity following clearance of sediments, may form part of a suite of adaptations to chronic sedimentation (see Chapter 7, where the ability of this species to modify its behaviour and increase its rejection efficiency has been described).

Sediment influxes from turbulence and other disturbances can cause substantial sediment accumulations on a wide range of coral species where morphology allows. For example, in Chapter 4 it was reported that storm conditions at Lizard Island could result in deposits of several millimetres of fine sediments on *Pectinia* and *Echinopora* colonies. The energetic arguments applied to *Leptoria phrygia* can equally be applied to other symbiotic corals. Thus, without invoking any other effects of increased ambient sediment loads (such as light attenuation due to turbidity, increased respiration due to rejection activities, or infection, etc.), light attenuation from increasing densities of overlying sediments can quickly reach levels causing a serious energetic imbalance for underlying tissues of a range of species.

Species differences in the importance of sediment-related light attenuation will depend on a range of factors including those which influence the build-up of sediments on their tissues (e.g. morphology,

turbulence, sediment rejection capability, etc.), but also the mechanical strength of the tissues (if the tissues die from abrasion, light attenuation has no relevance) and their tolerance to other factors such as disease. Assuming that tolerance to these factors is adequate, light attenuation may become significant. In the case of *Leptoria phrygia*, fine sediment accumulations of >1mm probably exceed the mechanical tolerance of the tissues, but at lower levels, light attenuation may significantly affect the energy budget of underlying tissues, and probably contributes to tissue stress. For *L. phrygia* and other corals, sediment rains of silts and sediments of very low density onto inclined surfaces may also cause significant light attenuation even if there is no build-up of sediments on the tissues. Accumulations of light-weight materials on tissues often cause very little bleaching but may still have a substantial effect on light attenuation. This influence may be particularly important to predominantly autotrophic species.

CHAPTER 9

GENERAL DISCUSSION

DISCUSSION

INTRODUCTION

This thesis examines some of the major influences of sediment on the behaviour, morphology, physiology and ecology of a selection of reef corals of the central Great Barrier Reef of Australia. The subject is very complex because sedimentation may be acute or chronic, it involves particles which vary enormously in size and composition, and its effects may be direct, accumulative or synergistic, almost always occurring in association with qualitative and quantitative attenuation of light resulting from turbidity. The direct effects of turbidity and the effects of organic sedimentation have not been addressed during the present studies although, where appropriate, reference is made to pilot studies in these fields. This thesis is restricted to the effects of natural carbonate and silica sediments on a taxonomically wide range of corals from the same area. Detailed studies are further restricted to a single species, *Leptoria phrygia.* Experimentation has been carried out *in situ* wherever possible, to avoid abnormal effects of artificial environments, and the results are related to natural environments and the distribution and abundance of corals within these environments.

Natural environmental parameters responsible for prevailing sediment regimes include substrate sediment distributions, turbidity and rates of sedimentation, all of which are highly correlated with wind-generated turbulence. Of these influences, the principal experimental variables examined in these studies have been sediment size, load, frequency and persistence, in relation to a wide range of behavioural, morphological and physiological attributes of corals in both natural and artificial situations. Correlations between these various natural and experimental parameters have been controlled and/or appraised as discussed in the relevant Chapters above.

Sediment-related strategies adopted by Australian reef corals

Australian corals adopt a range of strategies to counter the effects of sedimentation. These involve aspects of behaviour, morphology or physiology, which may be either fixed, or actively modifiable in the event of changes in sediment regime.

Behaviour.   All Australian corals, to a greater or lesser degree, use active behaviours to reject sediment. With minor additions and variations, sediment rejection mechanisms closely resemble those described for Caribbean species (Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976). Principal mechanisms involve tissue expansion, manipulation by ciliary currents, tentacles and mesenteries, mucus secretion, and pulsed contractions of the tissues.

When subjected to fine sediment or silt, corals secrete mucus. Mucus can assist sediment removal by holding particles together so that they can be moved en masse, but it is not universally beneficial and can actually obstruct sediment rejection from concave areas of corals (Chapter 2). This has also been observed for Caribbean corals (Bak & Elgershuizen, 1976). Tissue pulsing, and incidental movement by mesenteries, can also affect sediment removal in some Australian species (Chapter 2). For most species, silt and fine sediments are moved by cilia in the presence of mucus, whereas tissue expansion and, less commonly, direct tentacle manipulation, become more important as particle size increases.   Species with larger polyp and calice dimensions tend to be more capable of rejecting sediment accumulations. Where small-polyped species are good sediment rejectors, they generally have particularly strong ciliary mechanisms (Chapter 2). With the exception of faviids, most congeneric species which also have similar morphology, show close resemblance in their active rejection of sediments (Chapter 2).

Of Australian corals, Pectinia species show the most dramatic behavioural response to sediments, while Porites and Montipora species show least active rejection behaviour (Chapters 2-4).   At least two Australian species (Pocillopora damicornis: Appendix A, and Leptoria phrygia: Chapter 7) show behavioural adaptation to sediment influx, becoming more efficient sediment rejectors over time.

Morphology.   The importance of gross morphology has been stressed by most authors dealing with coral/sediment relations (Marshall & Orr, 1931; Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976; Loya, 1976; Veron & Pichon, 1980, 1982; Veron, 1981; Rogers, 1983; etc.).   In

general, vertical or highly ramose species will have an advantage over massive or encrusting ones in areas of high sedimentation, thus, branching growth forms are relatively prevalent in lagoons and turbid regions. The present studies also emphasise the importance of morphology at much smaller scales. Surface protrusions on *Montipora* spp. and *Hydnophora microconos* hindered the rejection of sediment (Chapter 2), while tissue mortality in many species was strongly correlated with minor variations in colony convexity (Chapters 4 and 7).

Colonies with few horizontal or sediment-trapping areas of tissue have a lower risk of sediment accumulation and therefore a lower chance of tissue damage and energy imbalance from nutritional stress. The speed with which applied sediments were lost from ramose colonies (principally through passive mechanisms) in comparison to flat colonies (almost solely through active mechanisms) quantitatively demonstrates the advantage of growth form changes (Chapter 3).

Species which show intra-specific variation with environmental conditions are of particular interest. Across the spectrum of coral species, there are those which show very little environmental variation (e.g. *Diploastrea heliopora*) to those which show enormous variations (e.g. *Echinopora mammiformis*, which can range from submassive to plate-like to fully arborescent). The role of sedimentation in this spectrum is often not clearly differentiated from that of turbidity and light attenuation except in some extreme situations where patches of tissue death appear to be responsible for upward directional growth in some foliaceous species (*Echinopora lamellosa*, *Mycedium elephantotus* and *Merulina scabricula*, see Chapter 4)

Physiology. Australian corals show a wide range of inter-species variation in physiological tolerance to overlying sediment. *Porites* and *Montipora* species, in particular, are very tolerant of sediment accumulations, while *Favia stelligera*, *Leptoria phrygia*, *Echinopora lamellosa* and *Merulina scabricula* are relatively intolerant (Chapters 3 and 4). Wide tolerance variation has also been found in other Indo-Pacific regions by Hodgson (1990) from *Montipora*

verrucosa (very tolerant) to *Oxypora glabra* (very intolerant) and in the Caribbean (Rogers, 1983).

The reaction of coral tissue, if any, to sediment accumulations is usually bleaching (Chapters 2-4 and 7): no species has been observed to show darkening of tissue. Increases in chlorophyll per unit area, which are typical low-light responses to depth, shading, and probably turbidity, were not observed to occur in direct response to overlying sediment (Chapter 8). It follows that other stresses associated with overlying sediments are probably overriding the normal physiological response to low light.

Interspecific differences in the tolerance of coral larvae and spat to environmental conditions relating to sediment are likely to be critical to local distributions, especially on inshore reefs. Although overall species diversity may be high on these reefs, they are seldom *Acropora*-dominated as are offshore reefs. Nothing is known about the separate roles of turbidity and sedimentation on recruitment and very little is understood about any aspect of settlement and early development.

Effects of quality and quantity of sediment

Sediment size. All corals studied showed major variations in active removal behaviours according to particle size (Chapters 2 and 3) and indeed, one of the most basic findings of this study is that particle size is of paramount importance to virtually every aspect of sediment removal.

All corals are able to move silt-sized sediment particles, but the number of species capable of manipulating larger particles is progressively reduced as sediment size increases. Studies of Caribbean corals show generally similar size-correlated behavioural variations (Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976). The ability of Australian corals to reject larger sediments is correlated with calice size, species with larger calices being the more efficient (Chapters 2 and 3). Hubbard and Pocock (1972) found a similar trend for Caribbean corals and further claimed that calice morphology (on a sequence from plocoid to meandroid to cerioid) is

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also correlated. The present status of this notion is unclear: Bak and Elgershuizen (1976) could find no clear evidence, and although Johnson (1988) found differences in meander structure of *Manicina areolata* with different sediment regimes, these did not conform to predictions based on the present study. No effect of meander complexity was observed for *Leptoria phrygia* (Chapter 7), but intra-specific effects of this nature may be subtle and high experimental replication may be required for them to be observed.

Coarse sediments apparently present a greater mechanical obstacle to removal than fine sediment (Chapter 2), particularly for strong ciliary rejectors with medium to small polyps which do not have strong tissue expansion as an alternative strategy (possibly *Gardineroseris planulata* and small-polyped *Turbinaria* species). However, fine sediments may cause more intense and immediate physiological stress. (a) Fine sediment represents a more serious diffusion barrier than coarse (Brafield, 1964). (b) Mucus entanglement is more common with silt and fine sediment (Chapter 2; Hubbard & Pocock, 1972; Bak & Elgershuizen, 1976) and sediment/mucus accumulations can occur on flat and concave regions which further increase diffusion barriers (Chapter 2; Bak & Elgershuizen, 1976) and provide media for bacterial growth (Ducklow & Mitchell, 1979) which may be toxic to coral tissues (Hodgson, 1990). (c) Weight for weight, fine sediment attenuates more light than larger particles and will therefore have a greater influence on photosynthesis, especially at sub-lethal or sub-bleaching levels (Chapter 8). (d) Fine sediment accumulations are closely associated with high turbidity which will tend to exacerbate their effects. (e) Little-known micro-scale physical and chemical parameters including viscosity and electrostatic cohesion may be increasingly important with decreasing particle size. (f) Silts, at least when raining onto a surface, can affect the whole surface of colonies because they adhere to vertical and convex surfaces, not just horizontal or concave ones (Chapter 2).

Results of Chapter 3, where nine out of ten corals experiencing tissue death were treated with fine (63-250um) rather than coarse (500um-1mm) sediment, are indicative of the general effects of particle size differences.

Sediment type. Sediment particle density, contamination by pollutants and pathogens, and detrital content, are all potential influences on corals. The present study has showed that light attenuation by a mainland terrigenous sediment is greater than reefal sediment of equivalent size (Chapter 8). Terrigenous sediments from different regions will almost certainly show wide variation in qualitative properties, which may affect the biological oxygen demand of the sediments, increase the light attenuation, cause greater abrasion, or otherwise affect coral tissues.

Sediment load. In the Great Barrier Reef region, short term sedimentation rates measured over periods of days, weeks or months, can reach levels of $300mg.cm^{-2}.day^{-1}$ or more (Marshall & Orr, 1931; Willis, 1987; Mapstone et al, 1989; Chapter 5). For a majority of species, sediment load interacts with the period sediments overlie tissues to have a very strong influence on tissue mortality (Chapters 4 and 7). For a few species, such as *Porites lobata* and *P. lutea*, where the tissues withdraw into the skeleton, sediment load itself may be much less important and mortality may be dependent solely on the period that a load of minimum weight remains on the tissues (Chapter 4).

A single influx of up to $200mg.cm^{-2}$ is not normally a serious threat to convex or flat coral surfaces of those species examined, with the principal exceptions of *Leptoria phrygia*, *Favia stelligera* and *Gardineroseris planulata* (Chapters 2 and 3). On the other hand, concave surfaces of many corals can be at risk from much lower sediment loads, particularly where sediment accumulates and remains for several days (e.g. *Coeloseris mayeri*, *Merulina scabricula*).

Leptoria phrygia is a moderately efficient sediment rejector but is relatively intolerant of overlying sediments (Chapters 2-4). This species can adequately remove up to $10mg.cm^{-2}.day^{-1}$ in laboratory studies for 23 days, but is increasingly likely to suffer damage as daily sediment loads increase (Chapter 7). Thus a rate of $25mg.cm^{-2}.day^{-1}$ can cause some mortality to a proportion of the population over this period, and longer durations of lower sedimentation rates will probably also do so. Furthermore,

comparisons with experiments undertaken in the field suggest that these laboratory findings may underestimate potential field mortality at a given sedimentation rate.

Fungia repanda, Sandolitha robusta and *Diploastrea heliopora* can tolerate daily influxes of $400mg.cm^{-2}.day^{-1}$ for eight days without showing tissue damage or mortality, but *Mycedium elephantotus, Leptoria phrygia, Merulina scabricula* and *Echinopora lamellosa* may suffer some tissue damage at $50mg.cm^{-2}.day^{-1}$ for the same period, and higher levels of $200-400mg.cm^{-2}.day^{-1}$ may have a serious impact.

Periodicity and persistence of turbulence and sedimentation. Some corals (*Leptoria phrygia* and *Favia stelligera*) can be seriously affected by sediment accumulations over periods as short as 24-48 hours (Chapter 3). Others, such as *Gardineroseris planulata*, have higher tolerance but will succumb after a few days (Chapter 3). Even very tolerant species such as *Porites* and *Montipora* may have a limit to their tolerance to overlying sediments. Thus, for corals with relatively ineffective sediment rejection mechanisms which are strongly dependent upon turbulence, the occurrence and periodicity of sediment and turbulence may be much more critical than the *average* sedimentation rates over monthly or yearly cycles.

Sedimentation in perspective

Sedimentation is only one of an array of parameters describing the ambient sediment regime of coral reefs. Substrate sediments, suspended sediments, currents and wave action, interact to create a very wide range of different sediment environments. Reef environments may, for example, be highly turbid with relatively low sedimentation rates (particularly where suspended sediments pass through a region on currents); highly turbid with high sedimentation rates (particularly in regions influenced by river discharges); relatively clear with periodically high sedimentation rates and abrasion (such as in regions of heavy wave action); or very clear with very low sedimentation rates (such as on the exposed outer regions of the Great Barrier Reef).

Effects of increases in ambient sediment can be considered in five principal categories: (a) sedimentation and sediment resuspension; (b) particulate matter permanently in suspension causing turbidity; (c) abrasion; (d) sediment overlying substrates otherwise suitable for coral larval settlement; and (e) net substrate sediment accretion. Each type of influence may affect corals in characteristic ways.

(a) **Sedimentation and sediment resuspension.** As previously emphasised, the capacity of corals to reject sediment is enormously influenced by particle size. As very fine sediments reach the surface of corals they tend to be trapped in mucus and are removed by ciliary action. Coarser sediments, on the other hand, are mostly mobilised by tissue expansion and contraction. Most importantly, for many corals, silt-sized sediments which reach the surface singly or in a light rain, must normally be moved by cilia, even on almost vertical surfaces (Chapter 2).

Influxes of sediments of a size greater than 63μm can cause tissue mortality in some species in few days. In the short-term (at least up to 23 days), overlying sediments must be persistent rather than transitory before tissue death will occur (Chapter 7; Hodgson, 1990). Overlying sediments restrict light (Chapter 8), may encourage the proliferation of bacteria to toxic levels (Hodgson, 1990), and increase the boundary layer for diffusion of gases and nutrients. But sediment accumulations of these sizes are very strongly correlated with local morphology (Chapter 7) and rarely occur on strongly inclined or convex surfaces. It follows that the immediate effects from sedimentation of these particles sizes will normally be restricted to regions of a colony which are fairly flat or concave.

In theory, sediment accumulations could affect morphologically protected regions of the colony if effects extended to peripheral regions. There are a number of ways in which damage to peripheral regions might occur including proliferation of bacteria or toxins leading to a spread of infection from one region to another; translocation of materials from peripheral tissues to those directly affected by overlying sediment, causing stress in peripheral tissues; and fragmentation of the colony resulting from death of

sediment-trapping areas to the point where the whole colony can no longer survive.

In practice, all evidence so far available indicates that tissue death from sediment accumulations does not spread to peripheral regions (Chapters 3, 4 & 7; Bak & Elgershuizen, 1976; Rogers, 1983; Hodgson, 1990) and that tissue necrosis is contained within morphologically vulnerable areas of the colony. Normally, therefore, it seems very unlikely that whole colonies will be severely affected by sediment larger than 63µm unless the sediment-trapping region comprises most of the total colony area. Assuming that strong active rejection becomes increasingly unnecessary where tissue inclination is greater than about 30°, rejection activity for most species studied would be restricted to substantially less than half of the total surface area. The proportion of very vulnerable tissue was as little as 1% for *Leptoria phrygia* (Chapter 5).

In the short-term, accumulations of silts and finer particles are less likely to occur because sediment removal can be carried out promptly from all tissue surfaces. Where sedimentation overwhelms rejection abilities, exhaustion more readily occurs on concave surfaces than on vertical ones and accumulations of finer particles on coral tissues can cause morphology-specific mortality (Heron Island, *pers. obs.*). Most significantly, however, sedimentation of silts and finer fractions will also cause a more serious and persistent energy drain on the entire colony because rains of these sizes can affect much more of the whole colony surface, and are less morphology-specific (Chapter 2).

At the present time it is not clear whether sediment *resuspension* has additional effects to those of downward sediment flux although it seems likely that they can be considered together. Constant sediment resuspension from the substrate will increase the perceived downward flux onto tissues and increase rejection costs and possibly abrasion (see below). Cyclic downflux and resuspension from coral tissues could cause energetic costs due to the consistent need for rejection and to greater irritation, but considerable turbulence is needed to resuspend sediments from coral tissues due to micro-topography and mucus-entrapment (Chapter 3). Thus it seems

probable that resuspension causes much the same response as a
sediment rain for most corals. However, the resuspension rate
affects the level of downward sediment flux experienced by the coral
and the particle size is affected by the distance from sediment
source, local turbulence and depth. Thus, for sediment sensitive
species, resuspension characteristics may influence the coral's
position on the reef with respect to these factors.

(b) **Turbidity.** Turbidity increases light attenuation and causes
spectral changes (Jerlov, 1970; Kirk, 1983). Increases in turbidity
would, therefore, be expected to reduce photosynthesis (e.g.
Dallmeyer *et al*, 1982), and affect calcification, skeletal density
and linear growth (e.g. Dustan, 1975; Graus & Macintyre, 1976, 1982;
Chalker, 1983; Wellington & Glynn, 1983).

In contrast to many aspects of sedimentation turbidity can,
through reduced photosynthesis and calcification, potentially affect
the whole colony rather than subsections, and increases in turbidity
could therefore cause widespread changes in abundance of species
intolerant of lowered light levels.

A second important aspect of turbidity is the effect of very
fine particles and suspended materials just above the tissue
surface. These may be actively or accidentally caught in mucus
secretions or adhere to tentacles and tissue surfaces. As with
sedimentation of silts described above, rejection of these particles
can require active participation even on strongly inclined surfaces
and some clays may pose additional problems because of unknown
effects of charged particles and cohesion. Under these
circumstances, sediment rejection may, again, adversely effect
energy budgets.

(c) **Abrasion.** The significance of abrasion to corals is unknown but is
likely to be severe where large quantities of angular sediment are
suspended by strong turbulence. Abrasive effects of sediments will
constitute an energy drain to a colony if substantial mucus is
secreted to protect tissues, or if energy is diverted for tissue
repairs.

(d) **Effects of sediment on larval settlement.** Coral planulae rarely settle out onto unconsolidated substrates (e.g. Fadlallah, 1983). Colonisation of substrates affected by fine sediments has been little studied, but larvae typically search for a substantial area of hard substrate before settling and metamorphosing. Even species whose adults normally occur on sand, such as *Heteropsammia*, initially settle on the shells of gastropods (Veron & Pichon, 1980). Babcock and Davies (*in press*) have shown that settlement of *Acropora millepora* larvae is significantly reduced on surfaces exposed to high sedimentation rates as compared to controls in lower sedimentation regimes. This aspect of sedimentation is clearly profoundly important to species distributions and requires further study.

(e) **Increases in sediment accretion rates.** Where absolute sediment accretion rates are high, the rate of upward growth will be an important factor in colony survival. Species, such as *Echinopora lamellosa*, which have the ability to direct growth upwards (thus reducing active rejection requirements and potential tissue mortality, Chapter 4) and have high linear growth rates, may be particularly suitable for such environments. Under natural conditions, dramatic changes in accretion rates are probably rare and would be of only local importance. On the other hand, changes in local hydrodynamics or major increases in sedimentation rates due to human activities could cause serious increases in accretion rates, and under these extreme conditions corals could be gradually buried from the base upwards.

These summaries highlight the importance of area effects on coral colonies. Local sediment accumulations on corals can cause limited, mostly morphology-specific damage. Sedimentation of very fine particles, turbidity, and layers of sediment on the substrate, have effects that are not morphologically limited but are likely to affect the survival of entire colonies. It is these effects which will have the greatest impact on the local distribution of individual species and, ultimately, on the composition of whole coral communities. The present study, in combination with a synthesis of relevant literature, points to the conclusion that the most serious impact of sedimentation occurs when

sediments are fine enough to have a continuing effect on turbidity and, at the same time, affect whole colony surfaces.

Significance of sedimentation in the control of individual species distributions

The local control of species distribution on reefs is a complex subject which remains poorly understood. The suite of species selected for the present study includes some which appear to be totally excluded from a number of habitats and some which show little or no such preferences. Almost all are relatively abundant and the study therefore selected against species which had very restricted distribution ranges at Lizard Island. The species that were selected, however, belong to a wide taxonomic spectrum and probably encompass most of the range of active rejection mechanisms employed by scleractinians. Some of the relationships between distribution and environment are clear, others are disguised due to, for example, the poorly understood role of rare but very high impact events such as cyclones or, especially for very fine sediments, the ill-defined distinction between the effects of sedimentation, turbidity and light attenuation.

Species which are poor sediment rejectors (such as *Porites* or *Montipora* species), or those which show sporadic or short-lived rejection activity (such as *Gardineroseris planulata*), can only survive in areas of high sedimentation if they are able to reduce the vulnerability of their tissues to overlying sediments by exploiting mechanisms for passive rejection, or by developing a tolerance to sediments. Morphology and turbulence are the two most important aspects of passive sediment rejection. Both are interrelated with other environmental controls on distribution: morphology is very strongly influenced by both turbulence and light, and turbulence has a primary controlling influence on the sedimentary regime.

Porites cylindrica and *P. nigrescens*, which are very common in lagoons and other turbid environments (Chapter 5; Veron, 1986), are invariably ramose, and thus, via their morphology, largely avoid problems resulting from overlying sediments. *Echinopora mammiformis* and *E. lamellosa*, both have flexible morphologies which allow them to

optimise their growth strategy for the prevailing environmental conditions of light and sediment. Species such as *Leptoria phrygia*, may rely on turbulence to clear sediment from sediment-trapping regions, becoming less common in areas of lower turbulence. *Porites lobata* and *P. lutea*, on the other hand, can exist in a wide range of habitats because they are tolerant of overlying sediments for many days, their tissues withdrawing into the skeleton until sediments are removed by wave action. The tolerance of *Gardineroseris planulata* is more limited, and this species is probably excluded from regions of moderate to high sedimentation of fine and larger particles where calm conditions persist for substantial periods of time.

The distribution of some species show no clear correlations with sediment. Of the species studied, *Acropora hyacinthus* has one of the more restricted distributions, being very rare except in turbulent environments at Lizard Island. It is absent (or uncommon) from turbid inshore fringing reefs, in regions of moderate to high sedimentation, and in lagoons, yet it has a corymbose growth form which is very effective in passive sediment rejection. This is a species which is adapted to fairly narrow environmental constraints and shows low tolerance of other environments, whether morphologically adapted to them or not. *Diploastrea heliopora* is a good sediment rejector but neither its morphology, nor its position on the reef with respect to turbulence, offer substantial passive rejection advantages. This species occurs in a wide range of habitats and its distribution does not appear to be closely correlated with sediment. Its rejection capability may be sufficient for it to cope with most sediment environments, leaving control on its distribution to unrelated factors.

It must be emphasised that, in natural environments, high ambient sediment loads should not be viewed as a uniquely negative environmental attribute. Inshore fringing reefs of the Queensland coast which are subject to high sedimentation and turbidity, are very diverse ecosystems with high coral cover (Ayling & Ayling, 1987; Veron, 1987; Veron, pers.comm.). Furthermore, growth rates of some species (such as *Porites*) can be higher in these regions than elsewhere (Isdale, 1983). As corals are capable of utilising suspended materials as a food source (e.g. Lewis, 1976), it is extremely likely that some species are specifically adapted to exploit this resource in inshore waters. This

view is supported by evidence from the Caribbean where the growth rate of the massive coral *Siderastrea siderea* was positively correlated with sedimentation rate (Foster, 1980). Foster suggests that this species may be deriving energy from organic particles in the sediment.

Management implications

Naturally-occurring reefs which are not subject to human influence exhibit at least some characteristics which relate in a dynamic way to environmental conditions. Aspects of the community such as species composition, or intra-species morphology and skeletal density, vary with light, turbulence, turbidity, sedimentation, temperature or other factors. Most of these communities have formed over many years, decades or centuries. In contrast, human activities often dramatically alter ambient environmental conditions over time-periods of hours, days, or months.

Coral morphology has been shown to be critical, even at a very fine scale, to the vulnerability of tissues to fine and larger sediment sizes, but as many species are morphologically versatile, they can alter the *vulnerability of their tissues* by morphological adaptations. However, the relatively slow growth rates of corals (from a few millimetres to about ten centimetres per year), limit the speed with which they can change their morphology to less vulnerable forms. Under many natural conditions where changes in sediment/turbulence regimes are relatively slow, many species may have the time to fully exploit the range of morphological variation or physiological adaptation available to them. Where human activities cause widespread and dramatic changes over short time periods, even these species which have the intrinsic capacity to adapt may be adversely affected.

Potential for species and species-attributes as indicators of sediment
· stress. Fulfilling the criteria for the ideal 'indicator' (see the General Introduction) is not an easy task and especially not for a stress with the complexity of sediment, and for coral reefs whose species composition may be different from one site and region to another. Nevertheless, the present studies have laid a foundation and point to several potentially fruitful areas of further research:

(a) In midshelf reef habitats, sediment-intolerant species such as
    Leptoria phrygia, *Favia stelligera*, *Echinopora lamellosa* and
    Merulina scabricula (probably also *Oxypora* sp., Hodgson, 1990)
    may be useful indicators of sedimentation rate changes
    (Chapters 3, 4 & 7).

(b) Sediment-trapping morphology of these species should be targeted
    (Chapter 5).

(c) Colonies most quickly affected will be those with a high
    proportion of sediment-trapping to total tissue surface area in
    areas where passive assistance from turbulence is low. Thus,
    colonies at greater depth will normally be more useful than
    those in shallow depth if the increased sedimentation is
    imported from elsewhere (e.g. from construction).

(d) Targeting morphology of a number of morphologically responsive
    species (such as *Leptoria phrygia*, *Echinopora mammiformis*, *E.
    lamellosa*) in pre-impact studies may provide very useful
    background information about recent sedimentation regimes in
    the area to augment necessarily brief sedimentation rate
    studies. These morphologies will have integrated the normal
    sedimentation regime over much longer periods and, to some
    extent, may make up for the lack of seasonal sedimentation rate
    data (Chapter 5).

(e) Recent changes in sedimentation regime may be indicated by
    targeting concave regions of sediment-sensitive species. Very
    white, uneroded skeleton beneath sediment accumulations on
    Favia stelligera (see Appendix Plate 1.1), *Leptoria phrygia*,
    Echinopora lamellosa, *Merulina scabricula*, will probably
    indicate recent changes caused by increases in sedimentation.
    On species such as *Echinopora lamellosa* and *Pachyseris speciosa*
    (probably also other plating species such as *Oxypora* sp.)
    accumulations of sediment in concave areas may be accompanied
    by new growth upwards and over the top of the accumulations.
    The present studies have shown that these responses can occur
    as a direct result of sediment accumulations (Chapters 2-5 &
    7).

(f) Schuhmacher (1977, 1979) found that *Fungia* species with strong
ciliary rejection mechanisms become exhausted from persistent
sediment influxes. Exhaustion was not observed after eight
days for the ciliary rejector, *Fungia repanda*, during the
present study (Chapter 4), but might have occurred under more
chronic sedimentation. If rejection behaviour does constitute
a serious energy drain on a colony, those species which are
most active, perhaps strong ciliary rejectors in particular,
will be the most prone to exhaustion. In the present study,
Pectinia spp., *Fungia* spp., *Gardineroseris planulata*, and to a
lesser extent *Favia pallida* and *Turbinaria* spp. were some of
the most active ciliary rejectors (Chapter 2). Several of
these species (especially *Pectinia* and *Turbinaria* spp.)
normally have very little tissue vulnerable to downward
sediment fluxes and may thus avoid exhaustion. But *Fungia* is
not as well adapted morphologically, and several species of
this genus may prove to be useful chronic indicators of
sediment stress. This coral group has the added, and very
significant, advantage of being detached, and can therefore be
easily moved from one reef region to another, or from
peripheries to central impact zones. If stress-specific
responses could be found for these species, the rigour of
experimental designs for impact studies could be dramatically
increased with very little extra cost or effort. Concentrated
research to characterise the responses of a variety of fungiids
to turbidity, sedimentation of different grain sizes and
intensities, eutrophication, and other forms of pollution could
be very fruitful.

(g) Mesenterial extrusion, mucus and bleaching are both commonly
offered as potential indicators of stress in corals (see Brown
& Howard, 1985). The present work argues that mesenterial
extrusion can be ambiguous and may have limited value in the
detection of stress from downward sediment flux. Mesenteries
are extruded both as a feeding and a stress response but are
normally inconspicuous (Chapter 2). By the time mesenteries
are extruded as a stress response, other indications of stress,
such as tissue death, are normally already obvious and would
offer greater information on the extent of the problem.

Further research may show that mesenteries can be useful indicators of irritation from suspended sediments (particularly if they are contaminated), but at present this possibility remains unclear.

The presence of mucus in sediment accumulations probably adds to the likelihood of tissue death but, again, other indicators of potential stress (such as increases in the physical expanse of sediment accumulations, or of tissue death) will offer more immediate information. On the other hand, clouds of mucus in the water may be indicative of stressful levels of suspended particulates for some corars.

Bleaching is the most obvious sub-lethal effect of overlying sediments on tissues. In relation to sediment accumulations, bleaching is morphology-specific. It is not known whether bleaching occurs when convex and angled tissues become exhausted, or as a result of turbidity, as experiments exploring these aspects were outside the scope of the present studies.

Describing the sediment impact. These studies also emphasise the need for information about the specific type of impact (in particular the turbulence regimes, and sediment type and particle size), in order to predict the effects of sediments on communities.

(a) Differing temporal tolerances to overlying sediments of coral species makes the interaction between morphology, turbulence and sedimentation events of critical importance both in explaining existing species compositions and in predicting effects of sediment influxes on the community. Chapter 4 demonstrates the significance of even relatively short periods of calm on the survival of morphologically sensitive tissues of intolerant species: on the one hand, had turbulence risen dramatically during the first two days of this experiment, mortality of these species would almost certainly have been less extensive; on the other, had the calm period persisted, mortality would have been substantially increased. Heavy

influxes of sediments across wide areas of reef during calm weather may be very dangerous to tissues of sensitive species.

(b) A knowledge of impact sediment type and size spectrum is very important, not only to models of resuspension for the area, but also because of the size-specific responses of corals. Despite the relative difficulty of moving coarse grain sediments from coral tissues, this does not mean that fine sediments are less dangerous. Fine sediments, though possibly causing less direct mechanical damage, affect the coral through many indirect routes.

CONCLUDING REMARKS

The level of stress on a colony from sedimentation is related to its morphology. For a given species, sediment-trapping tissues will be the most vulnerable to mortality, and the extent of these tissues can give a measure of both the current sediment regime, and the vulnerability of the local population to immediate sediment threat. But the cost of rejection to the remaining tissues of the colony will depend upon the area of tissue intercepting downward flux of sediment and the extent of passive gravitational assistance. If the energetic costs of rejection for tissues at different angles could be established, it is possible that rejection costs for some species could be modelled from morphology indices which combined morphological characters such as size, mean tissue angle and projected to total surface area ratios. With this information, plus a measure of energy reduction (from spectral change and light attenuation) due to turbidity, energy budgets could be constructed which may allow predictions of the species' survivorship.

· Very little is known about inter-species differences in tolerance to turbidity. Some low-light tolerances can be inferred from species distributions. with respect to depth or shade, but combined effects of low light and spectral changes, or irritation from suspended particles, is very little understood. These areas are priorities for future research.

On reefs that are normally moderately clear, sediment-trapping regions of key species may be sufficiently common to be usefully targeted in impact studies. In inshore areas, communities already take advantage of morphology to reduce interception of sediments and sediment-trapping tissues may be scarce. In such regions, morphological measures such as mean plate angles, may be of much greater importance. In all cases, however, the selection of taxa to measure depends on identifying sensitive and responsive species.

Predictions of community changes related to alterations in sediment regime will almost certainly require an array of measurements which cover light intensity and quality, suspended particulate matter, sedimentation, sediment resuspension, turbulence, sediment type and size available for resuspension, and a number of other site-specific parameters such as nutrients or salinity which cannot, in reality, be separated from the sediment stress. At the present time, few of these parameters can be usefully interpreted as their importance and influence to individual species is unknown. However, the studies of responses to sedimentation described in this thesis, provide a foundation for the understanding of at least one aspect of this array of sediment complexity.

APPENDIX A

SEDIMENT   RESPONSES   OF   AUSTRALIAN   SCLERACTINIAN

CORALS − SPECIES SUMMARIES

SEDIMENT RESPONSES OF AUSTRALIAN SCLERACTINIAN CORALS - SPECIES SUMMARIES

INTRODUCTION

This Appendix summarises information available for each species from all Chapters. on a species by species basis. Information under each section heading is primarily based on observations from experiments described in particular Chapters as follows:

Sediment rejection behaviour:	Chapter 2
Sediment rejection efficiency:	Chapter 3
Sediment tolerance:	Chapter 4
Lizard Island:	Chapter 5

Descriptions of methodology can be found in the appropriate Chapter along with discussions of general points which help to place the present species descriptions into context.

Species identifications were kindly confirmed by Dr. J. Veron. and species descriptions. species names and authorities follow those of Veron (1986). Where other authors have described behaviours of species under other synonyms. every effort has been made to identify these accurately and both names have been given as. for example, *"(Fungia=) Heliofungia actiniformis"*.

A detailed examination of ciliary currents and feeding mechanisms was not a principal objective of this study. Many researchers studying feeding. used silt sized particles (principally carmine or carborundum) to study ciliary mechanisms and thus their work is directly relevant to the ciliary rejection of silts. During the course of the following species descriptions. reference has been made to these investigations when appropriate. Further comment based on personal observations has been included only where it augments existing knowledge.

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SPECIES INVOLVED IN EACH GROUP OF EXPERIMENTS

Species	Mechs	Eff	Tol	Dist	Other
Pocillopora damicornis	*	*[1]		*	
Montipora danae	*			*	
Montipora foliosa	*				
Montipora aequituberculata	*	*			
Acropora hyacinthus	*		*	*	
Acropora florida	*				
Astreopora myriophthalma	*	*		*	
Porites lobata	*	*	*	*	
Porites lutea	*	*	*	*	
Porites cylindrica		*		*	
Goniopora lobata	*				
Psammocora contigua		*			
Gardineroseris planulata	*	*		*	
Coeloseris mayeri	*	*		*	
Pachyseris rugosa		*		*	
Pachyseris speciosa	*			*	
Fungia repanda	*	*	*	*	
Sandolitha robusta	*	*	*	*	
Galaxea fascicularis	*	*		*	
Mycedium elephantotus	*		*	*	
Pectinia lactuca	*		*	*	
Pectinia paeonia	*				
Acanthastrea echinata	*	*		*	
Lobophyllia hemprichii	*				
Lobophyllia corymbosa	*				
Symphyllia recta	*			*	
Symphyllia radians	*	*		*	
Hydnophora microconos	*	*		*	
Merulina scabricula	*		*	*	
Favia stelligera	*	*		*	
Favia pallida	*	*[1]		*	
Favites abdita	*			*	
Goniastrea retiformis	*			*	
Platygyra lamellina	*			*	
Leptoria phrygia	*	*	*	*	*
Oulophyllia crispa	*	*		*	
Montastrea curta	*			*	
Plesiastrea versipora	*	*		*	
Diploastrea heliopora	*	*	*	*	
Cyphastrea serailia	*	*		*	
Cyphastrea chalcidicum	*			*	
Echinopora lamellosa	*		*	*	
Echinopora mammiformis	*	*		*	
Turbinaria peltata	*			*	
Turbinaria mesenterina	*			*	

Table A.1. Summary of experiments in which each species was involved. *Mechs*: Chapter 2, sediment rejection mechanisms. *Eff*: Chapter 3, sediment rejection efficiency. *Tol*: Chapter 4, tolerance to daily sediment influxes. *Dist*: Chapter 5, species distribution around Lizard Island. *Other*: Chapters 6-8, biochemical composition, sediment threshold tolerance, physiological responses to sediment.

[1]Carried out in the laboratory, not *in situ*.

SPECIES SUMMARIES

1. *Pocillopora damicornis* (Linnaeus, 1758) (Appendix Plate 1a)

> *SUMMARY: Rejection is overwhelmingly dominated by passive
> mechanisms because of morphology, with laboratory tests of
> rejection resulting in clearance of >80% of test areas within
> one hour. Ciliary activity occurs for fine and silt sediments
> when they are caught in the angle of branches. Pulsed
> contractions of the tissues are common. This species is
> present in all major habitats of Lizard Island and is dominant
> on a few patch reefs.*

Sediment rejection behaviour. Polyps retracted immediately on
contact with sediment. Active rejection was relatively
unimportant due to morphology. Most sediment immediately fell
off the colony. Polyps re-expanded almost immediately,
removing further quantities of sediment. Loss of fine and silt
sized sediments caught in angles or flatter portions of colony
was assisted by cilia. Silt was also actively removed from
strongly angled surfaces. Mucus was present but generally not
obvious for these grain sizes. General movements of tentacles
were important in dislodging sediments, particularly of the
larger grain sizes, but these did not appear to be a direct
sediment response. Minor tissue expansion occurred
occasionally (<1mm), particularly in response to larger
sediment sizes, but was observed only rarely. Pulsed
contractions of the tissues was moderately common and effective
at dislodging sediments. Polyps were expanded day and night
and no diurnal rejection differences were noted.

Ingestion of uncontaminated sediments was not observed for any
grain size. When ground fish was presented, on the other hand,
ingestion was universal. The mouths opened wide, becoming
conical and polyps extending well out of the calice. Silt and
fine sediments contaminated with fish were ingested. Tentacles
were involved in capture of contaminated sediments but not for
fish alone. Mesenteries were not observed for this species.

Sediment rejection efficiency. Although not reported in detail
in this thesis, *Pocillopora damicornis* was the subject of a
laboratory study of sediment rejection. 6 colonies were
randomly allocated to each of three treatments, control, coarse
sediment (0.5-1mm) and fine sediment (63-250um), at a total

daily dose of 400mg.cm^{-2}.day^{-1} divided into two portions of 200mg.cm^{-2}.day^{-1} applied morning and evening. The experiment was run for a total of 21 days, during which time there was no mortality of any part of any colony. Approximately 50% required no active removal due to morphology. Sediment loss was fast, with >80% loss of either sediment grain size within one hour. Rejection of fine sediment was significantly faster than that of coarse measured after 40 minutes (2 sample t-test, $n_1 = n_2 = 6$. $p < 0.01$: fine sediment clearance: 95.8<97.8<99.1%; coarse sediment clearance: 73.9<78.7<83.2%, $\bar{x} \pm SE$). Over the period of the experiment, the rate of sediment rejection significantly increased between the first and second, and the second and third weeks for both sediment sizes ($p < 0.05$).

Lizard Island. This species was common in most habitats and dominant on several patch reefs fronting the research station. Tissues of *P. damicornis* were never observed naturally within 1cm of substrate sediments. Although this species was branching, colonies varied in the degree and dimensions of branches in habitats around Lizard Island.

Comment and discussion. Changes of density and dimensions of colony branches for this species in different habitats have been noted elsewhere on the Great Barrier Reef (Veron & Pichon, 1976: p.47). The influence of morphology on passive rejection will depend very much on these factors. Ciliary currents are described by Yonge (1930) and by Abe (1938). Marshall & Orr (1931) examined this species (as *P. bulbosa*) with similar conclusions. *Pocillopora damicornis* has been suggested as an early coloniser by Connell (1973). It was common on reefs offshore from Jeddah (Saudi Arabian Red Sea) which had previously been sediment-stressed (IUCN, 1985). However, it is possible that this species invaded after the strongly detrimental stress had abated. There is some evidence to suggest that this and other members of this genus may not be highly tolerant of turbid conditions and high sedimentation (Mayer, 1918; Dahl & Lamberts, 1978; Maragos, 1987; Hodgson, 1990).

2. *Montipora danae* (Edwards & Haime, 1851)

SUMMARY: Shows very little rejection activity, particularly for larger grain sizes. Silts and fine sands can move slowly on ciliary currents. Tissue expansion occurs but is not very effective. Rejection of large sediment sizes is very poor.

Sediment rejection behaviour. Polyps retracted on contact with sediment of all sizes. Under heavy loadings polyps were unable to expand. But otherwise polyps re-expanded through sediment which would remain at their bases. Polyps were able to expand around coarse and granule sized grains provided that density was not too high (less than one grain thick). Active rejection of large grain sizes was often almost non-existent over the first two to three hours although single grains would occasionally move a millimetre or so. Movement of fine and silt sizes in mucus by cilia was observed but poor. Significant movement was always in a gravitational path. Tissue expansion was observed, but slight (<1mm) and more common with larger grains sizes. Many polyps were extended during the day and no difference in rejection was noted from day to night.

Some isolated fine grains were ingested, but ingestion of uncontaminated sediments was generally uncommon. Response to ground fish was standard (see *Oulophyllia crispa* and Plate 2.4). Polyp mouths opened to expose hollow interior and fish was drawn in on ciliary currents. Contaminated silts and fine sediments were also ingested. Contaminated larger sizes were not tested. Only one mesentery was observed on one colony.

Lizard Island. This species was not distinguished from *M. verrucosa* during field surveys. The species pair was present to common in most habitats of Lizard Island.

Comment and discussion. The microtopography of this coral appeared to hinder sediment rejection as larger grain sizes became trapped between tuberculae. Yonge (1930) describes the ciliary currents for *Montipora ramosa* (probably *M. digitata*[1]). Hodgson (1990) examined the sediment tolerance of *M. verrucosa* in Hawaii and found that this species was not injured by levels of $30mg.cm^{-2}.day^{-1}$ and $0.5g.l^{-1}$ of 'fine marine sediment'. He argues that this species may possess physiological tolerance to effects of sediment.

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1.   *Montipora ramosa*, investigated by Yonge (1930), is a synonym for both *M. digitata* and *M. angulata* (Veron & Wallace, 1984). However, Yonge's corals were identified by Vaughan, whose corals were revised as *M. digitata*.

3. *Montipora foliosa* (Pallas, 1766)

SUMMARY: As for M. danae *but microtopography is even more of a hindrance to sediment rejection.*

Sediment rejection behaviour. Generally as for *M. foliosa*. However, pulsed contractions of the polyps was observed for this species which assisted in mobilising sediment. Some expansion of tissues was observed but was minor.

No ingestion of uncontaminated sediments observed. Ingestion of ground fish was standard (see *Oulophyllia crispa* and Plate 2.4).

Comment and discussion. Microtopography was even more of a hindrance with this species than with *M. danae*, especially with larger grain sizes.

4. *Montipora aequituberculata* Bernard, 1897 (Plates 2.11 & 2.12, Appendix Plate 1b)

SUMMARY: As for M. danae *but microtopography is again even more of a hindrance to sediment rejection. This is one of the poorest active sediment rejectors of all species tested. However, it appears to have high sediment tolerance.*

Sediment rejection behaviour. Generally as for *M. danae*. Larger sediment sizes became lodged between tubercles in the same way as for *M. foliosa*. Silt and fine sediments moved readily by cilia. No major tissue expansion was observed for any grain size. Mucus was common with fine and silt, but could hinder ciliary loss of these sizes in concave regions. Polyps expanded between single or a few grains of coarse sediment or granules with no obvious attempt to remove them. Tentacles were apparently not important.

Ingestion of uncontaminated silt and fine sediments was rare. Response to ground fish was standard (see *Oulophyllia crispa* and Plate 2.4) and generally as for *M. danae*. Mesenteries were occasionally apparent around coarse sediment and granules but only briefly.

Sediment rejection efficiency and tolerance. Of 22 species examined in the field, *M. aequituberculata* was found to be one of the three poorest active sediment rejectors (with two *Porites* spp.). However, sediment tolerance of this species

appeared to be relatively high as tissues underlying sediment
accumulations did not die after several days. Bleaching under
these conditions was common, but tissues recovered if the
sediment later dispersed. Two individuals of this species that
were tested opportunistically during the course of the field
tolerance experiment described in Chapter 4, also showed a
bleaching response after several days of sediment accumulation.
These tissues also recovered when water movement later cleared
the sediment from the tissues.

Comment and discussion. As for *M. foliosa*, tubercles trapped
sediments and hindered their removal. Two species of brittle
stars were observed to cause incidental cleaning of fine
sediment from this coral. · The experiments on *M.
aequituberculata* support the conclusions reached by Hodgson
(1990) for *M. verrucosa* discussed above. It is possible that
sediment tolerance is a generic characteristic.

5. *Acropora hyacinthus* (Dana, 1846) (Plate 4.1)

SUMMARY: *Loss of sediment is dominated by passive rejection
due to the corymbose plate morphology of the species. At
Lizard Island it is very abundant in shallow-water exposed
locations where wave action is considerable. Mucus strands in
combination with wave action greatly assist loss of fine and
silt sediments in situ. Ciliary movements are important for
small sediment sizes when they become lodged between branches.
Coarse and granule sized particles were generally dislodged by
undirected polyp movements and wave action.*

Sediment rejection behaviour. Loss of sediment was dominated
by passive mechanisms for this species. Polyps were usually
expanded during the day prior to sediment influx. When
influxes of sediment occurred on part of a branch, polyps of
the entire branch usually retracted. Loss of sediment was
assisted by movements of the polyps and tentacles though these
did not appear to be strongly sediment-directed (i.e. general
movements increased and were not localised in areas of sediment
influx). Tentacles and polyp tissues were observed to pulse
during sediment influxes. Pulsing occurred at other times but
more rarely. No differences were noted between responses at
night and during the day.

Silt and fine sediment were moved by cilia in flatter regions
of the colony. Mucus was apparent for these sediment sizes.
Coarse sediments and granules were principally mobilised by

gross polyp and tentacle movements. Expansion of the coenosarc was minor. The response of the coral to silt and fine sediments was to produce a series of thin mucus strands. A few to 20 grains would be attached along the length of the strand. Commonly one end of the strand would become detached and get caught by wave action. Eventually the other end would detach, allowing the strand to be washed away.

Ingestion of uncontaminated sediments was not observed for this species. Introduction of ground fish caused polyp mouths to gape and fish to be drawn in on ciliary currents. Mesenteries were not observed.

Sediment tolerance. Individuals of this species subjected to 50, 200 or 400mg.cm^{-2}.day^{-1} for eight days showed no signs of stress or tissue. Water movement was considered to play a substantial role in sediment rejection for this species even in calm water because of the shallow location of most colonies. However, incidental observations on this species and other *Acropora* species suggest that they may be intolerant of high levels of suspended material in the water.

Lizard Island. *Acropora hyacinthus* was observed at one lagoon site and one moderately-exposed site. However, this species was substantially more common in exposed habitats and normally occurred in shallow water (1-2m).

Comment and discussion. A commensal crab created local currents which assisted loss of sediments in its vicinity. At Lizard Island, tissues of *A. hyacinthus* were never close to substrate sediments. Wave action was considered to be important for this species. Yonge (1930) describes the ciliary currents of *Acropora (hebes=) aspera*. Bull (1982) found this species in the inshore waters of Magnetic Island, but (at the same Island) it has also been reported to suffer severe damage from increased suspended sediment (Bennett, 1971 and Brown, 1972, cited by Endean, 1976). Marshall & Orr (1931) found that *Acropora* always cleaned itself of sediment in 24 hours, but Mayor (1924b) considered this genus less able to clean itself of fine silt than *Pocillopora*. However, there are many species of *Acropora* some of which are better able to flourish in silty lagoonal waters than others (Veron, 1986). It is therefore probable that considerable variation in rejection capabilities exists in this genus.

6. *Acropora florida* (Dana. 1846)

*SUMMARY: Passive   rejection   is   important   but   not   as
overwhelming as for* A. hyacinthus. *General tentacle and polyp
movements   are   the   principal   mobilising   force   for   coarse   and
granule   sized   sediments   though   these do   not   appear   to   be
closely   directed.   Fine   and   silt-sized   sediments   can   be
manipulated   easily by cilia.   Mucus in conjunction with wave
action   is considered important for this species but mucus may
also   have exacerbated stress under Calm conditions   when   some
tissues   died.   Minor   tissue expansion of the coenosarc   occurs
and may be important for rejection of larger grain sizes   under
Calm conditions.*

Sediment rejection behaviour. polyps were expanded during the day and retracted when a sediment influx occurred. Considerable sediment loss occurred as a result of branching morphology, but branches were much thicker than those of *A. hyacinthus* and this form of passive loss was less effective. Sediment could get caught in angles between the branch projections though even slight wave action dramatically assisted loss when this occurred. Wave action was considered to be important. Mucus was produced and trapped silt and fine sediments were later swept away by water movement. However, greater active sediment rejection was observed for this species than for *A. hyacinthus*. Silt and fine sediment were removed by ciliary activity but also by tentacles. It appeared that cilia on the sides of the tentacles moved fine sediment and silt towards the tentacles tips as the tentacles bent outwards. When the sediment reached the tips it dropped off the polyp altogether. Minor tissue expansion was observed. No differences in rejection between night and day were noted.

After one sediment influx it was apparent on several occasions that mucus had been secreted into a matrix just above the tissue. Further influxes were caught in the matrix and sloughed off before they reached the tissue surface.

No ingestion of uncontaminated sediment was observed for this species. No mesenterial response was observed.

Comment and discussion. Although some specimens of *A. florida* appeared to be flat and solid from a distance, closer examination showed that many areas of the tissue surface were not flat or concave. Once mobilised, therefore, most sediment could move under the influence of gravity with relatively little active requirement. However, on colonies where flat

regions did occur, active rejection of coarse and granule sizes was poor. Parts of two individuals showed stress after two days when fine sediment had been introduced under Calm conditions. The sediment had become clogged with mucus into a solid mass. At Lizard Island, tissues of this species were never observed close to substrate sediments.

See also *Acropora hyacinthus* above.

7. *Astreopora myriophthalma* (Lamarck, 1816) (Appendix Plate 1c)

> *SUMMARY: Apparently a poor active rejector. Cilia and mucus are involved in rejection of silt and fine sediment. Tissue expansion capability appears weak and the ability to move coarse sediment and granules is poor. However, rejection efficiency studies tend to dispute this finding as sediment clearance was not particularly poor.*

Sediment rejection behaviour. Active rejection movements by this coral species were slow for all sediment sizes. Silt and fine sediment could be manipulated by cilia but were assisted by localised tissue expansion. Mucus was present for these sizes. Initial mobilisation of sediment was sometimes caused by partial expansion of polyps. Occasionally, pulsed contractions of tissues occurred. The observed expansion of coenosarc tissue in response to sediment was small ($^=$1mm) but, in view of the absence of more effective mechanisms, tissue expansion appeared to be of great importance in rejection.

Observations at dusk and at night showed that some polyps would expand through overlying sediments provided that the layer was not too thick. As corallites were plocoid, sediments tended to be lost from the polyp area before the surrounding coenosarc and the polyp was able to expand. When fine sediments formed a layer about 4 grains thick above the polyps only some could expand and often only partially. However, even partial expansion assisted in sediment loss. Grains were mobilised and rejection more effective. However, polyps did not fully expand during the day to cause sediment loss.

Ingestion of uncontaminated sediment was not observed for test individuals although the response to ground fish was standard (see *Oulophyllia crispa* and Plate 2.4). Mesenteries were not seen in response to sediment.

Sediment rejection efficiency. Despite the relatively poor

rejection behaviour described above, rejection efficiency was not found to be particularly poor for this species. Most colonies showed slow rejection during the first two hours but had rejected more than 95% by 24 hours. It is possible that night-time rejection is high for this species and accounts for some of these differences. Turbulence had a significant effect on sediment rejection for this species (p<0.05).

Lizard Island. *Astreopora* was present in all regions of Lizard Island, but was perhaps less common in the lagoon than elsewhere. Few colonies were large, and most were small with distinctly rounded, convex surfaces. This morphology would encourage passive sediment loss resulting from water movement.

During the course of field observations it was noted that at least some tissues of 17 colonies examined at Lizard Island (n=43) were flush with the substrate. Generally the substrate was slightly vegetated coral rock but in five cases the substrate was mixed but mostly coarse sand of a minimum depth of 0.5cm. Tissues at the colony edge were slightly bleached but living and the colony did not penetrated more than one polyp depth into the sand. Presumably they are able to clear the edges sufficiently well to survive. It seems probable that this was carried out by polyp and tissue expansions and contractions with the assistance of local water movement.

Comment and discussion. Early observations suggested that general sediment transport would be poor for this species unless assisted by passive influences. Furthermore, the skeletal microtopography hampered the movements of sediments, particularly of fine sediment. However, rejection efficiency experiments indicated that the species was not significantly poorer than most other species and, in the field, many colonies were sufficiently convex to encourage passive loss.

Yonge (1930) describes the ciliary currents for *Astreopora ocellata*. He also noted for this species that the rugged surface of the coenosarc greatly hindered ciliary loss of silts, the material being lost very slowly.

8. *Porites lobata* Dana, 1846 (c.f. Plate 4.2)

SUMMARY: A relatively inactive sediment rejector. Active rejection is poor for all sediment sizes although silt and fine sediment can be manipulated by cilia. Mucus is present in response to silt and fine sediments. Pulsed contractions of

*the polyps and tissues can be important in sediment
mobilisation.* With P. lutea *and* Montipora aequituberculata, P.
lobata *showed the poorest sediment clearance from test areas
but may compensate by having relatively high tolerance to
overlying sediments.*

Sediment rejection behaviour. Silt and fine sediment could be
manipulated by cilia and were removed from inclined surfaces.
On flat surfaces some fine sediment and silt were held in mucus
and rejected by cilia. However, rejection was rarely swift and
in many cases little mucus was apparent. Pulsing of tissues
was important in mobilising sediments. Coarse and granule
sized sediments were principally moved by tissue expansion but
expansion was weak. Generally this species was relatively
inactive. Where sediment load was light, polyps (many of which
had previously been expanded, but contracted on contact with
sediment) re-expanded through the overlying sediment.
Generally, however, overlying sediment inhibited polyp
expansion. No differences were noted between day and night.

Ingestion of uncontaminated sediment was not observed for this
species. Nor were mesenteries observed in response to
sediment. Response to ground fish was standard (see
Oulophyllia crispa and Plate 2.4).

Sediment rejection efficiency and tolerance. With *P. lutea* and
Montipora aequituberculata, this species was the poorest
sediment rejector of all 22 species tested. However, it
appears to have considerable tolerance to overlying sediment
accumulations, suffering no tissue death despite substantial
sediment loads and accumulations for many days. The tissues of
colonies enduring overlying sediments for more than a couple of
days almost always bleached heavily and withdrew deep into the
skeleton. When sediment later dispersed, bleached tissues
recovered slowly but completely and after 2-4 weeks were
indistinguishable from their neighbours.

Lizard Island. During brief field surveys *P. lobata*, *P. lutea*,
and other large massive *Porites* were not distinguished from one
another. Massive species of the genus were present in all
habitats around Lizard Island but were less ·common in the
lagoon than elsewhere. Individuals were often large (surface-
area >10m^2). Only for two of a sample of 29 colonies were
tissues flush with a sandy substrate (the colonies had not
fallen, their edges were growing naturally close to the
substrate). The edge tissues were bleached but living, but
living tissues did not occur below the surface of the sediment.

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Comment and discussion. In the field, individuals of *Porites
lobata* and other species in the genus were regularly observed
with a mucus sheet covering all or part of their tissues. Such
sheets, both in texture and appearance, were quite unlike the
mucus secreted as an immediate response to sediment by this or
other species although one may be a precursor to the other.
Porites sheet formation apparently took many days, whereas
those referred to here for *Diploastrea heliopora*, *Mycedium
elephantotus* and *Favia pallida*, etc., developed in less than
20 minutes and were thicker, more fluid, and less 'brittle' in
appearance.

Several individuals of a small brittle star species were
observed in active cleaning of the space around their crevices.

Hodgson (1990) examined the sediment tolerance of this species
to 'fine marine sediment' and found that it was rapidly damaged
by $30mg.cm^{-2}.day^{-1}$ and $0.5g.l^{-1}$ for 10 days. There is some
conflict between his results and those reported here. The
difference highlights the difficulties of generalising from
single studies of sedimentation. *Porites lobata* may simply
have different responses to different types of sediment and its
inherent contaminants; it may be affected more profoundly by
laboratory conditions; it may show trans-Pacific genetic
differences: or the tolerance experiments described in Chapter
4, may not have been run for long enough for death to occur
(see discussion in Chapter 4 which suggests that the period of
time sediments overlie tissues of this species may be more
important than the sediment load). Almost all colonies had
bleached but death had not occurred after 8 days.
Nevertheless, *Porites* does occur in high abundance in very
turbid conditions in Australia (Bull, 1982; Potts *et al*, 1985;
Collins, 1987; Veron, 1987) and elsewhere (Maragos, 1974), and
it shows high growth rates in turbid inshore regions (Isdale,
1983). All of these observations suggest that it must have
some useful adaptations for turbid environments.

Marshall & Orr (1931) considered water movement to be an
important influence in sediment rejection from *Porites* and more
significant than ciliary action. In their investigations,
mucus was secreted in response to influxes of mud but ciliary
rejection was incomplete. They considered *Porites* a poor
active rejector. The semi-massive Caribbean species *Porites
astreoides* was considered a competent sediment rejector of up
to 2mm grains by Hubbard & Pocock (1972) but not by Bak &
Elgershuizen (1976). Johannes and Tepley (1974) have examined

the feeding mechanisms of this species by time-lapse photography. Yonge (1930) examined the feeding mechanisms for *Porites solida*.

For further discussion refer to Chapters 2-5 where sediment-related features of *Porites* spp. are discussed at some length.

9. *Porites lutea* Edwards & Haime. 1860 (c.f. Plate 4.2)

> SUMMARY: *General rejection behaviour is identical to P. lobata. Active rejection is poor for all sediment sizes although silt and fine sediment can be manipulated by cilia. Mucus is present in response to silt and fine sediment. Sediment can be mobilised by pulsed contractions of the polyps and tissues. With P. lobata and Montipora aequituberculata, P. lutea showed the poorest sediment clearance from test areas, but may compensate by having relatively high tolerance to overlying sediments.*

Sediment rejection behaviour. Sediment rejection behaviour of *P. lutea* was indistinguishable from that of *P. lobata.*

Sediment rejection efficiency and tolerance. Rejection of sediment after 24 hours was marginally less than *P. lobata* but in other respects their responses and tolerance were similar. *P. lutea* colonies also tolerated overlying sediments, with tissue bleaching but no tissue death.

Lizard Island. See *P. lobata* above.

Comment and discussion. See *P. lobata* above.

10. *Porites cylindrica* Dana, 1846 (Plate 3.2)

> SUMMARY: *Sediment rejection is strongly dominated by passive loss due to ramose morphology. This species is uncommon in exposed regions but very dominant in the lagoon.*

Sediment rejection behaviour. Active sediment rejection was minor because of the overwhelming dominance of passive loss of sediment. Tentacle and polyp movements were important in dislodging sediments to the sides of branches.

Sediment rejection efficiency. More than 50% of fine or coarse sediment immediately dropped through the branches, and more

than 80% had been lost in total after only 10 minutes. Active rejection was relatively unimportant even in calm water conditions.

Lizard Island. This species was very dominant in the lagoon, moderately common in Watson's Bay, but rare in exposed locations. It was generally found with *P. nigrescens.*

Comment and discussion. Veron (1986) describes this species as being very common and often a dominant component of lagoons or back reef margins.

11. *Goniopora lobata* Edwards & Haime, 1860

SUMMARY: Colony morphology and tissue fleshiness , greatly enhances passive rejection. Both ciliary activity and tissue expansion are also well-developed. All sediment sizes are removed effectively.

Sediment rejection behaviour. Passive rejection was a major influence for all colonies observed. The colonies at Lizard Island were columnar with rounded, convex ends. Coenosarc tissues were smooth and punctuated by long fleshy polyps which were in constant motion. Much of the sediment dropped off the colony immediately, or was kept mobile by polyp movements and removed by strong ciliary currents on the column and coenosarc. Polyps retracted in response to sediment but re-expanded later, further dislodging sediments. The tissues surrounding retracting polyps were often seen to expand, effectively scraping sediment from the column as retraction took place. All sediment sizes were effectively removed by this combination of active and passive process. It is unlikely that water movement would be of much further benefit. Polyps were expanded by day and night and no diurnal rejection variations were noted.

Ingestion of uncontaminated sediments was not observed for this species. Nor were mesenteries extruded in response to sediment. No feeding tests were carried out.

Comment and discussion. Yonge (1930) examined the feeding responses of *Goniopora tenuidens*. *Goniopora* as a genus is common in highly turbid waters and can form huge stands (Veron, 1986). It was clear that, in addition to a morphology that encouraged passive rejection, *G. lobata* showed strong active rejection mechanisms, making it well suited to sediment-laden waters.

12. *Psammocora contigua* (Esper, 1797)

SUMMARY: Sediment rejection is strongly dominated by passive loss due to ramose morphology. This species is very common in some areas of the lagoon.

Sediment rejection behaviour and efficiency. Active sediment rejection was minor because of the overwhelming dominance of passive loss of sediment. Detailed studies of behaviour were not undertaken. More than 85% of fine or coarse sediment had been lost in total after only 10 minutes, even in calm water conditions.

Lizard Island. This species was common in some areas of the lagoon. Its distribution elsewhere was not examined.

Comment and discussion. Marshall and Orr (1931) examined a species of this genus and found it to be a relatively poor rejector.

13. *Gardineroseris planulata* (Dana, 1846) (Appendix Plate 1d)

SUMMARY: An active ciliary rejector. Tissue expansion is minor, but ciliary activity is very strong. Silt and fine sediments are manipulated with ease, and coarse and granule sized grains are also manipulated by cilia, but with increasing difficulty. Despite the strong rejection behaviour, this species does not maintain rejection activity over longer periods and may become exhausted relatively quickly. Its tolerance may nevertheless be higher than species such as Leptoria phrygia or Favia stelligera as death does not necessarily occur for several days. At Lizard Island, this species is relatively uncommon and only occurs in exposed locations.

Sediment rejection behaviour. This species showed very strong ciliary currents up the inner walls of the calices towards the edge of the colony. All sediment sizes could be manipulated by cilia although movement of granules was slow and laboured. Mucus was not readily apparent with small sediment sizes unless a build-up of sediment occurred in the calices. Tissue expansion was minor, cilia being more important. Tentacles seemed to be important in supporting larger grains during manipulation. Polyps in calices containing substantial loadings of sediment did not expand. However, as expansion was rare even under normal conditions, it was difficult to say with certainty that sediment inhibited expansion.

No ingestion of uncontaminated sediments was observed. Mesenteries were observed on dying specimens but not as an immediate response to sediment. Response to ground fish was standard (see *Oulophyllia crispa* and Plate 2.4).

Sediment rejection efficiency and tolerance. Although this species showed strong rejection activity during the first hour, this reduced substantially during the following three hours until sediment became almost static. Only two colonies (n=10) cleared more than 90% of the test area after 48 hours, and bleaching of six of the remaining colonies was severe. Two subsequently showed some tissue death. Rejection of coarse sediment tended to be considerably slower than that of fine sediment but tissue death occurred under fine rather than coarse sediment. This species may become exhausted quickly but tolerance is still probably higher than for *Leptoria phrygia* or *Favia stelligera*. both of which showed tissue death after 24 hours.

Lizard Island. This species was not seen either in the lagoon or the moderately-exposed sites around Lizard Island but generally occurred at low abundance in shallow, turbulent water. It was also found in one area of local abundance at 10m in Coconut Bay.

Comment and discussion. Several small brittle stars were seen to move fine sediments from the tissues of this coral. Veron (1986) indicates that *Gardineroseris planulata* prefers clear water on the Great Barrier Reef.

14. *Coeloseris mayeri* Vaughan, 1918 (Appendix Plate 1e)

SUMMARY: A moderately active rejector of silt and fine sediment, although sometimes these sizes can cause difficulties. A poor rejector for larger sediment sizes. Silt and fine sediments are agglutinated in mucus and moved slowly by cilia. Larger sizes move slowly, principally by tentacle expansion and movement, but also by local tissue expansion.

Sediment rejection behaviour. In contrast to many species, the individuals of *Coeloseris* observed showed little initial retraction of tentacles as sediment influxes reached the tissue surface. Silt and fine sediment became slowly clogged by mucus and then moved by ciliary activity slowly across the surface. Larger sizes were moved slowly by movements of the tentacles and localised tissue expansions. The tentacles themselves

expanded and contracted to assist sediment mobilisation. Coarse particles appeared, on occasion, to be passed from one tentacle to another. Pulses occurred across the tissues, particularly obvious in the tentacles. Parts of two colonies died after fine sediment influxes. The sediment became heavily matted with mucus and collected in a slight dip in the colony. The sediment/mucus ball became solidly agglutinated and was almost certainly then too large to be easily manipulated. Tissues beneath became strongly distended, presumably in an unsuccessful attempt to move the mass. They later bleached, mesenteries appeared, and they finally died. This occurred under calm conditions in the field. It would probably not have occurred if turbulence had existed. Polyp expansion at night was minor and although some sediments were dislodged this was not a dominant influence on rejection.

Ingestion of uncontaminated sediment was not actually observed but it was difficult to determine whether ingestion took place in this species as sediments collected over the polyp mouths and often obscured the view. Mesenteries were not observed in response to initial sediment influxes, but were seen around regions of tissues dying as a result of overlying sediment.

Sediment rejection efficiency. In comparison to other tested species Coeloseris was a relatively slow sediment rejector in calm conditions for both coarse and fine sediments. Nevertheless, most colonies had cleared >90% of test areas within 24 hours. Turbulence had an influence on rejection at p<0.10 for this species.

Lizard Island. Coeloseris mayeri was present in all regions of Lizard Island but was relatively rare in the lagoon in comparison to more exposed locations.

Comment and discussion. Many colonies of this species show a relatively convex morphology which would assist in the mobilisation of sediments. Nevertheless, the relatively deep calice centres encouraged sediment to collect and active manipulation was required to lift sediments over adjacent walls. Yonge (1930) describes the feeding mechanisms and ciliary currents of this species. His results also suggest that Coeloseris is not a good rejector, even of silt sized carborundum powder.

The tissues of Coeloseris colonies (n=30) were never flush with the substrate.

15. *Pachyseris rugosa* (Lamarck, 1801)

SUMMARY: Sediment rejection is strongly dominated by passive loss due to ramose morphology. This species is rare in exposed regions, but common in the lagoon.

Sediment rejection behaviour. Active sediment rejection was minor because of the overwhelming dominance of passive loss of sediment. Action · rejection behaviour was not studied in detail.

Sediment rejection efficiency. More than 50% of fine or coarse sediment immediately dropped through the branches, and more than 75% had been lost in total after only 10 minutes. Active rejection · was relatively unimportant even under calm water conditions.

Lizard Island. *Pachyseris rugosa* was rare in exposed regions, not observed in Watson's Bay, relatively common on patch reefs off the Research Station, but common in the lagoon.

Comment and discussion. This species may form large colonies in shallow turbid water, but smaller colonies occur in a wide variety of habitats (Veron, 1986).

16. *Pachyseris speciosa* (Dana, 1846)   (Plate 2.5 and Appendix Plate 1f)

SUMMARY: Mucus is important in the removal of silt and fine sediment, forming sheets which are usually removed by turbulence. Cilia are active for these sizes, less so for coarse sizes. Tissue expansion is minor but assisted in movement of larger sizes. This species has a growth strategy to overcome accumulating sediments. It is less common in the lagoon and highly exposed areas than moderately-exposed regions.

Sediment rejection behaviour. Silt and fine sediment was caught in a mucus sheet which lay somewhat above the tissue from the top of one ridge to another. Minor wave action could catch this sheet and lift it off the coral. Rejection was also aided by relatively strong ciliary currents. Larger sediment sizes were manipulated slowly by cilia but assisted by tissue expansion of the walls on a small scale. Mesenteries were present close to fine and silt sediment sizes and may assist in movement of sediment. No expansion of tissues or polyp occurred at night and no diurnal differences .in sediment rejection were noted.

Ingestion of uncontaminated sediment was not observed for this species although mesenteries were common. Ground fish was not tested.

Lizard Island. Fairly common in gullies between North Point to Pidgin Point, but not observed on the exposed Coconut Bay reefs. Fairly common also in moderately-exposed regions, but less common in the lagoon.

Comment and discussion. In the field, the orientation and morphology of this species often enhanced passive rejection. Many almost flat plating forms when examined closely were not entirely flat or concave but sloped downwards on one side to form a natural channel for sediment rejection. Several specimens were found where central concave sections had become filled with sediment and died, but further skeleton and tissues had grown up over the dead and dying patch (i.e. the plane of growth at the edge of the dying patch had altered). It was clear that the aragonite beneath sediment had been part of the colony and had died because identifying features of the species were still present.

Both Yonge (1930) and Abe (1938) describe feeding mechanisms and ciliary currents for this species.

17. *Fungia repanda* Dana, 1846 (Appendix Plate 1g)

SUMMARY: A very strong ciliary rejector: all sediment sizes are removed speedily. Tissue expansion also occurs but is relatively unimportant because ciliary currents are generally sufficient. Mucus is obvious for fine sediments and silt. Rejection is the fastest of all non-ramose species tested. In tolerance experiments this species did not suffer damage or mortality.

Sediment rejection behaviour. This species was one of the most active rejectors investigated. Sediments were moved from the upper surfaces of the septa to the dips. Fine sediment and silts were heavily clogged with mucus. Ciliary currents were very strong indeed, moving from the mouth outwards along the vertical walls of the septa. Movement of silt and fine sediment was very fast. Expansion of the wall, oral disc and basal tissues between the septa could be substantial (3-4mm) but seemed generally superfluous to ciliary rejection of all sediment sizes except perhaps granules.

Ingestion of large quantities of uncontaminated sediment was common when an influx first met the surface. Once rejection had begun fresh sediment was no longer drawn into the mouth. The response to ground fish was standard (see *Oulophyllia crispa* and Plate 2.4). The mouth expanded greatly and the food was passed inside by ciliary currents.

Sediment rejection efficiency and tolerance. This species showed the fastest sediment rejection of either coarse or fine sediment of any of the non-ramose species tested. Turbulence did not affect the rate of rejection. It suffered no bleaching damage or mortality during field endurance tests.

Lizard Island. This species was not positively distinguished from *F. concinna* during brief field surveys. The species pair was common from North Point to Pidgin Point, but rare in Coconut Bay. Individuals were present on north-western reefs of Watson's Bay and off the Research Station, but much less common. Their abundance in the lagoon was uncertain. No individuals were recorded at two sites, but abundance was not recorded elsewhere.

Comment and discussion. Other *Fungia* spp. were examined briefly (*F. fungites* and *F. concinna*) and showed identical sediment responses to *F. repanda*. Feeding and/or sediment rejection mechanisms have been studied in fungiids by a number of authors. Yonge (1930) examined *Fungia danae* and Abe (1938) added (*Fungia=)Heliofungia actiniformis*, *Fungia repanda* and *F. echinata*. Fisk (1981) reports on feeding and sediment rejection in two sand-dwelling fungiids (*Heteropsammia cochlea* and *Heterocyathus aequicostatus*). Yamasu and Mizofuchi (1989) examined the effects of red clay and detergents on the oxygen production of *F. repanda* and found that concentrations of 500ppm suspended clay had distinguishable effects on photosynthesis and on respiration.

Schuhmacher made a more comprehensive study of sediment rejection for the group covering 14 species (Schuhmacher, 1977) and 18 species (Schuhmacher, 1979). These included *Fungia fungites*, but excluded *F. repanda* and *F. concinna*. He found that sediments falling on several of the convex *Cycloseris* species simply fell off and did not require significant active rejection. Active mechanisms fell into two categories: (a) mucus entanglement combined with ciliary action: and (b) inflation of the polyp. He found that the majority of solitary species tested were ciliary rejectors (Schuhmacher, 1977), only (*Fungia=)* *Heliofungia actiniformis*, *Cycloseris marginata* and

Diaseris distorta using polyp inflation. He also considered
ciliary mechanisms to be more efficient than polyp expansion
for these corals. But longer-term tolerance to continuous
sediment influxes was greater in convex and polyp-inflating
species than the initially efficient ciliary rejectors.
Tolerance of ciliary rejectors depended upon the capacity of
mucociliary cells and the shape of septa, species with sharp
septa being less tolerant than those with broad septal edges.
He placed *F. fungites* into the vulnerable category and, on the
basis of septal edge width, *F. repanda* and *F. concinna* would
also fall into this group. Marshall and Orr (1931) examined
the sediment shedding ability of *Fungia danai* and
(*Fungia=)Heliofungia actiniformis*. While ciliary rejection was
also found to be strong for *F. danae*, they also found a decline
in its rejection ability over time. However, daily doses of
sediments to *F. repanda* for eight days in the field was not
sufficient to exhaust this species.

18. *Sandolitha robusta* Quelch. 1886   (Plate 2.6)

*SUMMARY: A moderately active rejector for silt and fine
sediment, but slow for larger sizes. Silt may become clogged
in mucus. Fine sediments are held in mucus and removed by
cilia and tissue expansion. Mucus was not apparent for coarse
sediments or granules. These sizes are removed by cilia and
tissue expansion. Initial sediment rejection rates tend to be
slow but after 24 hours most colonies had cleared >95% of the
test areas. No colony showed any sign of tissue damage or
death at any time. The species is present in all habitats
around Lizard Island.*

Sediment rejection behaviour. This fungiid did not demonstrate
the highly developed ciliary currents of other *Fungia* spp.
Nevertheless, cilia were important for all sediment sizes.
Silt was immediately caught in a mucus net and clogged.
Movement was subsequently by ciliary currents. Fines were
similar although the mucus was less apparent and tissue
expansion was also involved. Coarse and granule sized grains
could also be manipulated slowly by cilia but tissue expansion
(though weak) was also important.

Ingestion of uncontaminated sediments was extremely common in
this species. In fact. throughout all experiments ingestion of
sediment was probably more common and consistent for this
species than for any other. Mesenteries were not observed
however. Feeding response to ground fish was standard (see
Oulophyllia crispa and Plate 2.4).

Sediment rejection efficiency and tolerance. Sediment rejection rates were relatively slow during the first four hours in comparison to most other species tested, but rejection after 24 hours was generally higher than 95%. Expansion during the dusk period may have greatly assisted loss of sediment. No individuals showed any ill effects at any time during tolerance or other experiments in the field.

Lizard Island. This species was present in all habitats around Lizard Island at relatively even abundance.

Comment and discussion. It is possible that this species tolerates some sediment on its tissues during the day, especially as many colonies were found with low levels of sediment naturally occurring on their tissues. At the scale of the sediments, rejection paths in *Fungia repanda* were unimpeded. In contrast, the microtopography of *Sandolitha* formed a series of terraces (where the polyps were found) which seemed to hinder the loss of sediment.

Both Yonge (1930: as *Doderleinia irregularis*) and Abe (1938: as *Halomitra robusta*) examined the feeding and ciliary currents of this species. Yonge (1930) reports that inedible matter was removed with great speed from the surface. Given the observations described above, it is probable that he was referring to silt sized particles.

19. *Galaxea fascicularis* (Linnaeus, 1767) (Plate 2.7 and Appendix Plate 1h)

SUMMARY: A relatively strong active rejector. Ciliary currents are the principal mechanism for silt and fine sediment. Mucus secretion occurs but is minor. Large sediment particles are actively manipulated by tentacle tips, apparently using adhesive glands. Tissue expansion is also important. Sediment rejection is relatively fast in comparison to most species. Morphology of the polyps is a major factor in rejection. The species is common in all habitats around Lizard Island.

Sediment rejection behaviour. Ciliary currents were strong on the oral disc and on the coenosarc at the base of the projecting corallites. Silt and fine sediments were readily swept away by these currents. Mucus was secreted but sediment was rarely present on the polyps for long enough to become well clogged. At the bases mucus clogging was more apparent.

However, for all sediment sizes, but particularly for coarse sediment and granules, tentacles played an active and direct role in sediment rejection. Two principal mechanisms were involved. For silt and fine sediment, ciliary currents moved sediment away from the mouth and to the bases of tentacles. From there currents continued to carry sediment towards the tips. At the same time the tentacles bent outwards away from the oral disc. Sediment moved towards the tips and fell over the edge.

For larger particles, the tip of the tentacle expanded forming a club shape. The tentacle bent over towards the oral disc and picked up a single grain with its tip. The tentacle first straightened and then bent outwards, away from the oral disc. Finally the particle was released to fall to the coenosarc below. This action was very common for large sediment sizes. There were many changes in tentacle size and expansion during the course of sediment loss. Polyp mouths often expanded upwards into a cone to assist gravitational sediment loss towards the edge of the oral disc. Pulsed contractions of tentacles and tissues also assisted in mobilisation of sediment. Tentacles were expanded day and night and no diurnal differences in rejection were detected.

Tissue expansion of the coenosarc was occasionally apparent at the base of the corallites. However, the principal rejection mechanism from the coenosarc appeared to be ciliary currents.

Ingestion of uncontaminated sediments was not observed in this species. Ground fish caused polyp mouths to open and expose hollow interior. Food was drawn in on ciliary currents. Mesenteries were not observed.

Sediment rejection efficiency. Sediment rejection was generally fast in this species in comparison to non-ramose species. Morphology played a significant part in the loss of sediment from projecting polyps, allowing normal activities of the polyps to continue unimpeded.

Lizard Island. This species was common in all habitats of Lizard Island. The similar species *G. astreata* was also present in most locations but substantially less abundant.

Comment and discussion. Loss of sediment from the polyps was clearly assisted by the height of the corallites. Once mucus-clogged silt and fine sediment began to fall over the edge of the oral disc, gravity would assist in the loss of other sediment held in the same mucus bundle. Loss from the bases

was slower, but potentially also less important as photosynthesis and heterotrophic feeding would no longer be severely affected.

Yonge (1930) examined the feeding mechanisms and ciliary currents of this species but does not refer to the directed tentacle rejection of sediment described above. It was not observed for small sediments which may explain the disparity. It seems likely (though it was not observed) that tentacle tips would also be used for capturing large prey. Observations of a specimen of *G. astreata* confirmed that it, too, used directed tentacle manipulations to reject large sediment particles. Brief observations of this related species suggested that ..,,.ction mechanisms were generally similar to *G. fascicularis*.

Marshall & Orr (1931) found that this species cleaned itself rapidly and considered that ciliary activity was of substantial importance.

20. *Mycedium elephantotus* (Pallas, 1766) (Appendix Plate 1*i*)

SUMMARY: A relatively strong active rejector, principally using ciliary currents and mucus for fine sediment and silt, and ciliary currents with tissue expansion for larger sizes. The species shows moderately low tolerance of sediments overlying its tissues. It is generally rare around Lizard Island, but locally common in semi-protected gullies in the exposed reef front.

Sediment rejection behaviour. This species was very effective at the removal of silt and fine sediment using mucus with strong *ciliary currents. Cilia appeared to be able to manipulate larger sizes but less effectively. Tissue expansion* capacity was substantial ($\pm$5mm) and greatly assisted loss of large particles. Individual polyps were occasionally partially expanded to reject sediment. Pulsing did not occur. Tissue and polyp expansion at night helped to dislodge static sediments.

Ingestion of uncontaminated sediments were not observed. Mesenteries were not observed. Ground fish caused polyp mouths to open and expose hollow interior. Food was drawn in on ciliary currents.

Sediment tolerance. Several colonies of this species suffered tissue damage during the field endurance experiment when

sediments remained on the tissues for a few days. However, this is possibly a response to substantial build-ups of sediment. Sediments were not normally observed on the tissues of this species under natural conditions and it shows strong rejection capability. It may cope well with rains of sediments (and particularly silts) but less well with sudden very heavy influxes (particularly of larger sizes).

Lizard Island. This species was generally rare in all habitats. It was, however, locally common in semi-protected gullies in the reef front between North Point and Pidgin Point.

Comment and discussion. Angled orientation of skeletal plates often encouraged passive rejection. Furthermore, the tissues were fleshy and 'slimy', encouraging fluid streaming of mucus-entangled sediment. Wave action may be a significant influence when mucus sheets are well-developed.

21. *Pectinia lactuca* (Pallas, 1766) (Plate 4.4)

SUMMARY: An extremely active sediment rejector. This species shows very strong tissue expansion and ciliary activity for all sediment sizes. With Pectinia paeonia, it was the most active rejector of all tested species. It is also tolerant of overlying sediment.

Sediment rejection behaviour. With *Pectinia paeonia*, this species was the most active sediment rejector of all species tested. Ciliary currents were very strong, and could manipulate all sediment sizes although small sizes were moved more readily. Mucus was apparent for fine sediment and silt. Tissue expansion was extremely impressive. On occasion tissues were observed to expand off the underlying skeleton by as much as 3-4cm (an order of magnitude greater than most other species) in response to sediment. Tissue expansion was used for removal of all sediment sizes. Sediments would collect in quantity at the base of the polyp (carried by gravity and ciliary currents). The underlying tissue then expanded upwards on one side of the sediment mass, causing it to tip down to the opposite side. Mouths occasionally formed conical projections, causing sediment to fall down the sides. When sediments were added at night the polyp retracted and sediment rejection followed as described above except that partial polyp expansion generally accompanied the wall tissue expansion. As one polyp was cleared of sediment it re-expanded.

Ingestion of uncontaminated sediments was not observed for this species. Ground fish caused polyp mouths to open and expose hollow interior. Food was drawn in on ciliary currents. Mesenteries were not observed.

Sediment tolerance. Tested colonies showed considerable tolerance given the accumulations of sediment on their tissues but some tissue death occurred.

Lizard Island. *Pectinia lactuca* was generally rare in exposed locations but was locally common in semi-protected gullies between North Point and Pidgin Point. Smaller colonies were observed on north-western and lagoon reefs but nowhere was the species dominant.

Comment and discussion. Overall morphology was found to be significant. *P. lactuca* colonies commonly showed 'gravitational drains' in their morphology. In other words, the skeleton had formed in such a way that a downward channel could be found from most points to an edge of the colony. Often the route was very convoluted and spiralled, but there were no really major obstacles. Walls that existed in its path were lower than adjacent walls. Thus, whilst having the most dramatic active mechanisms of any species examined, these species often also had considerable assistance from passive gravitational forces.

P. lactuca is a common coral in turbid habitats on the Great Barrier Reef (Veron, 1986).

22. *Pectinia paeonia* (Dana, 1846)

SUMMARY: An extremely active sediment rejector with very strong tissue expansion and ciliary activity for all sediment sizes. With Pectinia lactuca, *this species is the most active rejector of all species tested.*

Sediment rejection behaviour. Identical to *P. lactuca.* but sediment drains in colonies were more convoluted.

Ingestion of uncontaminated sediments was not observed for this species. Ground fish caused polyp mouths to open and expose hollow interior. Food was drawn in on ciliary currents. Mesenteries were not observed.

Comment and discussion. *P. paeonia* is a common coral in turbid habitats of the Great Barrier Reef (Veron, 1986).

23. *Acanthastrea echinata* Dana, 1846 (Plate 2.2)

SUMMARY: A reasonably effective sediment rejector of all sediment sizes. Silt, fine and coarse sediments are rejected in mucus with ciliary currents and considerable tissue expansion. Granules can be manipulated weakly by cilia but are principally rejected by tissue expansion. Rejection rates fell in the mid-range of species tested. The species was not observed in central lagoon areas of Lizard Island and large colonies are restricted to the shallow exposed reef front.

Sediment rejection behaviour. Mucus was secreted around silt and fine sediments which were rejected by ciliary activity. Tissue expansion was particularly significant for larger sediment sizes but was commonly observed with fine sediment and silts. Tissue expansion of several millimetres could occur quickly (30-60 seconds). Mucus sheets or bundles were obvious for silt, fine and coarse sediments. Static sediments were mobilised as polyps expanded at night, but rejection effects of polyp expansion were incidental to feeding.

Ingestion of uncontaminated sediments occurred in all tested colonies for all sediment sizes. Ejection of these sediments took place about 30 minutes later. Ground fish caused polyp mouths to open and expose hollow interior. Food was drawn in on ciliary currents. Sediments coated with ground fish were ingested and held in the mouths for up to 2 hours.

Sediment rejection efficiency. Rejection rates of this species fell in the mid-range of those species tested. There was little difference between coarse and fine sediment rejection.

Lizard Island. This species was not observed at lagoon sites but was moderately common elsewhere. Large colonies appeared to be restricted to shallow water exposed reef areas.

Comment and discussion. Of 31 colonies examined in the field, the edges of 19 were flush with the substrate, 6 of these being mixed sand of more than 0.5cm depth. Only the very edge (2mm or so) of the marginal tissues were bleached and none were dead. The corals were able to maintain the clear zone by cleaning.

Yonge (1930) examined the feeding mechanisms and ciliary currents of this species.

24. *Lobophyllia hemprichii* (Ehrenberg, 1834)

SUMMARY: Ciliary currents are detectable but tissue expansion is significant for all sediment sizes. Expansion capacity in response to sediment is relatively large (1.5cm) but this species does not always reject sediment immediately. Often tissues simply expand around sediment obscuring it from view. Remaining sediment is likely to be lost when the polyps are expanded at night.

Sediment rejection behaviour. It was clear that this species had the capacity to move silt and fine sediment. readily by ciliary activity and tissue expansion. Tissue expansion capacity observed in response to sediments was high (1.5cm) and sediments *of all sizes were readily mobilised. Rejection of* all sizes was possible. However, rejection did not necessarily take place immediately. Often tissues simply expanded around the sediment accumulations, obscuring them from view. When massive influxes of sediment were simulated (400-1000mg.cm^{-2}, far greater than used for other species), tissue expansion was concentrated on sediment rejection initially but often ceased before rejection was complete. It is probable that minor sediment accumulations on this species cause only minor irritation (if any) to the fleshy tissues. Expansion around accumulations would ensure that autotrophic feeding could be maximised. Night-time observations indicated that much of the remaining sediment could be lost when polyps fully expanded during the dusk period. Pulsing was occasionally observed.

Ingestion was largely uncertain as the expansion of tissues regularly obscured the polyp mouth and sediment altogether. Ground fish caused polyp mouths to open and food was drawn in on ciliary currents. Mesenteries were not observed for any individual.

Comment and discussion. The morphology of this species enhanced passive rejection to some extent. The phaceloid structure of the corallites ensured sediment lost from one polyp would fall off the colony entirely and would not affect any region.

Rejection by all of the large mussids was similar (*L. hemprichii, L. corymbosa, Symphyllia recta* and *S. radians*).

25. *Lobophyllia corymbosa* (Forskal, 1775)

SUMMARY: *Silt and granule sizes were not examined for this species. Otherwise it is identical to L. hemprichii. Tissue expansion in response to sediment is somewhat less (0.8cm).*

Comment and discussion. Yonge (1930) examined feeding mechanisms and ciliary currents of this species.

26. *Symphyllia recta* (Dana, 1846)   (c.f. Appendix Plate 1J)

SUMMARY: *Strong ciliary currents are present but tissue expansion is very significant for all sediment sizes. Expansion capacity in response to sediment is relatively great (1cm) but, as with* Lobophyllia hemprichii, *this species does not always reject sediment immediately. Often tissues simply expand around the sediment obscuring it from view. Remaining sediment is likely to be lost when the polyps are expanded at night.*

Sediment rejection behaviour. Very similar to *Lobophyllia* species. It was clear that this species had the capacity to move silt and fine sediment readily by ciliary activity and tissue expansion. Tissue expansion capacity observed in response to sediments was great (1cm) and sediments of all sizes were readily mobilised. Rejection of all sizes was possible. However, rejection did not necessarily take place immediately. Often tissues simply expanded around the sediment accumulations, obscuring them from view. As for the lobophyllids, when massive influxes of sediment were simulated tissue expansion was concentrated on sediment rejection initially but often ceased before rejection was complete. Again it is probable that minor sediment accumulations on this species cause only minor irritation to the fleshy tissues. Expansion around accumulations would ensure that autotrophic feeding could be maximised. Night-time observations indicated that much of the remaining sediment could be lost when polyps fully expanded during the dusk period. Pulsing of the fleshy tissues was occasionally observed.

Movement of sediment from one meander to another followed a pattern similar to *Platygyra* and *Leptoria.* Sediments collected at a dead end and underlying tissues expanded greatly to lift the sediment mass over the end wall. Tissue expansion was, however, considerably more dominant in this species than in the

meandroid faviids for which ciliary activity was very important.

Ingestion was largely uncertain as the expansion of tissues regularly obscured the polyp mouth and sediment altogether. Ground fish caused polyp mouths to open and food was drawn in on ciliary currents. Mesenteries were not observed for any individual.

Lizard Island. The species pair *S. recta* and *S. radians* was observed in all regions but was rare in the lagoon.

Comment and discussion. Yonge (1930) describes the feeding mechanisms and ciliary currents of this species. Marshall & Orr (1931) examined sediment rejection and found that it always cleaned itself in 24 hours.

27. *Symphyllia radians* Edwards & Haime, 1849 (c.f. Appendix Plate 1*l*)

SUMMARY: Essentially identical to S. recta *except that the expansion observed in response to sediment is a little greater (1.2cm). Sediment rejection is relatively fast.*

Sediment rejection efficiency. This species showed moderately fast rejection rates in comparison with other non-ramose species.

Lizard Island. The species pair *S. recta* and *S. radians* was observed in all regions but was rare in the lagoon.

Comment and discussion. Of 30 colonies, the tissues of only one individual of this species were flush with the substrate which was coral rock.

28. *Hydnophora microconos* (Lamarck, 1816) (Appendix Plate 1*k*)

SUMMARY: Moderately active for silt and fine sediment, very slow for larger sizes. Silt and fine sediment are consolidated in mucus and moved by ciliary currents. Movement of coarse sediments and granules is relatively poor, but is carried out principally by tissue expansion. These grain sizes sometimes become jammed between hydnophores and occasionally can cause lesions. This species is restricted to exposed regions at Lizard Island where it is most common in shallow, turbulent water.

Sediment rejection behaviour. Silt was trapped in mucus and moved on ciliary currents. Fine sediments were also treated similarly but movement was slower. Neither coarse sediment nor granules were moved at all in the first 10-30 minutes, after which movement was very slow. Several of the larger particles became jammed between the hydnophores. On two occasions the sediment particle was seen to cause damage to the tissue. Tissue expansion was apparent on the hydnophores and the basal regions for the larger sediment sizes in particular but active sediment transport of these particles appeared to be slow. Mesenteries were extruded in abundance around granules and coarse sediment. On occasion they appeared to have an 'active influence on the rejection of. the sediment although this could have been fortuitous. Some dislodgement of sediments occurred during the dusk period as tissues expanded.

Ingestion of uncontaminated sediments was not observed for this species although mesenteries were abundant around coarse and granule sized particles. Responses to ground fish were standard (see *Oulophyllia crispa* and Plate 2.4). The polyp mouths opened and food was drawn in on ciliary currents.

Sediment rejection efficiency. Rejection was relatively slow during the first four hours, but clearance was better than 95% after 24 hours.

Lizard Island. This species did not occur in the lagoon or the western reefs. It was only present in any abundance in shallow (1-2m) highly exposed areas of south-east and north-east facing reefs from South Island round Pidgin Point to North Point. In these habitats wave action would normally have a significant role.

Comment and discussion. Yonge (1930) examined the feeding mechanisms and ciliary currents of *Hydnophora exesa* and Abe (1938) investigated *H. rigida.*

29. *Merulina scabricula* Dana, 1846 (Plate 4.3)

SUMMARY: Moderately active of silt using mucus and ciliary currents. Similar for fine sediments, but with a weaker rejection. Rejection of larger sizes is poor and tissue expansion is very weak. Sediment tolerance appears to be relatively low. The species occurs in all regions of Lizard . Island.

Sediment rejection behaviour. Silt and fine sediment were clogged in mucus and moved on ciliary currents. Cilia seemed to be less effective for fine sediment than for silt which moved moderately fast and could be adequately rejected. Tissue expansion was slight even for larger sediment grain sizes. Movement of coarse sediments and granules was generally poor.

No ingestion of uncontaminated sediments. Ground fish was not tested. No mesenteries were observed.

Sediment tolerance. This species showed poor sediment ⁺glerance, more than half of tested colonies suffering some tissue necrosis.

Lizard Island. Present in all habitats but never dominant.

Comment and discussion. Yonge (1930) describes the feeding mechanisms and ciliary currents of this species. He suggests that the movement of silt sized particles was effective and fast as found in the present study.

30. *Favia stelligera* (Dana, 1846)   (Plate 2.3 and Appendix Plate 1j)

SUMMARY: A moderately active rejector of silt and fine sediment using mucus and ciliary currents. Tissue expansion is minor for coarse and granule sizes although coarse can be weakly manipulated by cilia. Mesenteries may occasionally play an active role in moving larger sediment grains. Tentacle tips occasionally pick up larger sediments from the oral disc and deposit them on the coenosarc. Rejection rates are average, but this species appears to be very sensitive to overlying sediments. Around Lizard Island, it is common in shallow, turbulent areas of exposed reefs, but colonies are much smaller and less abundant elsewhere.

Sediment rejection behaviour. Mucus agglutination was clear for silt and fine sediments and particles were removed by ciliary currents. Only minor tissue expansion was-observed for larger sediment sizes. Tentacles tips were observed to pick up sediments from the oral disc and deposit them on the coenosarc. Night-time expansion of polyps only marginally assisted sediment loss. If sediment loads on the polyps were heavy the polyp had difficulty expanding.

Ingestion of uncontaminated sediments was very common in tested individuals of this species. Single coarse grain sediments were commonly ingested and polyps even expanded upwards to engulf granules (which were often larger than the inner calice diameter, see Plate 2.3). Ground fish caused polyp mouths to open and food was drawn in on ciliary currents. The response to food by polyps previously presented with sediment was noticeably slower than the response from polyps with no prior sediment history. Mesenteries were relatively common in response to larger sediments. Mesenteries sometimes appeared to assist ejection of coarse sediment from the mouth.

Sediment rejection efficiency and tolerance. Rejection rates were neither particularly slow nor particularly fast, but this species was very sensitive to overlying sediments, irreversible tissue damage occurring after only 24 hours.

Lizard Island. The species was common in exposed regions, particularly in shallow, turbulent water. It was present in other regions but colonies were smaller and much less abundant.

Comment and discussion. The morphology of the colonies was often a stubby columnar shape with substantial convexity which would also encourage passive loss of sediment. Of 38 colonies, none had tissues flush with any substrate, and not within 3cm of sediments. Bouchon (1981) describes this species as being characteristic of wave-exposed areas.

31. *Favia pallida* (Dana, 1846)   (Appendix Plate 2a)

> *SUMMARY: A strong ciliary rejector.   This species can manipulate all sediment sizes with cilia, although manipulation of granules is slow. Colonies generally use cilia and tissue expansion for granules; principally cilia for coarse sediments; and mucus and cilia for silt and fine sediments. Tentacles occasionally manipulate single larger grains with their tips. The gentle curvature of colonies also encourages passive loss. Colonies were regularly observed with small pockets of mucussy fine/silt sediment in their calices.*

Sediment rejection behaviour. All colonies investigated ingested sediments strongly. To this end, sediments falling in the calices were drawn to the mouths and silt, fine and coarse sediment falling on the inter-calice region were moved up the outer calice wall on ciliary currents and fell towards the mouths. Commonly the inner top tissues of the calice wall

would contract as the sediment rounded the top, making the angle more vertical and encouraging the mucussed sediment to fall to the centre of the polyp. Movement of granules was much slower, but grains could be manipulated by cilia. Tissue expansion was observed for all sediment sizes but was more common for granules. There was some evidence of direct tentacle manipulations of the type described for *Favia stelligera* and *Galaxea fascicularis*, particularly for larger sediment sizes. Once the colony began to reject strongly, it was clear that significant ciliary currents existed across the coenosarc. Silt, fine and coarse sediments were moved readily by these ciliary currents. Silts and fine sediments were heavily mucussed. Although 'sheets' of the type and magnitude described for *Diploastrea*, covering polyps and coenosarc, were not formed, mucus agglutination of smaller sediment sizes was important and greatly assisted ciliary transport.

Ingestion of uncontaminated sediments was common and occurred in all specimens examined. Ground fish caused polyp mouths to open and food was drawn in on ciliary currents. A mesentery was observed on one occasion wrapped around a bolus of mucus and fine sediment as it was ejected from the mouth following ingestion. Mesenteries were not observed at any other time.

Sediment rejection efficiency. A laboratory study of sediment rejection (not reported in this thesis) suggested that this species is very competent, clearing >85% of test areas within one hour. As several species showed faster rejection in the laboratory than in the field (see Chapter 3) this may be an overestimate, but this species would nevertheless rank highly in its clearance rates against the species investigated in Chapter 3.

Lizard Island. This species was not observed in the lagoon and was most common in exposed locations. Colonies were rarely large.

Comment and discussion. Most colonies observed in field, even rare colonies of >50cm diameter, had a gently curving surface with few, if any, concave patches. The coenosarc also appeared to be 'slippery', perhaps due to the abundance of cilia and the presence of mucus. In general, therefore, gravitational forces would greatly assist in the loss of sediment once rejected from the calice, and even granule sized particles were rejected successfully.

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Colonies of this species were regularly observed with small quantities of sediment in their calices during the day. This low level of sediment appeared to be tolerated as no active rejection was taking place. In contrast to areas of the coenosarc, where passive rejection would greatly assist rejection, the polyp centres were deep and much greater energy would need to be expended in order to reject the sediment. Nighttime observations indicated that polyps generally had little difficulty expanding through sediment even when the sediment filled the calice to the brim. Perhaps, therefore, this species rids itself of enough sediment that photosynthesis is not seriously impaired but simply tolerates the remaining grains until nightfall when normal expansion activities would naturally remove the remainder.

Yonge (1930) investigated the feeding mechanisms and ciliary currents of this species.

32. *Favites abdita* (Ellis & Solander, 1786)   (Appendix Plate 2*b*)

> *SUMMARY: A strong ciliary rejector, capable of moving silt, fine and coarse sediment with ease. Granules can also be moved by cilia but more slowly. Tissue expansion occurs for all sediment sizes but is much more common for larger grains.*

Sediment rejection behaviour. This species was a strong ciliary rejector with capabilities similar (though perhaps not as active) to *Favia pallida*. However, being cerioid, *F. abdita* did not have the advantage of smooth coenosarc tissues along which to move sediments *en masse*. All sediment sizes could be manipulated by cilia though movement of granules was slower than other sizes. Tissue expansion was observed for all sediments, but relatively rarely for coarse and smaller sizes for which ciliary currents were adequate. Expansion of calice wall tissues was rare, partial expansion of the central polyp region being more common. Direct tentacle manipulations were not observed during the day, but were common at night. Static sediment was dislodged as the polyps expanded at night but this was incidental to feeding activities.

Ingestion of uncontaminated sediments was not observed for this species. The response to ground fish was standard (see *Oulophyllia crispa* and Plate 2.4).

Lizard Island. During field surveys *F. abdita* and *F. halicora* were not distinguished. The species pair was rare in the lagoon, but present in all other habitats.

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Comment and discussion. Most colonies of *F. abdita/halicora* were hillocky, with few horizontal or slightly concave regions. This morphology contributed to passive sediment loss.

Yonge (1930) examined the feeding mechanisms and ciliary currents of several *Favites* species and found that their structure and behaviour closely resembled *Favia pallida*.

33. *Goniastrea retiformis* (Lamarck. 1816) (Appendix Plate 2c)

> SUMMARY: A moderately active rejector of silt and fine sediment using cilia and mucus. Manipulation of coarse and granule sizes is poor. Generally these particle sizes are removed by tissue expansion, although this is relatively weak.

Sediment rejection behaviour. Silt and fine sediments were caught in mucus and removed by ciliary currents. Ciliary manipulation of coarse and granule sized grains was poor. Tissue expansion was apparent for these sizes but was relatively weak. Tentacle manipulations were not observed. Polyp expansion during dusk assisted to dislodge sediments although expansion could not always occur fully when sediment density was high. Fine and coarse sediments appeared to give the most difficulty. The gaps between granules offered openings through which partial tissue expansion could occur, shifting sediments and allowing further expansion.

Ingestion of silt and fine grains occurred occasionally. Ingestion of larger particles was not observed. Ground fish was not tested. Mesenteries were not observed on this species.

Lizard Island. *Goniastrea retiformis* was observed in all regions although it was less common in the central lagoon than elsewhere. It was not always common within transects in moderately-exposed sites. but this was an anomaly of sampling as it was generally common throughout the north-western region.

Comment and discussion. Yonge (1930) examined the feeding mechanisms and ciliary activity of species of *Goniastrea* and found that they closely resembled *Favites* and *Favia*.

34. *Platygyra lamellina* (Ehrenberg, 1834) (Appendix Plate 2d)

> SUMMARY: Moderately active for all sediment grain sizes. Fine sediments and silts are removed by a combination of mesenterial

activity, mucus, cilia and tissue expansion. Coarse and granule sized grains are removed primarily by tissue expansion and cilia.

Sediment rejection behaviour. Sediment rejection by this species was similar to that of *Leptoria phrygia*. Sediments of all sizes were moved by a combination of gravity and ciliary movement, with some minor tissue expansion and contraction, from the site of initial contact, off the walls and into the valleys beneath. Once in the valleys cilial transport occurred along the valley base until the sediment met a dead end. At this point the sediment accumulated against the wall, and the underlying tissues and polyp began to expand upwards. Cilia were still active and assisted to lift the sediment grains over the wall and into the adjacent meander. This process was repeated until the sediment fell off the colony. Pulsing of the tissues was occasionally observed in this species.

In the area encompassed by sediment (all sizes) mesenteries were often extruded through the sides and upper surfaces of the walls (and less regularly the inter-mouth regions of the valleys). Generally mesenteries were less abundant than observed in *Leptoria*, but they were similarly mobile and appeared to help to control the direction and movement of the fine sediment and silt. Mesenteries did not appear on areas of the colony unaffected by precipitating sediments. As the sediment was removed from the local area the mesenteries retracted.

Tissue expansion was an essential part of rejection for all sediment sizes in order to move from one meander to another. Tentacles were not observed to participate in sediment rejection.

No ingestion of uncontaminated sediments was observed for this species. Response to ground fish was standard (see *Oulophyllia crispa* and Plate 2.4). Mesenteries were common, but were relatively short and stubby and appeared to assist the movement of small sediment grains.

Lizard Island. *Platygyra* spp. were present in all habitats but rare in central lagoon sites.

Comment and discussion. Yonge (1930) examined the feeding mechanisms and ciliary currents of this genus (under the synonyms *Coeloria* and *Maeandra*).

35. *Leptoria phrygia* (Ellis & Solander. 1786) (Plates 2.8, 7.1. 8.1 and Appendix Plates 2e and 2f)

SUMMARY: Moderately active for all sediment grain sizes. Fine sands and silts are removed by a combination of mesenterial activity, mucus, cilia and tissue expansion. Coarse and granule sized grains are removed primarily by tissue expansion and cilia. Sediment rejection efficiency fell in the mid-range of species tested, but sediment tolerance of this species is low. Detectable damage occurred to Leptoria with daily sediment influxes of 25mg.cm^{-2}.day^{-1} and higher for 23 days. At Lizard Island it is most common in shallow, turbulent, exposed locations.

Sediment rejection behaviour. Sediments of all sizes were moved by a combination of gravity and cilial movement, · with some minor tissue expansion and contraction, from the site of initial contact, off the walls and into the valleys beneath. Once in the valleys ciliary transport occurred (downhill wherever possible) along the valley base until the sediment met a dead end. At this point the sediment accumulated against the wall, and the underlying tissues and polyp began to expand upwards. Cilia were still active and assisted to lift the sediment grains over the wall and into the adjacent meander. This process was repeated until the sediment fell off the colony.

Mucus was clearly important in the rejection of both fine sand and silt sized particles. Within minutes after sediment landed on the coral surface, two to several fine or many silt grains could be seen to stick together. Single or agglutinated groups of these grain sizes were readily moved by cilia, even upwards or across the vertical sides of the walls and septa. Entanglement did not appear to be as important for the larger grain sizes, although mucus may play a role in lubricating the route and protecting the underlying tissues from abrasion. The cilia of this species were able to manipulate both coarse and. granule sized grains but the resulting movement was considerably slower than for smaller grain sizes.

In the area encompassed by sediment (all sizes) mesenteries were extruded through the sides and upper surfaces of the walls (and less regularly the inter-mouth regions of the valleys). It is probable that their purpose was to test the foreign objects as a potential source of food. However, they were very mobile and appeared to help to control the direction and movement of the fine sediment and silt. Mesenteries did not

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appear on areas of the colony unaffected by precipitating sediments. As the sediment was removed from the local area the mesenteries retracted.

Tissue expansion was an essential part of rejection by this species. Tissues of the walls and valleys were observed to expand in response to sediment. However, the tissues most commonly involved in this activity were those of the polyp. oral disc and wall at the dead-end of a meander.

In the absence of food, *Leptoria* often ingested sediment grains, but more commonly rejection took place almost immediately. Large granule-sized sediment grains that could not be ingested were enveloped in mesenteries. When presented with food particles the polyps opened wide and ciliary currents. wafted the food into gaping mouths. The response of tissues to sediments contaminated with food was similar except that the sediment grains were also ingested with the food particles. *Leptoria* was a voracious predator at night, capturing planktonic worms, crustacea and other organisms with its tentacles (see Appendix Plate 2f). Sediments trapped in slight dips could prevent expansion.

Sediment rejection efficiency and tolerance. Sediment rejection by this species fell in the mid-range of non-ramose species tested, but tolerance was very low. Several colonies suffered some tissue death after only 24 hours during rejection efficiency experiments (Chapter 3), and a high proportion of colonies were affected during later tolerance experiments (Chapter 5).

Leptoria was the subject of further experiments to examine the level of sediment influx causing tissue damage and death. Over a period of 23 days, no colonies (all near-flat) suffered any tissue damage or death at sediment influxes of less than $25mg.cm^{-2}.day^{-1}$. From $25mg.cm^{-2}.day^{-1}$ the number of colonies affected and the extent of tissue damage progressively increased as input loads increased through 50, 100, 200, and $400mg.cm^{-2}.day^{-1}$, until at $1000mg.cm^{-2}.day^{-1}$ all colonies suffered total or almost total tissue death.

Lizard Island. This species was common along the exposed reef fronts, particularly in shallow, turbulent locations. It was present but considerably less abundant in moderately-exposed locations and entirely absent from the lagoon. Morphological studies of this species are reported in Chapter 5.

Biochemical constituents and physiological responses to
sediments. Analysis of lipid, chlorophyll and zooxanthellae
numbers for this species are reported in Chapters 6a and 6b.
Photosynthesis and respiration studies, and the potential
effects of sediments, are discussed in Chapter 8.

Comment and discussion. On Lizard Island under natural
conditions passive rejection is generally high either because
of its position on the reef where it is subject to high wave
activity, or in other areas, because it has relatively little
susceptible tissue. Its position and distribution, as well as
some of its morphological characteristics, are probably
controlled, at least partly, by the sedimentary regime. Of 211
colonies observed in the field only one had tissues flush with
the substrate (slightly vegetated rock), and no tissues were
within 2cm of sediments.

Yonge (1930) examined the feeding mechanisms and ciliary
activities of this species. He found that mesenteries were
frequently extruded through the mouth. In the present study,
most mesenterial extrusion was directly through the walls and
other tissues and only rarely from the mouth. He also found
that the tentacles were very active in food capture.

36. *Oulophyllia crispa* (Lamarck, 1816) (Plate 2.4 and Appendix
Plate 2g)

*SUMMARY: A strong active rejector of all sediment sizes.
Cilia, mucus and tissue expansion are involved in the rejection
of fine sediment and silt, cilia and tissue expansion for
coarse sediments and granules. Rejection from all but the most
central horizontal region of a colony is probably assisted by
passive gravitational loss. Of the non-ramose species studied,
active rejection rates are second only to* Fungia repanda. *The
species is absent from the central lagoon of Lizard Island but
present in other habitats.*

Sediment rejection behaviour. This species was a very strong
rejector of all sediment sizes tested. Sediments fell, or were
assisted by cilia, off the wall tissues to the bases of the
meanders. Fine sediments and silts were then-caught in mucus
and streamed along shallow gravitational paths on ciliary
currents. Coarse sediments and granules were moved principally
on ciliary currents but with occasional basal tissue expansion
were necessary. Once sediments of all sizes reached a meander
end, the tissues expanded as for *Leptoria phrygia* although the

expansion capacity was much greater (often about 8-12mm but twice observed to about 15mm). Tentacles were never observed to participate in rejection. As sediments passed along the meander valleys, polyp centres commonly expanded slightly (≈1mm) upwards to a pyramid shape with the mouth closed. This had the effect of keeping sediment together, and away from the mouths.

Ingestion of uncontaminated sediments was not observed although mesenteries did appear around granules on several occasions. In response to ground fish the polyp mouths opened widely and food was drawn in on ciliary currents as shown in Plate 2.4. The response was quite unlike that to sediments and no mesenteries were observed.

Sediment rejection efficiency. Of the 18 non-ramose species tested, the sediment rejection rate of *O. crispa* was second only to *Fungia repanda* and there was no distinguishable difference between coarse and fine sediment.

Lizard Island. Present in both exposed and moderately-exposed habitats but absent from the central lagoon.

Comment and discussion. Except in the most central horizontal regions of the colony, the floor of most meanders was not flat or concave. Although cilia were clearly active, streaming of sediment principally followed gravitational paths to the meander end and thus passive influences were relatively substantial.

37. *Montastrea curta* (Dana, 1846) (Appendix Plate 2*h*)

SUMMARY: Only moderately active for silt and fine sediment, using mucus, ciliary currents and tissue expansion. Tissue expansion is the principal mechanism for larger sizes but the response is variable, some individuals being relatively active and some very inactive. Absent from the central lagoon at Lizard Island and much more common in shallow, turbulent exposed reefs than moderately-exposed locations.

Sediment rejection behaviour. Silt and fine sediment were held in mucus and principally moved by cilia, although tissue expansion was also involved. On one individual, fine sediments were removed poorly, although generally rejection of fine sediment and silt was moderate. Coarse and granule sizes were mobilised by tissue expansion which was occasionally moderately

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substantial (≃4mm). It was not clear whether cilia were also involved. Two replicates dealt relatively well with coarse sizes and one with granule, while the remainder were poor for both sizes. Direct tentacle manipulations were not observed during the day, but were common at night.

Ingestion of fine sediment and silts was observed. Sediments which fell on the outside wall of the calice were carried away by ciliary currents, while sediment which fell on the inside wall were carried first to the mouth, and only later rejected. Ingestion of coarse and granule grains was not observed. No mesenteries were extruded by individuals of this species. Responses to ground fish were not tested.

Lizard Island. Absent from the central lagoon and considerably less common in moderately-exposed sites than along exposed reef fronts. Most abundant in shallow, turbulent locations.

38. *Plesiastrea versipora* (Lamarck, 1816) (Appendix Plate 2*i*)

SUMMARY: Moderately active for all sediment sizes although movement of granules is relatively poor. Cilia, mucus and tissue expansion are the principal mechanisms for rejection of silt and fine sediment, and cilia and tissue expansion for coarser sediments. Extrusion of mesenteries is common.

Sediment rejection behaviour. Cilia were capable of moving all sediment sizes although manipulation of granules was very slow. Tissue expansion was common for all sizes but mucus only clearly affected silt and fine sediment. Direct tentacle manipulations were not observed during the day, but were common at night.

Ingestion was common for all particle sizes. Coarse, fine and silt grains falling on the colony instigated an immediate response from the polyps which began to close up over the mouth trapping particles inside. The closure was incomplete and further sediment particles were lifted up the walls by cilia. As sediment was re-ejected the polyps opened up and tissues expanded considerably to aid sediment loss. Small (1-2mm) and elongate granules were also ingested but larger particles were enveloped by mesenteries. Mesenteries were also apparent among fine sediments that were stationary on the tissue surface. The response to ground fish was standard (see *Oulophyllia crispa* and Plate 2.4).

Sediment rejection efficiency. Rejection rates for this species were average.

Lizard Island. Not common around Lizard Island, but found sporadically in exposed and moderately-exposed regions. Not observed in the central lagoon.

Comment and discussion. This species is tolerant of a very wide range of environmental conditions, occurring in many habitats and at all latitudes around Australia (Veron, 1986).

39. *Diploastrea heliopora* (Lamarck, 1816)   (Plate 3.1 and Appendix Plate *2j*)

SUMMARY: A very competent rejector of all sediment sizes by cilia. Mucus strands or full mucus sheets are commonly formed with silt and fine sediments, which are subsequently moved by ciliary currents. Mucus entanglement is also relatively common with coarse sediment, although unbroken sheets are not formed. Tissue expansion is minor except where sediments are static for some time. Minor turbulence can cause entire mucus sheets and agglutinated sediments to be lost from the colony. Sediment rejection rates are relatively fast in comparison to other non-ramose species tested. This species shows little morphological variation and few sediment-trapping regions. It is present in all regions of Lizard Island but is less abundant in the lagoon than elsewhere.

Sediment rejection behaviour. A strong ciliary rejector. All sediment sizes could be manipulated by cilia although movement of granule and coarse grains was more laboured. Mucus appeared to be of particular importance to this species. Agglutination occurred for silt, fine and coarse sediments. For the two finer grain sizes mucus strands or full mucus sheets were formed which were subsequently moved by ciliary currents. Unlike *Favia pallida* whose plocoid corallites were comparatively jagged and broke potential sheets into smaller strips, the surface of *Diploastrea* was smooth and sheets forming a unbroken layer across the top of the corallites. were not uncommon. In the mucus, sediments spread out into a layer 1-2 grains thick and occasionally the sheets were extensive-covering many tens of polyps. Full sheets did not develop for coarse grains, but mucus entanglement was still significant. Tissue expansion was important for larger sizes (granules in particular) and significant expansion ($\simeq$4mm) was sometimes observed where sediment had been static for 20 minutes or so.

Direct tentacle manipulations were not observed during the day, but were common at night.

Ingestion of uncontaminated sediments was common. Particles of all sizes were observed to be actively moved up the outer corallite wall to the mouth on ciliary currents. As the sediment approached the top of the wall, the mouths opened and ingestion occurred. Ground fish caused the mouths to gape much more widely and food was wafted in on ciliary currents. Mesenteries were not observed for this species.

Sediment rejection and tolerance. Sediment rejection rates were high relative to most of the 18 non-ramose species tested. There was no distinguishable difference between coarse and fine sediment rejection rate, and no significant effect of turbulence on rejection rate. During longer-term sediment exposure (Chapter 4) accumulations of sediment on tissues of this species were rare because of the absence of sediment-trapping regions of tissue and the effectiveness of active rejection mechanisms. Very minor ($<1cm^2$) tissue damage occurred once but repaired quickly once sediment had dispersed.

Lizard Island. This species showed little morphological variation. It was present in all regions of Lizard Island but less abundant in the lagoon than elsewhere. In exposed locations, colonies were frequent from shallow water (2m) to the base of the dropoff (usually 10m). Large individuals ($>1m$ diameter) were common but rarely located in very shallow water.

Comment and discussion. Colonies were almost never concave at any point but moderate regions (20x20cm or larger) of flat or only very mildly convex tissue were not uncommon. Once mucus sheets had been formed, on several occasions mild turbulence was observed to lift the entire sheet off the colony without further need for active rejection. Of 30 colonies examined in the field none had tissues flush with the substrate and only one had tissues within 5cm of sediments.

40. *Cyphastrea serailia* (Forskal, 1775)

SUMMARY: Silt is moved readily by mucus and cilia, fine sediments less readily. Movement of coarse and granule sized sediments is very slow and laboured and generally initiated by tissue movements. Once on the move, the hillocky nature of the corallum probably helps to maintain the momentum for these larger sizes.

Sediment rejection behaviour. Silt was clogged in mucus and readily dispersed by cilia. Movement was often fast. Mobilisation of fine sediment was poorer but used a similar mechanism. No substantial movement of coarse or granule sizes was detected for over an hour for two of the three colonies, although one colony began after 20 minutes. Movement was caused by tissue expansion and probably also cilia (uncertain) but it was very slow. Tentacles did not appear to participate in rejection.

Ingestion occurred for all sizes except granule but was not universal. In response to ground fish polyp mouths expanded upwards to form a cone and opened widely. Food was drawn in on ciliary currents. Mesenteries were not observed for this species.

Sediment rejection efficiency. This species showed average rejection rates for non-ramose species tested.

Lizard Island. Found in all regions of Lizard Island.

Comment and discussion. Colonies of this species around Lizard Island were generally small and not smoothly rounded but full of small convex hillocks. This morphology seemed to assist sediment rejection. Although it was clearly difficult for the coral to initiate movement of larger particle sizes, once static friction had been overcome and grains were on the move, the steep slopes helped to maintain motion through subsequent flatter patches.

41. *Cyphastrea chalcidicum* (Forskal, 1775) (Appendix Plate 2*k*)

SUMMARY: Rejection is identical to C. serailia. Morphology of this species is also hillocky, which enhances passive rejection.

Sediment rejection behaviour. Rejection by this species was identical to *Cyphastrea serailia*.

Ingestion of all sizes but granule was again observed but no mesenteries were seen for any size. Responses to food were not tested.

Comment and discussion. The colonies of this species were also hillocky and may confer similar passive rejection advantages.

Rejection of silt and fine sediment was incidentally assisted
by the movements of a dorso-ventrally flattened polychaete worm
and several tanaid crustaceans.

Yonge (1930) examined the feeding mechanisms and ciliary
currents of this species.

42. *Echinopora lamellosa* (Esper, 1795)

*SUMMARY: Moderately active for small sediment sizes but
rejection of larger sizes is poorer. Silt and fine sediments
are moved by mucus, ciliary currents and minor tissue
expansion. Coarse grains are moved slowly by cilia and tissue
expansion. Granules are mobilised very slowly, if at all, by
tissue expansion. This species appears to be very sediment-
sensitive. It may use a growth strategy to cope with sediment
influxes. It is relatively common in all habitats around
Lizard Island.*

Sediment rejection behaviour. Silt and fine sediment were held
in mucus and were removed relatively easily by ciliary
currents. Mucus was much less apparent for fine sediment than
for silt. Sediment was removed from the polyps before the
coenosarc. Tissue expansion was apparent for small sediment
sizes but more commonly observed for movement of coarse and
granule sized grains. Coarse grains could be manipulated 'by
cilia but movement was slow. General movement of both coarse
and granule grains was poor.

Ingestion was not common but occurred for all sizes except
granules. Response to ground fish was standard (see
Oulophyllia crispa and Plate 2.4). Mesenteries were not
observed in response to sediment but were seen where a lesion
had been caused (not by sediment).

Sediment tolerance. The sediment tolerance of this species was
very poor (Chapter 4). Growth of edge tissues surrounding
regions that died as a result of sediment accumulations, was
angled upwards away from the dead patches. Growth may be an
important strategy for this species, allowing vulnerable areas
to die and putting energy into growth to lift new tissues away
from the substrate.

Lizard Island. Found in all habitats of Lizard Island and
locally common but colonies angled strongly in lagoon sites.
Very abundant in some semi-protected gullies on exposed reef

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fronts. Very commonly had dead patches at the base of foliose colonies close to the substrates.

Comment and discussion. The granular microtopography of the skeleton seemed to hinder sediment loss from this species. Plating colonies were occasionally extensive in moderately protected gullies on exposed north-east reefs. Here the colonies formed whorls and tiers, and often included regions that were concave or flat.

Both Yonge (1930) and Abe (1938) examined the feeding mechanisms and ciliary activities of this species.

43. *Echinopora mammiformis* (Nemenzo, 1959) (Plates 2.9 & 2.10)

SUMMARY: A very active ciliary rejector capable of moving all sediment sizes with ease. This species occurs in two distinct growth forms at Lizard Island: a finely branching form only found in the lagoon (where it is present in local abundance); and a plating form with occasional upward branches, occurring elsewhere around the island.

Sediment rejection behaviour. This species was able to manipulate all sediment sizes on cilia: silt, fine and coarse sediments with ease, but granules more slowly. It was a powerful ciliary rejector. Tissue expansion was redundant for silt and fine sediment but was occasionally observed for coarse sediments and more commonly for granules. In all cases distension was minor ($\approx 1mm$). Silts and fine sediment were matted in mucus prior to rejection. Mucus was not obvious for larger sizes. Tentacles were not observed to participate in rejection.

Ingestion of all sediments was common. Smaller sediments were often actively moved from the coenosarc, up the outer corallite wall and down to the mouth. Larger sediments were ingested when they had landed on polyps but rejected from the coenosarc. Mesenteries were not observed on laboratory specimens, but on two field colonies, long (2-3cm) filaments were observed on the tissue surface in the vicinity of sediments. Several mesenteries were apparent on each colony and occasionally wrapped around sediment particles (fine and coarse). The result was that the sediments moved, but this may have been incidental to a feeding function. Food was not tested for this species.

Sediment rejection efficiency. The ramose lagoonal morph was tested in rejection efficiency experiments for comparison against non-ramose species. Although active rejection mechanisms are well-developed in this species, at least 50% of both coarse and fine sediment dropped straight through the branches and more than 85% had been lost after 10 minutes.

Lizard Island. *Echinopora mammiformis* displayed two distinct morphologies on Lizard Island. In the lagoon, the species was exclusively ramose. It was relatively abundant and occasionally formed monospecific or part of multispecific stands. The branches were narrow and contorted. In contrast, colonies were principally plating with only occasional vertical branches in other locatic

Comment and discussion. Veron (1986) also refers to the two distinct morphs of this species. There is apparently no intermediate form.

44. *Turbinaria peltata* (Esper, 1794) (Appendix Plate 2*l*)

SUMMARY: A very strong ciliary rejector. Silt, fine and coarse sediment are all moved effectively by ciliary currents. Granules more slowly. Tissue expansion occurs in response to all sediment sizes, but is unnecessary for silt and relatively minor for other sizes. Not common around Lizard Island.

Sediment rejection behaviour. This species could manipulate all sediment sizes with its ciliary currents and was a very strong ciliary rejector although movement of granules was slow. Tissue expansion was observed for all sediment sizes but was rare for silt and uncommon for fine sediment. Tissues expanded only mildly in response to sediment (≃2mm). Polyps of this species were often widely spaced and the intervening coenosarc was smooth. Silt and fine sediment were consolidated in mucus and moved in ragged sheets or strands across the surface on ciliary currents, often *en masse* and fast. Mucus was also often apparent with coarse sediment. Direct tentacle movements were not observed. One polyp did display specific retraction behaviour. Fine sediment was building up against one side of the polyp (which was only expanded slightly) and, principally because grains were held together by mucus, became stuck. After several minutes the polyp retracted, the mucus/sediment mass slid overhead and the tissues immediately re-expanded. Pulsing of the tissues occurred occasionally. Polyps were regularly expanded during the day. After initial contraction

on polyps on sediment influx, some re-expanded mobilising sediments and some did not. No diurnal differences in rejection were noted.

Ingestion was not observed for this species. Food was not tested. Mesenteries were not observed in response to sediment.

Lizard Island. Not common around Lizard Island. Found at the base of the drop-off in exposed locations and rare on moderately-exposed reefs. Not observed in the central lagoon but occasional in peripheral regions.

Comment and discussion. It was notable that sediment collecting areas of *Turbinaria peltata* existed on many colonies *in situ*. A common form of the species at Lizard Island was an open cone with one side just off the vertical, and the other angled almost horizontally, sometimes slightly upwards, and sometimes slightly downwards. Generally the apex of the cone collected sediment and sediment was almost always present. Sometimes the tissues at the apex were dead. But often they, and much of the tissue between the apex and the outer edge in the horizontal direction were heavily bleached. Bleaching generally reduced from the apex outwards as might be expected. Perhaps more interestingly, polyps were much more widely spaced in this vulnerable region than over the rest of the colony.

Yonge (1930) examined the feeding mechanisms and ciliary currents of this genus.

45. *Turbinaria mesenterina* (Lamarck, 1816)

SUMMARY: *A strong ciliary rejector, particularly of silt, fine and coarse sediments. Mucus sheets form during rejection of silt and fine sediment and mucus is also apparent with coarse sediment. Tissue expansion is relatively minor. Rejection of granules is relatively slow. More common than* T. peltata *at Lizard Island and present in all regions.*

Sediment rejection behaviour. Tissues contracted on initial contact with sediment. As for *Turbinaria peltata*, this species was a strong ciliary rejector. Silt and fine sediment were caught in a mucus sheet and moved across the coenosarc on strong ciliary currents. Mucus was also apparent for coarse sediments. Cilia did not seem to be very effective at moving granules. Some minor tissue expansion was observed for all sediment sizes but was more significant in the rejection of larger grains.

. Ingestion was common for all sediment sizes, but mesenteries were not observed. When ground fish was added the polyp mouth formed a deep hollow. In some cased fish was caught on tentacles which retracted to the mouth and in others the oral disc began to protrude upwards and draw fish in on ciliary currents.

Lizard Island. Present in all regions of Lizard Island but generally not abundant. More common than *T. peltata.*

Comment and discussion. Many individuals of this species form vertical or angled whorls, and would benefit greatly from passive loss of sediment.

Yonge (1930) examined the feeding mechanisms and ciliary currents of this genus.

Appendix Plate 1

|		
(a)	(b)	(c)
(d)	(e)	(f)
(g)	(h)	(i)
(j)	(k)	(l)

a) *Pocillopora damicornis* (*x 0.2*)

b) *Montipora aequituberculata* showing laminar morphology and skeletal roughness (*x0.2*)

c) *Astreopora myriophthalma* (*x 0.07*)

d) Close up of corallites of *Gardineroseris planulata* (*x 1.5*)

e) *Coeloseris mayeri* (*x 0.5*)

f) *Pachyseris speciosa* showing encrusting to laminar or foliaceous morphology (*x 0.02*)

g) *Fungia repanda* (*x 0.3*)

h) *Galaxea fascicularis* (*x 0.05*)

i) Laminar colony of *Mycedium elephantotus* (*x 0.07*)

j) *Favia stelligera* showing sub-columnar growth form and central, recently dead tissue section (*x 0.02*)

k) *Hydnophora microconos* on the shallow exposed reef edge of Coconut Bay (*x 0.04*)

l) *Symphyllia* sp. (*x 0.05*)
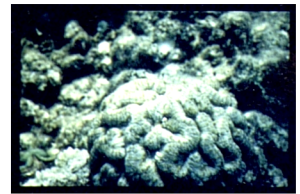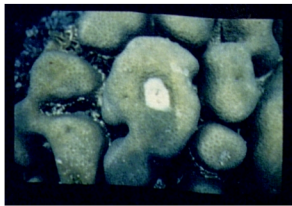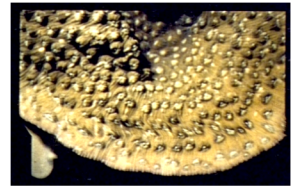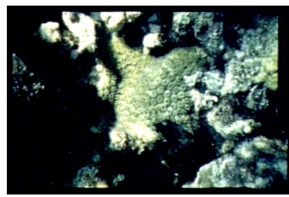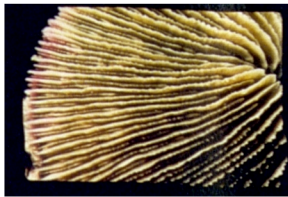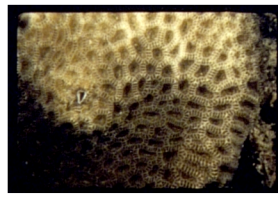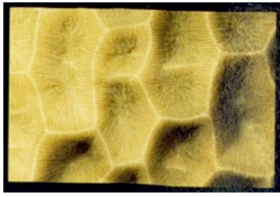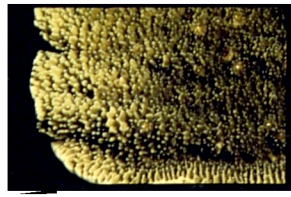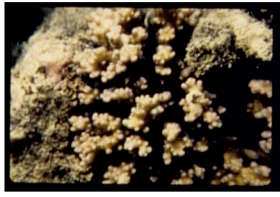
(a)   (b)   (c)

(d)   (e)   (f)

(g)   (h)   (i)

(j)   (k)   (l)

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a)   *Favia pallida (x 0.1)*

b)   *Favites abdita/halicora (x 0.2)*

c)   *Goniastrea retiformis (x 0.3)*

d)   *Platygyra lamellina (x 0.2)*

e)   *Leptoria phrygia* colony on the exposed reef front at Coconut Bay *(x 0.03)*

f)   *Leptoria phrygia* feeding hetero-trophically on polychaetes and other zooplankton at night *(x 0.1)*

g)   *Oulophyllia crispa (x 0.3)*

h)   *Montastrea curta (x 0.1)*

i)   *Plesiastrea versipora (x 0.3)*

j)   *Diploastrea heliopora* colony showing mucus sheet formation with fine sediment *(x 0.1)*

k)   *Cyphastrea chalcidicum (x 1)*

l)   *Turbinaria peltata (x 0.07)*
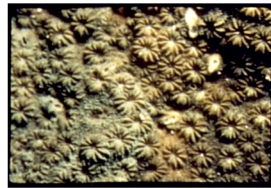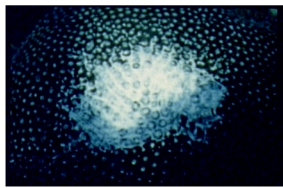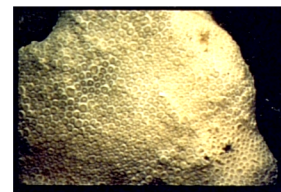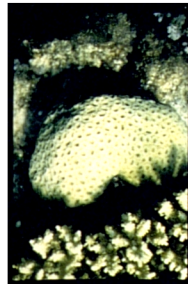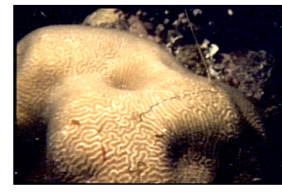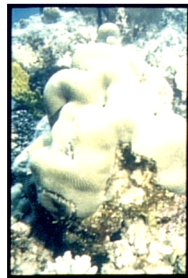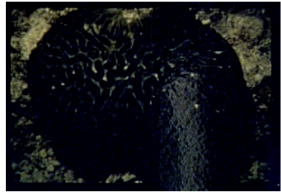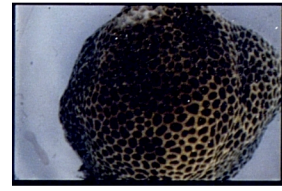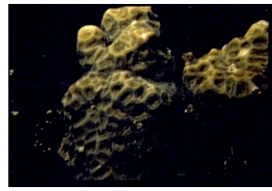
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