SEDIMENT RESPONSES OF CORALS FROM INSHORE REEFS, GREAT BARRIER REEF, AUSTRALIA

Thesis submitted by
Jeremy J. SOFONIA Bsc

for the degree of Master of Science in
the School of Marine Biology and Aquaculture at
James Cook University of North Queensland

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Jeremy. J. Sofonia
1 November 2006

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ABSTRACT

The role of turbidity and sedimentation is a key problem for nearshore coral reefs worldwide. However, little is known about how sedimentation interacts with other environmental factors such as hydrodynamics, temperature and light and how coral species vary in their sediment responses. Here, I investigate the response of corals to sediment under varying flow, temperature and light regimes in two controlled mesocosm experiments, and then preliminarily examine the role of sedimentation in structuring coral assemblages using a new method for manipulating sedimentation rates in field settings.

The first experiment was designed to test the specific hypothesis that coral stress (using the foliaceous *Turbinaria mesenterina* as a study species) associated with sedimentation is reduced under turbulent flow conditions that prevent long-term sediment deposition on coral tissues. To provide a rigorous assessment of the physiological response, three key physiological parameters were used: tissue lipid concentration, skeletal growth rate and photosynthetic performance (maximum quantum yield). The second experiment investigated interactions between sediment stress and stresses associated with high temperature and light – a problem highly topical in the context of climate change. Lastly, the field experiment consisted of an array of six erosive sediment blocks (plaster of paris and silicate-based sediment) suspended above the fringing reef at Pelorus Island (Queensland, Australia) to simulate replicate sediment gradients. The sediment responses of three coral species (*Acropora formosa*, *Montipora tuberculosa*, and *Porites cylindrica*) were followed and compared over a fifteen-day sedimentation even, using the relative surface area of tissue lesions/necrosis as the response variable.

Experiment 1 demonstrated that sediment concentrations (or sedimentation rates) of up to 110.7 ± 27.4 mg cm^{-2} d^{-1} had no effect on colony growth rate, lipid concentration or photosynthetic yield in *T. mesenterina* under high flow (23.7 ± 6.7 cm s^{-1}) or stagnant conditions. Also, interactions between flow and sediment treatments were non-significant. This is a surprising result that indicates that *T. mesenterina* is highly resistant to sediment deposition under low flow as well as sediment abrasion under wave action. Horizontal colonies subjected to sediment loads of up to 100 mg cm^{-2} under stagnant conditions were able to clear their surface within

two hours, suggesting that rapid and energy efficient clearing of sediment is a key mechanism of alleviating sediment stress. These results may explain the success of *T. mesenterina* on reef crests as well as deep reef slopes on highly turbid, inshore coral reefs in the Great Barrier Reef lagoon.

Results of experiment 2 showed that sediment treatments of up to 246 ± 47 mg cm^{-2} d^{-1} had no effect on colony growth rates, lipid concentrations or chlorophyll concentrations in either of the study species under the low (Control) light conditions (190 ± 60 μmol photons m^{-2} s^{-1}). In high light (270 ± 110 μmol photons m^{2} s^{-1}), however, lipid and chlorophyll concentrations declined significantly indicating a bleaching response. Interestingly, temperature treatments (25.5 ± 0.1 and 28.4 ± 0.1°C) had no effect on the lipid or chlorophyll responses of *T. mesenterina*. Also, sediment, temperature, and light treatments did not interact significantly, further demonstrating that the physiology of this species is highly robust to these environmental stressors. Of the three physiological responses measured, chlorophyll concentration proved to be the most sensitive.

The field experiment (experiment 3) showed contrasting sediment responses among the three study species, consistent with predictions based on growth forms. Specifically, the prevalence of tissue lesions in *M. tuberculosa* (flat, foliaceous) increased significantly with sedimentation rate, whereas *Acropora formosa* and *Porites cylindrica* showed minimal tissue lesions, which were not correlated with sedimentation rates. This result suggests that sediment can act as a selective pressure on coral reefs, potentially related to the functional morphology of the species in the assemblage.

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CHAPTER 1 GENERAL INTRODUCTION

1.1 Sediment Issues on Coral Reefs

Rivaling terrestrial rainforests in their biological diversity and providing major economic benefits from fisheries and tourism, coral reefs are complex and highly diverse ecosystems with tight resource coupling and recycling, allowing for extremely high productivity and biodiversity (Reaka-Kudla *et. al.*, 1997; Hoegh-Guldberg and Jones, 1999). Through commercial fishing and tourism activities alone, it is estimated that coral reefs may generate goods and services valued at up to $375 billion (USD) per year (Costanza *et. al.*, 1997; Johns et. al, 2001), and provide as much as one quarter of the food resources for the tens of millions of people living in developing countries (Norse, 1993; Jameson *et. al.*, 1995; Hoegh-Guldberg and Jones, 1999; Nyström, *et. al.*, 2000). Typically, corals live within certain zones of tolerance, or thresholds, and are sensitive to changes in environmental conditions including sedimentation, water temperature, ultraviolet (UV) radiation, salinity, and nutrient quantities (Coles, *et. al.*, 1976; Gleason and Wellington, 1993; Grigg *et. al.*, 1984; Grigg and Dollar, 1990; Berkelmans and Willis, 1999; Lirman *et. al.*, 2003). Depending on the magnitude, duration, and the life history strategies represented in the coral community, variation in the local (or global) environment may act as a significant mechanism for change in the biological composition and function of the reef (Roy and Smith, 1971; Acevedo *et. al.*, 1989; Sakai and Nishihira, 1991; Aronson and Precht, 1995; Hunter and Evans, 1995; Brown, 2000; Ostrander *et. al.*, 2000; Fabricius and McCorry, 2006). Changes to environmental conditions (locally or globally) may therefore have dramatic effects, both directly and indirectly, on the composition and function of these communities, potentially disrupting the 'services' they provide both biologically and economically. Understanding how corals respond to environmental change and how this change may effect the biological integrity, diversity, and productivity of reef ecosystems is therefore crucial, and of global concern.

Sedimentation is one of the most important disturbance factors on coastal coral reefs worldwide (Rogers 1990, Brown 1997) and has been repeatedly cited throughout the primary literature as a source of significant ecological impact. For example, Dodge and Vaisnys (1977) reported 'catastrophic' decline in coral population, specifically *Diploria labyrinthiformis*, following the 1941-1943 dredging of Castle Harbor, Bermuda. Nutrient rich sediments have been observed to increase primary production in the water column, shifting competitive interactions and reducing oxygen levels

(Pastorok and Bilyard, 1985; Richmond, 1993). Additionally, sediments have been observed to cause changes in colony morphology, decrease coral growth, decrease coral cover, alter species composition, and/or inhibit coral recruitment (Cortès and Risk, 1985; Pastorok and Bilyard, 1985; Richmond, 1993). Suspended sediment particles smother reef organisms, reduce light available for photosynthesis, and alter both physical (e.g. hydrodynamic characteristics) and biological (e.g. growth, morphology) processes of coral reefs (*reviewed by* Rogers, 1990). However, in some coastal reef areas where high levels of run-off and resuspension are in part due to natural processes (Kleypas, 1996) reef assemblages have developed under high natural sediment loads for millenia (Larcombe *et al.*, 1995). For example, the inshore waters of the Great Barrier Reef (GBR) are characterized by shallow turbid waters and exposed to episodic high inputs of particulate and dissolved matter during flood events that are reported to be an integral part of the near-shore reef system and strongly linked to biological composition and function (Devlin *et. al.*, 2000; Larcombe, *et. al.*, 2001).

Often, coral assemblages on nearshore turbid-zone reefs differ in composition from that of more offshore clear-water reefs (e.g. Done, 1982; Acevedo *et al.*, 1989), potentially reflecting differences in species niche characteristics (Anthony and Connolly, 2004). Although biodiversity in these areas may vary to reefs in clear water, total coral cover can remain unaffected demonstrating the success of coral species to find a niche within a large range of natural environmental conditions (Chappone *et. al.*, 1999; Lirman, *et. al.*, 2003).

It is argued that reefs exposed to high sediment influence are dominated by sediment tolerant coral genera, while reefs exposed to low sediment influence are dominated by sediment-intolerant genera (McClanahan and Obura, 1997). This is supported in that some coral species are able to tolerate sediment regimes well above what are normally considered threshold levels (Woolfe and Larcombe, 1998; Anthony and Fabricius, 2000). Such species may be considered ‘sediment specialists’, perhaps representing a life history strategy in which suboptimal (i.e. high sediment) environments are exploited to minimize competition (niche differentiation).

How a coral responds to sedimentation and turbidity, even a ‘sediment specialist’ species, however, may vary depending on how, if at all, other environmental conditions affect a stress response within the coral organism. In stagnant water conditions, a low water flow, for example, may facilitate particle settlement, creating a sediment layer capable of shading coral colonies and prohibiting gas exchange (e.g. metabolic respiration).

Alternatively, high water flow rates may assist corals in the removal of sediments from their tissue surfaces. Depending on sediment grain size, however, high flow rates may act as a stress mechanism by re-suspending sediments into the water column. These suspended particles can act to reduce photosynthesis (i.e. increased light attenuation), interfere with coral planktonic feeding, and/or increase the potential for tissue abrasion (Rogers, 1990; Teleki, 2000). Interestingly, some 'sediment specialist' corals, however, may take advantage of these high sediment conditions by utilizing particulate matter within the sediment as a secondary food source (Foster, 1980; Anthony, 1999).

Coral stress resulting from increasing water temperatures and UV light has been highly topical, and well documented, in the context of global climate change (Hoegh-Gulgberg and Jones, 1999; Pittock, 1999; Lough 2000; Pockley, 2000; Berkelmans, 2002; Pandolfi *et. al.*, 2003; Baker *et. al.*, 2004; Beardall and Raven, 2004; Lesser and Farrel, 2004; Rowan, 2004). Increasing water temperature and UV-B radiation have been correlated to physiological responses such as coral bleaching and mortality. It is unclear, however, how the ability of corals to manage sediment is affected by changes in temperature and irradiance. For example, is a 'sediment specialist' coral that is near its temperature and/or irradiance threshold more susceptible to sedimentation? Damage to the symbiotic algae (zooxanthellae) within coral tissues through temperature or UV may reduce the amount photosynthetic energy available to the coral host. The energy available to utilize active sediment removal mechanisms, such as mucus excretion and tentacle movement, may therefore be solely dependent on the energy reserves (e.g. lipid content) of the coral. Conversely, sediments may assist corals experiencing thermal and/or light induced stresses by proving shade and/or a supplementary food source by particle injection (Anthony and Fabricius, 2000).

In Chapter 2, I examine how flow conditions affect the sediment response of *Turbinaria mesenterina*, a hearty and sediment-tolerant reef coral from the turbid inshore reefs of the GBR lagoon. Building on the results of this pilot study, Chapter 3 then investigates the interactions between temperature and light on the sediment response of this species. Finally, in Chapter 4, I investigate the sediment response of *Acropora formosa*, *Montipora tuberculosa*, and *Porites Cylindrica*, *in situ*, utilizing a new method for sediment application. Results from this study are intended to contribute to the overall understanding of the role of sedimentation as a structuring mechanism of coral communities, and provide new and valuable tools for manipulative research into sediment effects on coral reefs.

CHAPTER 2 ASSESSING THE IMPORTANCE OF WATER FLOW ON THE SEDIMENT TOLERANCE OF THE REEF CORAL *TURBINARIA MESENTERINA.*

2.1 Introduction

Water flow has physical, chemical and biological effects on corals and coral reef communities. Therefore, determining the effect of water flow on corals is essential in understanding the abundance, distribution, and life history of a coral species. Physically, high water velocities may cause stress through abrasion (interaction with sedimentation) (Rogers, 1983; Pastorok and Bilyard, 1985), and/or even fracture corals entirely (Done, 1982; Graus and MacIntyre, 1989). Similarly, water flow directly affects the encounter rate of corals with zooplankton and other potential nutrient sources, and therefore the ingestion rates of such materials (Sebens *et. al.*, 1997; Anthony, 2000). Water flow can also play an important role in the efficiency of passive sediment removal from coral surfaces (Lasker, 1980; Rogers, 1990). Furthermore, water flow is also a primary force for particle re-suspension into the water column. The ability of water flow to re-suspend sediments, however, is dependent on several factors including particle grain size and density. Specifically, smaller and/or less dense the particles are more readily re-suspended given a particular water flow velocity. Physiological responses of corals to increased water flow can include: enhanced photosynthesis by symbiotic algae, increased respiration rates of coral tissues (Patterson *et. al.*, 1991; Atkinson *et. al.*, 1994; Lesser *et. al.*, 1994; Bruno and Edmunds, 1998; Dennison and Barnes, 1998), and increased coral growth rates (Jokiel *et. al.*, 1978; Montebon and Yap, 1992; Kuffner, 2001).

In this study, the effects of water flow and sedimentation on coral skeletal growth and energetics of *Turbinaria mesenterina* were examined in flow-through microcosms to test the effects of varying flow regimes and sedimentation rates on physiological condition. Because effects of sediment loading on the coral biology are likely to vary with flow regime (i.e. as deposition under low flow and resuspension under high flow), each sediment treatment was conducted under stagnant as well as high-flow conditions.

To rigorously characterize physiological condition, I used three physiological variables:

- *skeletal growth rate* (change in buoyant weight) – a good proxy for photosynthetic rate (e.g. Barnes and Chalker, 1990);
- *maximum quantum yield* (photosynthetic efficiency) – an indication of symbiot stress response (e.g. Hoegh-Guldberg and Jones, 1999);
- *lipid content* – as an estimate of energy storage and proxy for the trophci value of the coral's recent environmental conditions (Anthony and Fabricius, 2000).

We test the hypotheses that (1) all physiological response variables are reduced under extremely high sediment loads, but that (2) sediment effects will be stronger in depositional (low-flow) compared to in resuspension (high-flow) regimes. By using sediment with low (<1%) organic carbon content, we did not expect particle ingestion to compensate for energy costs associated with any of the sediment regimes.

2.2 Materials and Methods

2.2.1 Study Site and Coral Collecting

The coral collection site was located at Cockle Bay Magnetic Island (19.183°S, 146.8ºE), part of the inner-shelf of the GBR lagoon, Australia on 5 May (Austral winter), 2001 (*Figure 2.1*). Cockle Bay was chosen due to the abundance of *T. mesenterina* and steady inundation by highly turbid water from the adjacent West Channel (Larcombe, *et. al.*, 1995; Woolfe and Larcombe, 1998). The presence of this species within this area demonstrates its natural resilience to sedimentation and turbidity and therefore its appropriateness for testing in this study.

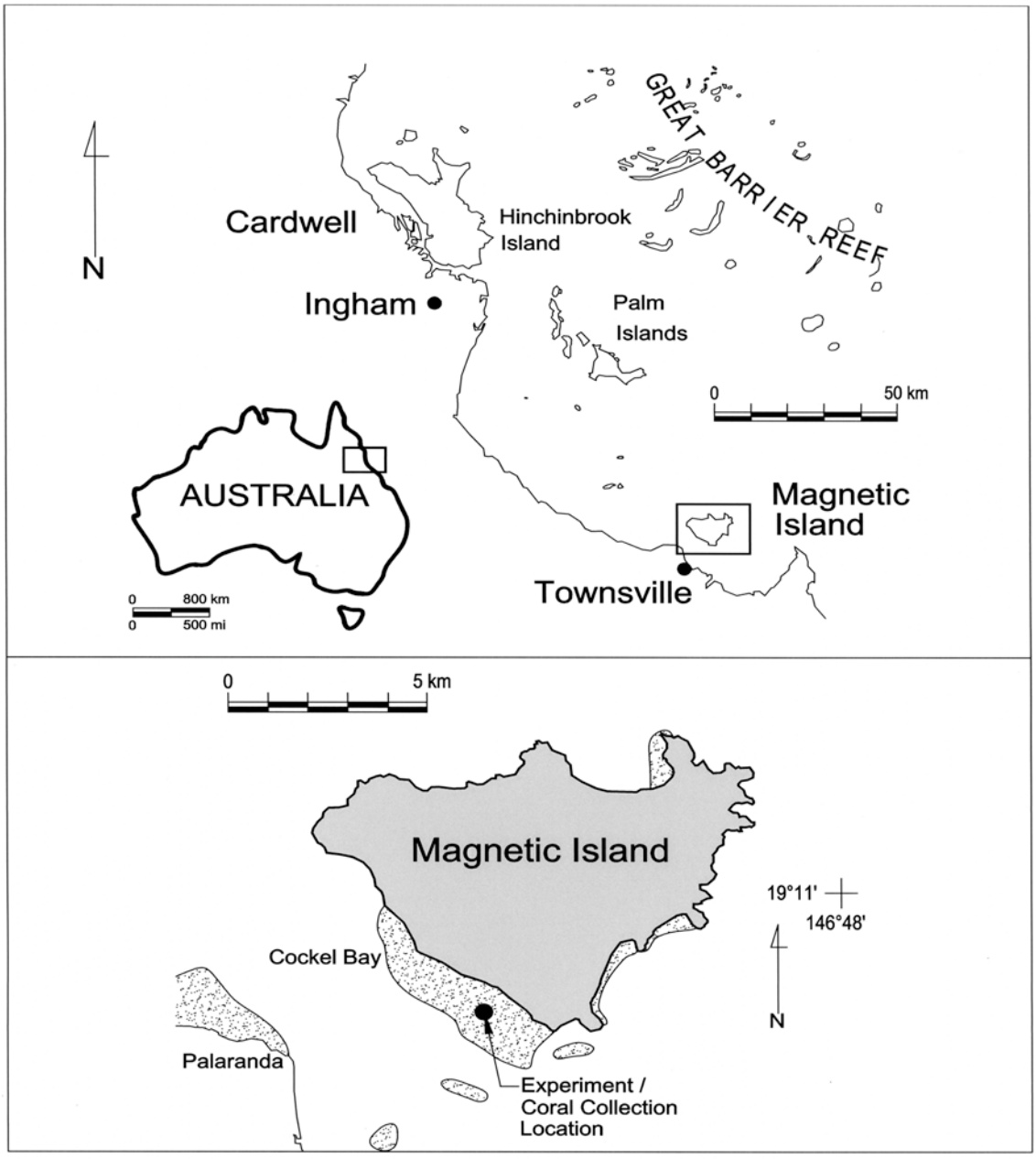


Figure 2.1: Map of Magnetic Island illustrating the coral collection and field experimentation location for this study (19.183º S, 146.8º E).

Cockle Bay is one of the most turbid reefs in the inshore region of the GBR lagoon (Anthony *et al.,* 2004), in part due to frequent re-suspension of sediment deposits in the shallow Cleveland Bay (Larcombe *et al.,* 1995) and downstream transport of mud from adjacent bays on Magnetic Island. Coral communities on the reef crest and slope (1-6 m depth) in Cockle Bay and adjacent bays are characterized by high abundance of *T. mesenterina*. In Cockle Bay in particular, this species forms large monospecific stands that may cover >90% of the reef (*Figure 2.2*).

Figure 2.2 Photograph of large monospecific stands of *Turbinaria mesenterina* within Cockle Bay, Magnetic Island.

Approximately 100 fragments (around 8 cm by 8 cm) were collected from large colonies of *T. mesenterina* at 2-4 m depth (below lowest astronomical tides) in Cockle Bay. The fragments were cut from colony peripheries using surgical bone cutters, and a small (3 mm diameter) hole was drilled at the edge of the fragment for attachment to stands. To minimize effects of varying light history on sediment responses corals were collected predominantly from colonies in open (unshaded) habitats. To allow the collected corals to heal and recover from handling stress prior to experimentation, they were left on racks in the field for nine weeks. Each coral was attached to a stand (8 cm by 8 cm PVC ring cut in half) using a cable tie (2 mm wide). During the recovery period and experimental phase, downwelling irradiance *in situ* at the level of the experimental colonies (fragments) ranged between 50 and 300 _ mol quanta m^{-2} s^{-1}

(daily averages) based on continuous monitoring using two light loggers (Dataflow 392 recorders with cosine corrected PAR sensors) attached to the coral racks. The sensors were equipped with automated wipers to prevent fouling. Rates of sedimentation at the site approximated 7-12 mg cm^{-2} d^{-1} (dry weight of GF/C filtered material) estimated from weekly deployment of six sediment traps (3.25 cm wide and 30 cm tall, Jurg 1996). Flow speeds *in situ* were estimated using dissolution rates of plaster blocks (e.g. Jokiel and Morrissey, 1993). Six hemispherical blocks (base diameter 53 mm) of known dry weights were placed on the coral racks at three occasions (one-day exposures). Dissolution rate was converted to flow speed after calibrating blocks in a flow chamber (n = 8) with known flow velocities determined by particle tracking. Flow rates at the sites ranged from 3 to 11 cm s^{-1}.

2.2.2 Laboratory Experiment

Experimentation took place at the Marine and Aquaculture Research Facilities Unit (MARFU) at James Cook University, Townsville, Australia. A 10,000 liter closed seawater system supplied eighteen (25 liter) plastic aquaria tanks with 35 ppm sea water at 23-24º C. Six 400-watt lamps provided a light regime ranging from 140 - 190 Einsteins m^{-2} s^{-1} for 10 hours each day corresponding to the average growth irradiance at the field site.

The experimental design consisted of two fixed factors (hydrodynamic regime and sediment treatment) replicated by three aquaria tanks per treatment. Each tank contained four coral colonies to reduce variation between tanks (*Figure 2.3*). Tanks were assigned one of three sediment treatments: High: >100 mg cm^{-2} d^{-1}; Low: 10-20 mg cm^{-2} d^{-1}; and Control: <1 mg cm^{-2} d^{-1} and two hydrodynamic treatments: Low- and High-flow ($0.73 \pm 0.01 cm^{-1}$ s^{-1} and 23.7 ± 6.7 cm^{-1} s^{-1} respectively). Replicate numbers were based on the results of a power analysis described by Anthony (PhD Thesis, 1999) and were calculated to be of sufficient power ($1-\beta \geq 0.80$) at a precision level of $\alpha = 0.05$. Additionally, four coral colonies per treatment were calculated as sufficient to reduce variation between measurements such that the maximum likely error (e) is ≤ 4.7% while effectively minimizing the required sampling effort (*Table 2.1*). Tanks with High-flow treatments were fitted with two Aquaclear 402-powerheads. Pumps were positioned along the top and bottom of each tank, and fitted with PVC spray bars, such that particulate material was suspended evenly throughout the tank (*Figure 2.3*). Low-flow tanks did not include the 402-powerhead pumps or spray bars.

Sediments were applied daily for 34 days and measured using small cylindrical sediment traps (3.6 cm wide, 4.5 cm tall) along with 50 ml grab samples obtained by syringe. These samples were filtered through pre-weighed, Whatman GF/C filters (~1 µm pore size), rinsed in distilled water, then dried at 80º C till constant weight and re-weighed. To exclude effects of light attenuation, only particles greater than 60 µm were used. However, to enable particle re-suspension using realistic flow regimes, only particles smaller than 120 µm were used. Sedimentation rates in the High, Low, and Control treatments were of 110.7 ± 27.4; 16.2 ± 4.4; and 0.8 ± 0.3 cm^{-2} d^{-1}, respectively.

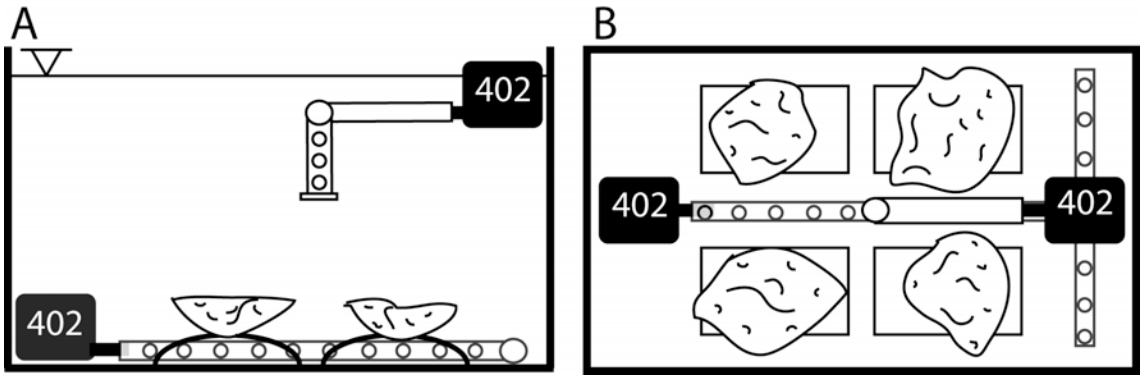


Figure 2.3: Side (A) and plan (B) profiles of the high flow tank design. Four colonies of *Turbinaria mesenterina* anchored to PVC stands were placed into each treatment. Each tank included two 402-powerhead pumps and spray-bars.

Table 2.1: Calculated maximum likely error (e) in measuring coral response with a given sample size (n). Based on a power analysis described by Anthony (PhD Thesis, 1999), a sample size of n=12 was determined to reduce the maximum likely error to an acceptable level (e=3.00%) while maintaining a practical sampling effort (72 coral colonies).

n	e	Total # Corals
6	6.57	36
12	4.65	72
18	3.79	108
25	3.22	150
35	2.72	210
45	2.40	270
55	2.17	330
65	2.00	390
75	1.86	450
100	1.61	600

2.3.3 Determining Flow

The flow regime inside the chambers was estimated using dissolution rates of blocks of plaster of paris (Jokiel and Morrissey, 1993). Three blocks (hemispherical, with a base diameter of 53 mm) of known dry weights were placed in each of the hydrodynamic treatments and replicated with two tanks. After 4 hours, the blocks were

removed and placed into an oven, dried for 48 hours at 60°C, and reweighed. Flow calibration was conducted in a flow chamber with known flow velocities ranging from 0 to 12 cm s^{-1} for 4 hr, and at the same temperature and salinity as used during the experiment. The relationship between weight loss per hour (ΔW) and water flow (U) during flow calibrations was estimated as:

$$U = a\,\Delta W$$

Where *a* is the conversion coefficient (slope) between weight loss and flow velocity. The erosion rates were linear over the flow velocity range with a slope (*a*) of 37.4 g cm^{-1}. The flow velocity in the Low-Flow tanks was 0.73 ± 0.01 (SE) cm s^{-1} while those in High-Flow tanks were more than 30 times higher at 23.6.7 cm s^{-1}.

2.3.4 Field Reference Group

To compare the physiological responses of corals in the experiments with those in the field, 20 fragments of *T. mesenterina* were left on the racks in Cockle Bay as a field reference group. Light intensity and sediment conditions were continuously monitored, as described above, for the duration of the 34-day experiment. Corals that remained in the field at Cockle Bay were exposed to a sedimentation rate of approximately 5.2 ± 0.8 mg cm^{-2} d^{-1}.

2.3.5 Coral responses

Sub-lethal coral stress was assessed by comparing the skeletal growth, lipid concentrations and photosynthetic efficiencies of colonies between treatments over time.

Skeletal growth rates were measured using the buoyant weight technique (Jokiel *et. al.*, 1978; Davies, 1989; Davies, 1990). Similar to the technique of Jokiel *et. al.* (1978) corals were placed into seawater of known density, and weighed prior to, during, and after the experiment.

Coral lipid concentrations were assessed using a technique modified from Folch *et. al.* (1957) and Harland *et. al.* (1992). Specifically, corals were homogenized using a bowl and pistol, and a 10 g sub sample (wet weight) was used for lipid extraction. Samples were dissolved in chloroform methanol (2:1) solution, with butoxylated hydroxy toluene (BHT) added to prevent oxidation. The sample was filtered through a Whatman glass fiber filter (GF/C), and treated with a potassium chloride solution (0.88%) to remove impurities (i.e. salts and other non-lipid material). Impurities were

evacuated from the upper layer via aspiration. The lower organic phase was then washed three times with a methanol: water solution (1:1), each time the upper phase removed. Finally, the remaining organic solution was poured into pre-weighed aluminum boats and allowed to dry. Total lipid was calculated by determining net weight divided by the area of coral fragment sampled (mg cm^{-2}). Changes in coral lipid concentrations over time were determined by comparing treated corals to a baseline group of twenty-two untreated corals. Specifically, this sub-group of corals was randomly selected from the initial 114 fragments collected from Cockle Bay prior to experimentation (i.e. not part of the field reference group or laboratory experiment); and analyzed immediately prior to experimentation in effort to establish baseline lipid concentrations and facilitate post-experiment comparisons. Stress responses of the endosymbionts were assessed by measuring changes in the performance (maximum quantum yield) of photosystem II. This was done using a Pulse Amplitude Modulation (PAM) fluorometer (DIVING PAM, Walz, Germany). Photosystem II is commonly accepted as the most vulnerable part of the photosynthetic apparatus and can be used as a sensitive indicator of photosynthetic performance and/or stress (Hoegh-Guldberg and Jones, 1999; Jones *et. al.*, 1999; Ralph *et. al.*, 1999). Measurements were taken in the laboratory before, during, and after treatments on dark-adapted colonies during the early morning hours prior to sunrise.

2.3.6 Data Analysis

Data was analyzed using a univariate ANOVA. All assumptions were tested using histograms and the Levene's test for homogeneity of variances (p=0.05). Analyses were performed using the SPSS (v. 10.0) statistical packages.

2.4 Results

2.4.1 Coral Skeletal Growth (change in buoyant weight)

Surprisingly, there were no significant differences in net rates of coral skeletal growth in either hydrodynamic flow or sediment treatments. However, there was a significant interaction between hydrodynamic and sediment treatments (*Table 2.2a*). Skeletal growth rates were somewhat variable, within/between hydrodynamic and sediment conditions (*Figure 2.4a*). High-flow treatments showed a slightly higher growth rate than their Low-flow counterparts in both High (Low-flow = 1.65 ± 0.14 g, High-flow = 2.32 ± 0.27 g) and Low (Low-flow = 1.69 ± 0.61 g, High-flow = 1.88 ± 0.71 g) sediment treatments. Skeletal growth rates for colonies in the Control groups were nearly identical (Low-flow/Control = 1.65 ± 0.12 g, High-flow/Control = 1.58 ± 0.182 g).

2.4.2 Coral Lipid Concentration

The highest concentrations of lipids within the experimental populations were observed in the Low sediment treatment level (Low-flow = 8.5 ± 0.9 mg cm^{-2}, High-flow = 8.0 ± 0.6 mg cm^{-2}) and in the Field Reference group (8.8 ± 0.6 mg cm^{-2}) (*Figure 2.4b*). All lipid concentrations, however, were less than those observed in the Day 1 population (10.1 ± 0.7 mg cm^{-2}). Differences in lipid concentration were not significant between any hydrodynamic or sediment treatment. Furthermore, no significant interaction occurred between hydrodynamic and sediment treatments (*Table 2.2b*).

2.4.3 Photosynthetic Efficiency

Low- and High-Flow treatments were virtually identical with PAM yields of 0.611 ± 0.005 and 0.621 ± 0.005 respectively. Differences in photosynthetic efficiency between Control (0.624 ± .006), Low (0.608 ± .009), and High (0.608 ± .009) were also non-significant (*Figure 2.4c*). Furthermore, there was no interaction between hydrodynamic regime and sediment treatment (*Table 2.2c*).

Table 2.2: Full factorial, univariate ANOVA testing for effects of water flow (Low- and High-Flow) and sediment treatments (Control, Low, and High) on (A) in skeletal growth rates, (B) lipid contents, and (C) maximum quantum yield of *Turbinaria mesenterina*. Data are analyzed using tanks as replicates.

A. Skeletal growth rates (% of initial buoyant weight)				
Source of variation	**Df**	**MS**	**F**	**p**
Flow	1	0.030	0.290	0.600
Sediment	2	0.243	2.362	0.136
Flow X Sediment	2	0.480	4.662	**0.032**
Error	12	0.103		

Data were normally distributed and variances were homogeneous (p=0.264)

B. Lipid contents (mg cm^{-2})				
Source of variation	**Df**	**MS**	**F**	**p**
Flow	1	0.311	0.248	0.628
Sediment	2	0.881	0.701	0.515
Flow X Sediment	2	0.150	0.120	0.888
Error	12	1.257		

Data were normally distributed and variances were homogeneous (p=0.995)

C. Maximum quantum yield				
Source of variation	**Df**	**MS**	**F**	**p**
Flow	1	0.000534	1.63	0.226
Sediment	2	0.000273	0.83	0.459
Flow X Sediment	2	0.000300	0.91	0.428
Error	12	0.000328		

Data were normally distributed and variances were homogeneous (p=0.726)

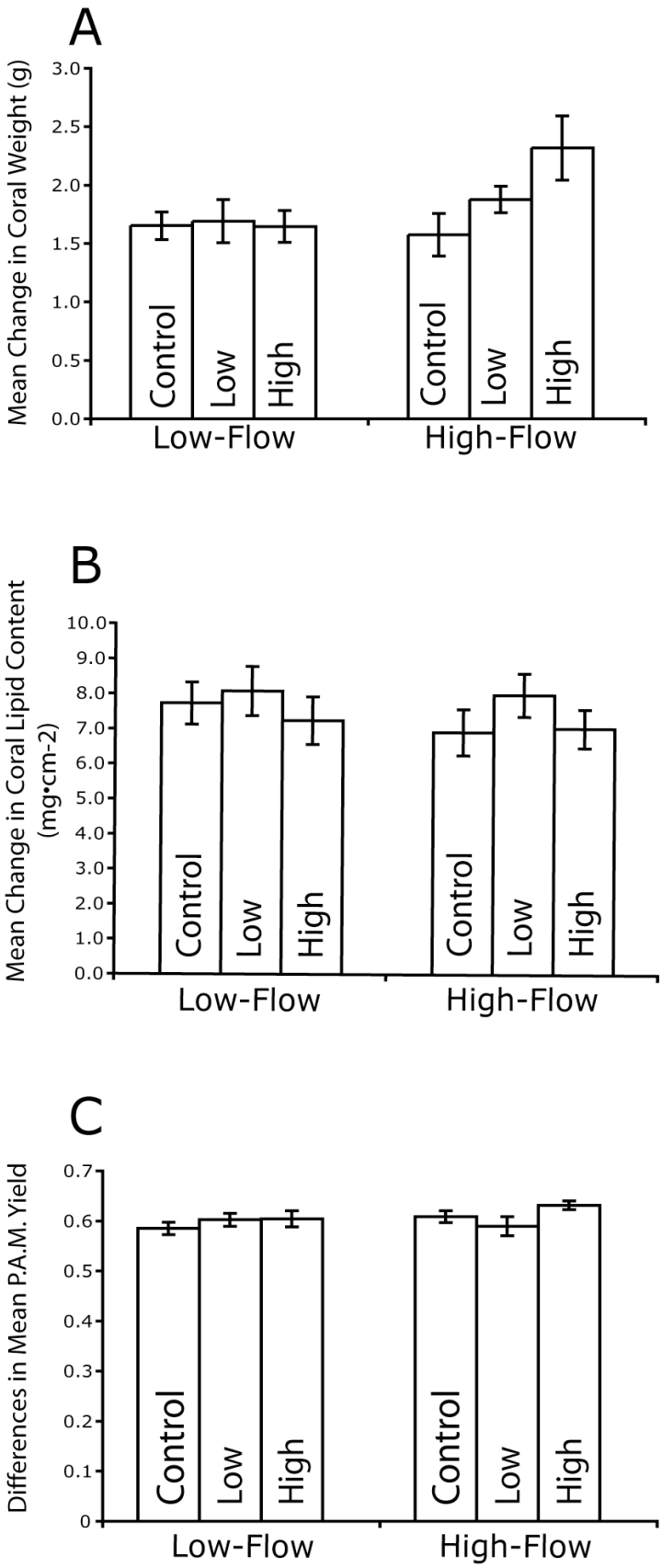


Figure 2.4: Mean differences ± SE of (A) colony buoyant weight, (B) lipid concentration, and (C) maximum quantum yield of symbiotic algae between (1) hydrodynamic (Low- and High-flow), (2) sediment (Control, Low, and High) and (3) interaction effects on *Turbinaria mesenterina*.

2.6 Discussion

Of the three techniques employed in this study, none detected a significant biological response in the sediment tolerance of *T. mesenterina* under varying hydrodynamic conditions. Generally, this study demonstrates that *T. mesenterina* tolerates high levels (110.7 ± 27.4 mg cm^{-2} d^{-1}) of sediments within a wide range of hydrodynamic conditions, and for an extended period.

Coral Skeletal Growth

Although there were no significant differences between hydrodynamic or sediment treatments, there was a significant interaction of these two treatments on the skeletal growth of *T. mesenterina*. While remaining relatively equal in static treatments, growth rates in dynamic tanks appear to increase in direct in proportion to sediment concentration (*Figure 2.4a*). Since growth rates in both Control groups were nearly equal, it is hypothesized that the observed increase in growth is due to a combination of both dynamic flow and increased suspended sediment particles. Skeletal growth rates could be increasing with flow and particle concentration due to an enhanced particle-feeding capacity, similar to that reported by Anthony (2000). Additionally, dissolved bicarbonates may have limited skeletal growth in Low-Flow treatments. According to Marubini and Thake (1999), skeletal growth is limited by dissolved inorganic carbon (DIC). DIC may have been limited in Low-Flow tanks simply due to the low input and circulation of water from the main seawater system.

Coral Lipid Concentration

Lipid concentrations showed no significant changes from the prescribed hydrodynamic or sediment treatments. This is a very interesting result, however, in that it demonstrates that *T. mesenterina* is a robust species that is able to tolerate sediment treatments that are typically assumed to be highly stressful to corals. It is hypothesized, however, that adequate nutrient and energy resources (e.g. abundant zooplankton/ consistent source of light energy) available within the laboratory may assist in supporting this high-sediment tolerance and that perhaps, under conditions of additional stressors (e.g. temperature stress); the resilience of this species may be reduced. All test groups did show a decrease in lipid concentration when compared to Day 1 samples, implying a handling stress during fragmentation, collection and transportation. This may be supported in that the field reference group (relatively less handled), indicated a relatively lower lipid concentration than the other experimental groups (*Figure 2.4b*).

Photosynthetic Efficiency

The photosynthetic efficiency was not significantly affected by sediment treatment or flow (*Figure 2.4c*). This is most likely the result of the environmental conditions within the laboratory. With adequate light energy and nutrient resources available, zooxanthellae were little affected by the sediment and hydrodynamic treatments. With little stress, it is not surprising that their photosynthetic efficiency did not fluctuate significantly. It is interesting to note, however, that the field reference group that was exposed to natural conditions showed relatively lower photosynthetic efficiency. Although not statistically different from the other experimental groups, this observation may reflect the more variable conditions of the field environment. For example, a series of cloudy days or high turbidity can increase light attenuation, potentially influencing photosynthetic efficiency.

Sediment Tolerance and Acclimatization

The high sediment tolerance of *T. mesenterina* is likely a result of a life history strategy that efficiently utilizes both passive and active sediment removal tactics. In this experiment, however, *T. mesenterina* has demonstrated that the passive removal of sediment is not vital to the success of maintaining a positive energy budget (e.g. continued growth) under sediment loads of up to 110.7 ± 27.4 mg cm^{-2} d^{-1} for over 30 days. According to Anthony and Larcombe (2001), the physiological condition of corals is closely related to variation in the environment. Furthermore, evidence from previous studies indicates that corals may be able to acclimatize to these changes, enabling the maintenance of a positive energy budget. Anthony (1999b) reports that coral species that are well acclimatized to high sediment loads, for example by utilization of particulate matter as a food source (Rosenfeld *et al.*, 1999), acclimatization to shifting light regimes (Anthony *et al.*, 2004) or by energy-efficient mechanisms of sediment handling (Lasker, 1980) are likely to have selective advantage on high-turbidity reefs. Results from this study (i.e. no physiological changes), provide further evidence that *T. mesenterina*, from the inshore reefs of the GBR, are conditioned to high sediment regimes and perhaps utilize such mechanisms to gain a competitive advantage. As many coastal reefs become subjected to increasing sediment loads due to coastal developments, poor land use practices (e.g. Furnas, 2003), and increased frequency of severe storms coral taxa with extreme sediment tolerances, such as *T. mesenterina*, are likely to be the key players in future coral communities on coastal reefs.

CHAPTER 3. EFFECTS OF LIGHT AND TEMPERATURE ON THE SEDIMENT STRESS RESPONSE IN CORALS

3.1 Introduction

Over the past twenty years, particularly in response to global warming concerns, the effects of temperature and irradiance on corals and coral reef ecosystems have been a major concern. In this, strong correlations have been demonstrated between temperature and light on biological conditions such as coral diversity, abundance and general health, particularly in relation to coral bleaching (Brown and Howard, 1985; Jokiel and Coles, 1990; Brown and Ogden, 1993; Buddemier and Fautin, 1993; Glynn, 1996). Environmental conditions and their effect on coral communities, however, are complicated in that they rarely, if ever, change individually. Storms, for example, may reduce water temperature, light availability, and salinity as a result of increased cloud cover and precipitation (Harmelin-Vivien, 1994; Mumby, *et. al.*, 2001; Schrage and Clayson, 2003). In addition, terrestrial runoff and wind-generated currents may act to increase local suspended sediment concentrations affecting light attenuation levels, influencing primary production, shifting competitive interactions, altering oxygen levels, and potentially smothering and/or scouring (Pastorok and Bilyard, 1985; *reviewed by* Rogers, 1990; Richmond, 1993). Understanding not just individual environmental conditions but their potential interactive effects is crucial in understanding how corals and coral reefs respond to environmental change.

Susceptibility to sediment stress on corals and coral reefs has not only been observed to vary inter-specifically but also intra-specifically, between reefs, between locations on the same reef, and even between the symbiotic algae (zooxanthellae) within a single colony (Rogers, 1979; Hudson, 1985; Fitt and Warner, 1995; Helmuth *et. al.* (a), 1997; Helmuth *et. al.* (b), 1997; Anthony and Fabricius (2000); Marshall and Barid, 2000; Meesters *et. al.*, 2002). It is likely that this reported variation in sediment response is due to variation in associated environmental variables (i.e. light, temperature) as well as differences in the life history of the organisms. The role and importance of such interactions on the coral sediment response remain unclear.

Changes in both light and temperature have been observed to have a direct link to changes in coral physiological response (Jones, *et. al.*, 1998). To date, however, no previous studies have specifically investigated the affect of the bleaching response (i.e. loss off zooxanthellae) on the sediment tolerance of corals. That is, sediments act to shade colonies reducing exposure to elevated irradiance and reducing water temperatures through reflection. Increased sediments may provide an additional food source supplying additional energy for growth, defense (e.g mucus production), and/or damage repair (Anthony,1999; Rosenfield *et. al.* 1999). I hypothesize that that corals near their light and/or temperature threshold will generally be more susceptible to sediment stress, however, the response will depend on multiple factors including the life history of the subject species, number environmental stressors, degree and speed which these stressors are applied, and the colony's ability to acclimatize to this change.

In this section of the study, *Turbinaria mesenterina* and *Montipora digitata,* two species common along the inshore reefs of the GBR, were subjected to various sediment loads under varying light and temperature treatments. The objectives were to:

- determine how these corals respond to these environmental factors individually; and
- to determine if these factors interact with one another to produce a greater coral stress response (i.e. synergistic effects).

Critical for effective and efficient coral reef research and management (particularly in regard to dredging, land reclamation, beach nourishment, and coastal development projects), a secondary objective of this study was to try and determine the sediment threshold of these two species and to observe the potential role of light and water temperature in this response.

3.1.2 Description of Study Species

T. mesenterina and *M. digitata* were selected for this project because of their dominance along the turbid inshore reefs of the GBR (Osborne, *et. al.*, 1997; pers. obs.). Differences in life history strategies (e.g. morphology) also allow for inter-specific comparisons (Veron and Wallace, 1984; Veron, 2000).

Turbinaria mesenterina (Lamarck, 1816) may be found in habitats ranging from shallow exposed reefs to protected lagoons and is most dominant in shallow turbid environments. Primarily dependent on light availability, colonies can be composed of unifacial laminae which are highly contorted and fused when growing in sub-tidal habitats, upright or tiered when on upper reef slopes, and horizontal in deeper water (Willis, 1985; Veron, 2000). Colonies are usually less than one meter across with exsert corallites (approx. 2.5 mm diameter) crowding the upper surface.

Montipora digitata (Dana, 1846) form colonies with digitate or arborescent anastomosing upright branches. Usually seen in green, orange, and brown color varieties, corallites are immersed and small, and the coenosteum is smooth. *M. digitata* are common in shallow reef environments and may be a dominant species of lagoons and/or shallow mud flats which are characterized by high sunlight irradiance, relatively low water turbulence, and high nutrient content (Veron, 2000).

3.1.3 Coral Collection Areas

Turbinaria mesenterina was collected at Cockle Bay Magnetic Island (19.183º S, 146.8º E), part of the inner-shelf of the GBR, Australia in early October 2002 (Austral spring) (*Figure 3.1*). Cockle Bay was chosen due to the abundance of *T. mesenterina*, easy access from the mainland, as well as a steady inundation by highly turbid water from the adjacent West Channel (Larcombe, *et. al.*, 1995; Woolfe and Larcombe, 1998). The presence of this species in this area suggests a natural resilience to sedimentation and turbidity and therefore its appropriateness for testing in this study.

Colonies of *M. digitata* occurred along the Pioneer Bay reef flat directly in front of the OIRS (18.611º S, 146.5º E) (*Figure 3.1*). Pioneer Bay was selected primarily because of its local abundance of *M. digitata*. Additionally, with a tidal flat of over five hundred meters, the reef at Pioneer Bay is almost completely exposed at low tide, subjecting the corals of this area to the extreme end of light and temperature conditions. The dominance of this species along this reef flat demonstrates the ability of *M. digitata* to tolerate extreme light and temperature conditions. This demonstrated range of tolerance was the primary reason *M. digitata* was selected for this study.

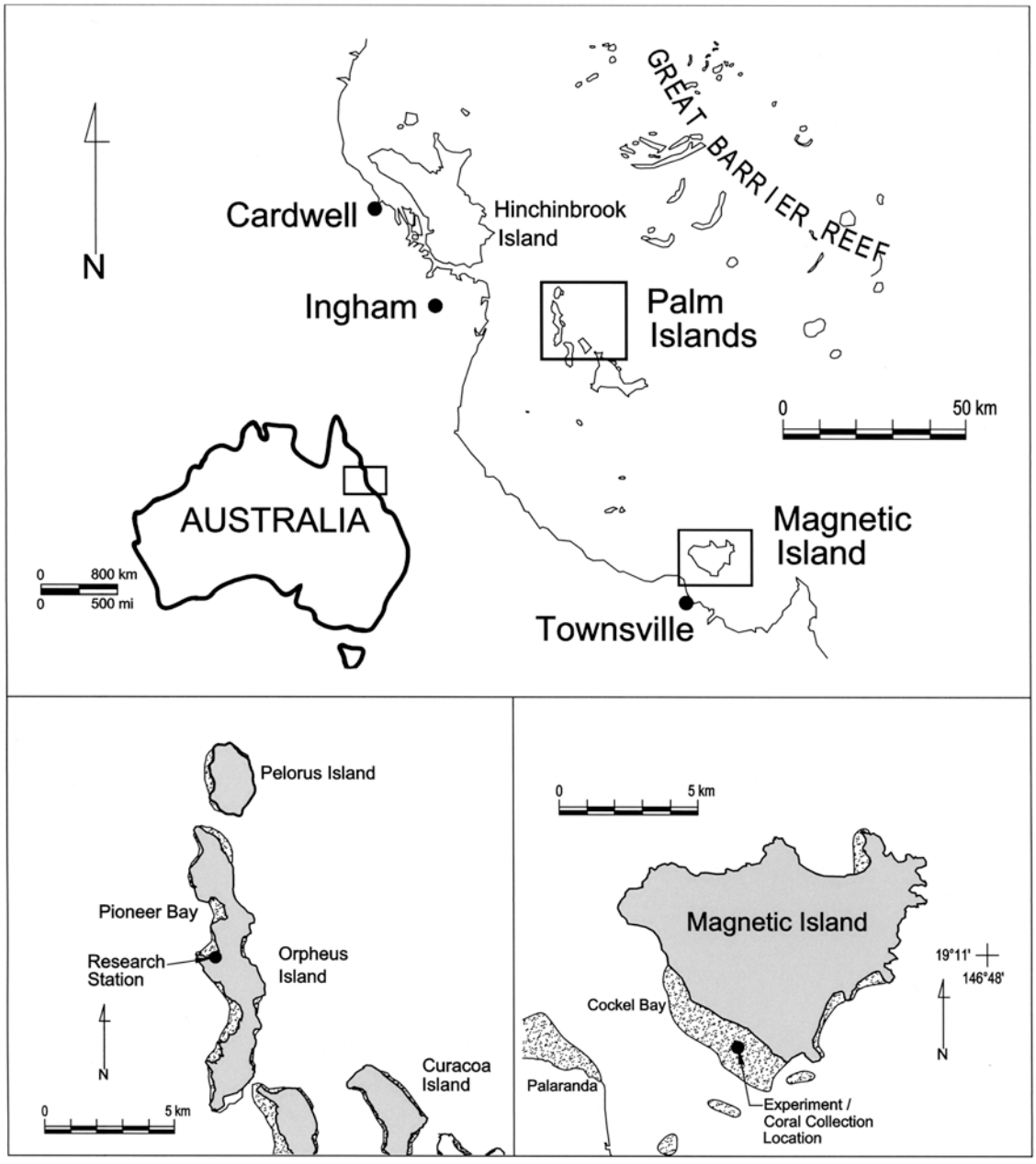


Figure 3.1: Map of Orpheus and Magnetic Islands illustrating the location for coral collection (Cockle Bay: 19.183º S, 146.8º E), and experimentation (Orpheus Island Research Station) for this study.

3.2 Materials and Methods

3.2.1 Experimental Set-up

One hundred and twenty colonies of *T. mesenterina* (measuring approximately 10 cm x 10 cm) were collected from a narrow depth range (3 to 5 m below datum) on the reef flat of Cockle Bay (Magnetic Island). The corals were immediately transported to the Orpheus Island Research Station (OIRS), placed into shaded, flowing seawater raceways, and allowed three weeks to recover from handling stress. In the interim, one hundred and twenty, medium-sized (approximately 5 cm x 5 cm) colonies of *M. digitata* were collected from the reef flat of Pioneer Bay, Orpheus Island (<1 m below datum). Again, these colonies were placed into raceways and allowed to recover from handling. Over 200 kg of surface sediments were collected along the near shore reefs of Pioneer Bay, and wet sieved to a grain size no greater than 120 µm.

Experimentation took place at the OIRS where an open seawater system supplied 36 plastic tanks (25 liters each) with a continuous flow of seawater. Temperatures during the acclimation period ranged from 25 to 26 ºC. Corals were shaded to the extent that light penetration matched the average growth irradiance at their collection sites. Irradiance was measured using a manufacturer-calibrated Li 192s sensor connected to a Li 1000 logger (Licor, Lincoln Nebraska, U.S.A.). Three colonies of each species were placed into each tank, which was assigned one of three sediment treatments: Control: <1 mg cm^{-2} d^{-1}, High: 100-150 mg cm^{-2} d^{-1}, and Very High: >250 mg cm^{-2} d^{-1}. Each tank was also randomly assigned a light treatment: Shaded: (<300 micro Einsteins m^{-2} s^{-1}) or Unshaded: (700-800 micro Einsteins m^{-2} s^{-1}), and one of two temperature treatments: Heated (28-29 ºC) and Unheated (25-26 ºC). Water temperatures were maintained using custom built, 800-Watt, submersible coil heaters with built in thermostats.

3.2.2 Experimentation

Sediment treatments were applied manually every eight hours for fifteen days and measured using small cylindrical sediment traps (3.6 cm x 4.5 cm). These samples were filtered through pre-weighed, Whatman GF/C filters (~1 µm pore size), rinsed with distilled water, and then dried at 80º C. When dry, samples were re-weighed and sediment weight was determined by subtracting the weight of the filter as previously recorded. The rate of sedimentation was expressed as mg cm^{-2} d^{-1}.

3.2.3 Assessment of the coral stress response

Coral response was assessed by comparing the skeletal growth, lipid concentration, and chlorophyll concentration of colonies between treatments and over time. Skeletal growth rates were measured using the buoyant weight technique (Jokiel *et. al.*, 1978; Davies, 1989; Davies, 1990). Similar to the technique of Jokiel *et. al.* (1978) corals were placed into seawater of known density, and weighed prior to, during, and after the experiment.

Coral lipid concentrations were assessed using a technique modified from Folch *et. al.* (1957) and Harland *et. al.* (1992). Specifically, corals were homogenized using a mortar and pestle, and a 10 g sub sample (wet weight) was used for lipid extraction. Samples were dissolved in chloroform methanol (2:1) solution, with butoxylated hydroxy toluene (BHT) added to prevent oxidation. The sample was filtered through a Whatman glass fiber filter (GF/C), and treated with a potassium chloride solution (0.88%) to remove impurities (i.e. salts and other non-lipid material). Impurities were removed from the upper layer via aspiration. The lower organic phase was then washed three times with a methanol-water solution (1:1), each time the upper phase removed. Finally, the remaining organic solution was poured into pre-weighed aluminum boats and allowed to dry. Total lipid was calculated by determining net weight divided by the area of coral fragment sampled (mg cm^{-2}).

Coral bleaching, examined by chlorophyll concentrations within zooxanthellae and coral tissues, was also used as a physiological indicator of stress. In accordance with Chalker and Dunlap (1981), efficient extraction can be achieved using a 90% aqueous acetone solution. 50 g of homogenized coral sample (wet weight) were extracted in 100 ml of solvent for a period no less than six hours, in darkness, at 4 °C. The extract was decanted and the procedure repeated twice to ensure maximum pigment removal. In accordance with Jeffery & Humphrey (1975), the absorbance of each extract was recorded at 630 and 663 nm with a spectrophotometer (Hewlett Packard).

3.2.4 Data Analysis

The experimental design consisted of three fixed factors: Light (Shaded; Unshaded), Temperature (Heated; Unheated), Sediment (Control; High; Very High) that were each replicated by three tanks. Individual tanks contained three coral colonies per species to reduce variation between tanks. Replicate numbers were based on the data from the previously conducted water flow study (Chapter 2) and were calculated to be of sufficient power ($1-\beta \geq 0.80$) at a precision level of $\alpha = 0.05$. Additionally, nine coral colonies per species per treatment were calculated as sufficient replication to reduce variation between measurements such that the maximum likely error (e) is $\leq 2.96\%$ while effectively minimizing the required sampling effort (*Table 3.1*). Data was analyzed using a univariate ANOVA. All assumptions were tested using histograms and the Levene's test for homogeneity of variances ($p=0.05$). All analyses were performed using Microsoft Excel (X) for Macintosh and SPSS (v. 10.0) statistical packages.

Table 3.1: Calculated maximum likely error (e) in measuring coral response with a given sample size (n). Based on the data from the previously conducted water flow study (Chapter 2), a sample size of n=9 was determined to reduce the maximum likely error to an acceptable level (e=3.00%) while maintaining a practical sampling effort (120 coral colonies).

n	e	Total # Corals
5	4.81	60
10	2.96	120
15	2.41	180
20	2.09	240
25	1.87	300
30	1.71	360
40	1.48	480
50	1.32	600
75	1.08	900
100	0.94	1200

3.3 Results

3.3.1 Light, Temperature, and Sediment Treatments

Light regime treatments, measured noon, averaged 190 ± 60 and 780 ± 110 micro Einsteins m^{-2} s^{-1} in Shaded and Unshaded treatments respectively. The mean water temperature of the Heated treatment was 28.4 ± 0.1 ºC (max: 30ºC, min: 27 ºC) while that of the Unheated was 25.5 ± 0.1 ºC (max: 26.5 ºC, min: 23.5 ºC). Results from sediment traps within tanks indicate sedimentation rates in the Control, High, and Very High treatments were 0.5 ± 0.2, 126.7 ± 29.8 and 246.3 ± 47.4 mg cm^{-2} d^{-1} respectively.

3.3.2 Coral Skeletal Growth (change in buoyant weight)

T. mesenterina did not show any significant changes in net skeletal growth rate in response to any of the treatments (*Table 3.2a, Figure 3.2*). Furthermore, there was no observable interactive effect of these treatments. Similarly, the growth rates of *M. digitata* remained statistically unchanged from the temperature and sediment treatments and their interactions (*Table 3.2b, Figure 3.2*). However, there was a significant decrease in the growth rate within the Shaded light treatment decreasing from 1.7 g d^{-1} to only 1.3 g d^{-1}. In general, *M. digitata* displayed a higher growth rate than *T. mesenterina*. The highest growth rate observed in *M. digitata* was in the Unshaded, Heated, Control group at a rate of 2.3 g d^{-1}. The highest growth rate for *T. mesenterina* in the Unshaded, Unheated, Control group was only 1.8 g d^{-1} (*Appendix B*).

Table 3.2: Results of the full factorial, univariate ANOVA testing for effects of light (Shaded and Unshaded), water temperature (Heated and Unheated), and sediment treatments (Control, Low, and High) on differences in buoyant weight of (A) *Turbinaria mesenterina* and (B) *Montipora digitata*.

A. *Turbinaria mesenterina*				
Source of variation	**Df**	**MS**	**F**	**p**
Light	1	0.134	0.328	0.572
Temp	1	0.250	0.636	0.431
Sediment	2	0.812	2.24	0.123
Light X Temperature	1	0.090	0.220	0.643
Light X Sediment	2	0.417	1.02	0.376
Temperature X Sediment	2	0.126	0.307	0.738
Light X Temperature X Sediment	2	0.301	0.735	0.490
Error	24	0.409		

Data were normally distributed and variances were homogeneous (p=0.090)

B. *Montipora digitata*				
Source of variation	**Df**	**MS**	**F**	**p**
Light	1	2.10	4.83	**0.038**
Temp	1	0.903	2.07	0.163
Sediment	2	0.580	1.33	0.282
Light X Temperature	1	0.467	1.07	0.311
Light X Sediment	2	0.831	1.91	0.170
Temperature X Sediment	2	0.158	0.362	0.700
Light X Temperature X Sediment	2	0.617	1.42	0.262
Error	24	0.435		

Data were normally distributed and variances were homogeneous (p=0.348)

3.3.3 Coral Lipid Concentration

Results indicated no significant response in the net lipid concentrations of either species to sediment treatments up to 250 mg cm^{-2} d^{-1}, or to temperature treatments of 29 ºC. However, there was a significant effect of the light treatments on *T. mesenterina*. Specifically, lipid concentrations decreased from 13.2 ± 0.5 mg cm^{-2} to 9.1 ± 0.3 mg cm^{-2} (*Table 3.3a, Figure 3.2*). Unlike the response observed in skeletal growth rate, *M. digitata* showed no significant changes in lipid concentration in relation to light or temperature treatments (*Table 3.3b, Figure 3.2*). There were no observable interactive effects between light, temperature, and sediment on either species. In general, the mean lipid concentration of *T. mesenterina* (11.2 ± 0.4 mg cm^{-2}) was twice that of *M. digitata* (5.5 ± 0.3 mg cm^{-2}) (*Appendix B*).

Table 3.3: Results of the full factorial, univariate ANOVA testing for effects of light (Shaded and Unshaded), water temperature (Heated and Unheated), and sediment treatments (Control, Low, and High) on differences in lipid concentrations of (A) *Turbinaria mesenterina* and (B) *Montipora digitata*.

A. *Turbinaria mesenterina*				
Source of variation	**Df**	**MS**	**F**	**p**
Light	1	153.4	46.4	**<0.001**
Temp	1	16.4	2.24	0.144
Sediment	2	1.89	0.530	0.595
Light X Temperature	1	2.51	0.701	0.411
Light X Sediment	2	0.304	0.085	0.919
Temperature X Sediment	2	1.52	0.424	0.659
Light X Temperature X Sediment	2	0.0169	0.005	0.995
Error	24	3.58		

Data were normally distributed and variances were homogeneous (p=0.054)

B. *Montipora digitata*				
Source of variation	**Df**	**MS**	**F**	**p**
Light	1	12.5	3.91	0.060
Temp	1	3.36	1.05	0.315
Sediment	2	1.05	0.329	0.723
Light X Temperature	1	0.640	0.200	0.658
Light X Sediment	2	0.350	0.110	0.897
Temperature X Sediment	2	2.33	0.729	0.493
Light X Temperature X Sediment	2	0.157	0.049	0.952
Error	24	3.19		

Data were normally distributed and variances were homogeneous (p=0.069)

3.3.4 Chlorophyll a concentrations

Results indicated no significant response of the chlorophyll *a* concentrations of either species to sediment treatments up to 250 mg cm^{-2} d^{-1}. However, strong effects of light and temperature were observed. Again, *T. mesenterina* showed a significant stress response, that is, a reduction in chlorophyll concentration in the Unshaded treatments (*Table 3.4a, Figure 3.2*). However, there was no apparent effect of temperature. In contrast, *M. digitata* demonstrated a significant increase of chlorophyll concentrations in the Shaded light treatment as well as in the Unheated temperature treatments (*Table 3.4b, Figure 3.2*). There were no observable interactive effects between light, temperature, and sediment on *T. mesenterina*, however, the combination of reduced light and temperature did interact to significantly increase the chlorophyll concentration in *M. digitata* (ANOVA: df=1, f=16.61, P≤0.001). Throughout all treatments, the mean chlorophyll concentrations of *T. mesenterina* (149.0 ± 7.3 mg cm^{-2}) were observed to be more than twice that of *M. digitata* (61.5 ± 4.0 mg cm^{-2}) (*Appendix B*).

Table 3.4: Results of the full factorial, univariate ANOVA testing for effects of light (Shaded and Unshaded), water temperature (Heated and Unheated), and sediment treatments (Control, Low, and High) on differences in chlorophyll concentrations of (A) *Turbinaria mesenterina* and (B) *Montipora digitata*.

A. *Turbinaria mesenterina*				
Source of variation	**Df**	**MS**	**F**	**p**
Light	1	37300.5	36.8	**<0.001**
Temp	1	226.0	0.223	0.641
Sediment	2	979.3	0.967	0.395
Light X Temperature	1	579.2	0.572	0.457
Light X Sediment	2	121.9	0.120	0.887
Temperature X Sediment	2	1137.2	1.12	0.342
Light X Temperature X Sediment	2	124.0	0.122	0.885
Error	24	1012.7		

Data were normally distributed and variances were homogeneous (p=0.107)

B. *Montipora digitata*				
Source of variation	**Df**	**MS**	**F**	**p**
Light	1	2114.5	7.32	**0.012**
Temp	1	4205.5	9.10	**0.005**
Sediment	2	125.1	0.210	0.812
Light X Temperature	1	4796.0	16.6	**<0.001**
Light X Sediment	2	326.0	1.13	0.340
Temperature X Sediment	2	228.0	0.790	0.465
Light X Temperature X Sediment	2	259.0	0.897	0.421
Error	24	288.8		

Data were normally distributed and variances were homogeneous (p=0.056)

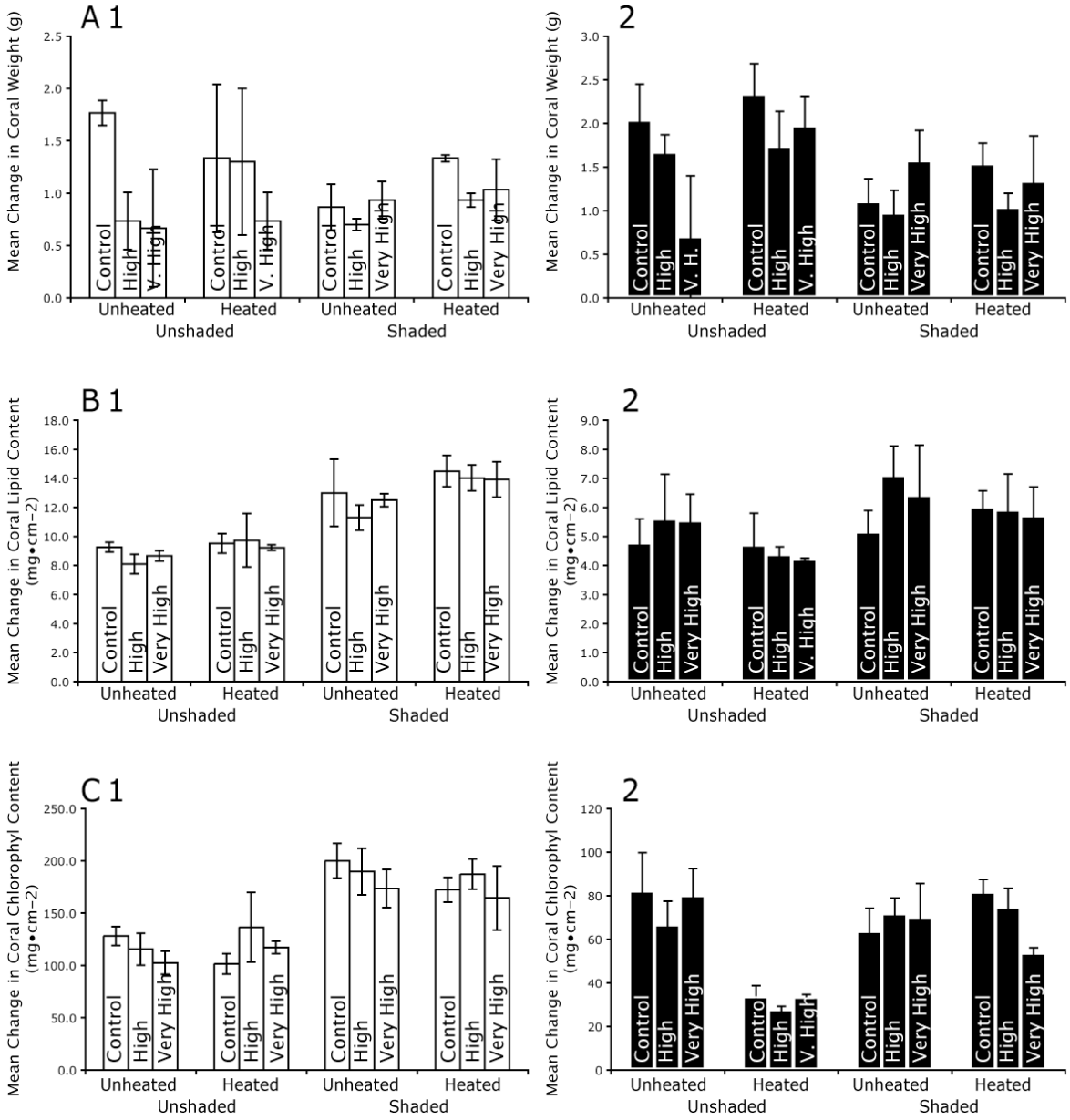


Figure 3.2: Mean changes ± SE in (A) coral skeletal weight, (B) coral lipid concentration, and (C) coral chlorophyll concentration between the interaction of light (Unshaded and Shaded), temperature (Unheated and Heated), and sediment (Control, High, and Very High) treatments on (1) *Turbinaria mesenterina* (white) and (2) *Montipora digitata* (black).

3.4 Discussion

Sediment Tolerance and Acclimatization

None of the three methods for assessing sub lethal stress utilized in this study indicated a significant biological response in *T. mesenterina* or *M. digitata* to any of the applied sediment treatments. This suggests that both *T. mesenterina* and *M. digitata* are able to tolerate very high levels of sediments (246.3 ± 47.4 mg cm^{-2} d^{-1}) within a wide range of water temperatures and light irradiances, for a period of up to fifteen days. I hypothesize that the high sediment tolerance of *T. mesenterina* and *M. digitata* are a result of life history strategies that efficiently utilize both passive and active sediment removal tactics. Further, it is likely that colony morphology, specifically the raised corallite structures of *T. mesenterina* and vertical cylindrical orientation of *M. digitata*, enhance passive sediment rejection, leaving more energy available for growth, repair, and reproduction. This is supported by Lasker (1980), who states that a morphology that assists in passive sediment removal can significantly reduce the amount of work a colony must perform to keep its surfaces clear of sediments. It was also observed that the corallite morphology of *T. mesenterina* aids in the active removal of sediments. Shortly after settling onto the coral surface, sediments aggregated on the tissues between polyps (coenosteum), typically toward the center of the colony (possibly facilitated by the passive function of relatively small, low-profile, closely grouped polyps). Here, sediments were coated with mucus that lifts vertically into the water column and off of the colony (pers. obs.). No excessive mucus production was observed in the colonies of *M. digitata.* Instead, active sediment removal was accomplished simply through polyp re-extension. Upon sediment application, the vast majority of sediment particles fell past without contacting the colony surface. When particles did make contact, the polyp tentacles would immediately retract, possibly as a protective mechanism. Five to fifteen minutes after sediment application, these tentacles would slowly extend, pushing the remaining particles off and effectively clearing the surface. Neither sediment removal mechanism described here appeared to require a high-energy investment on behalf of the coral colony. On the contrary, the excess mucus production and tentacle movement observed may be related to the mechanisms by which these species perform enhanced particle feeding (*see also* Anthony (1999), Rosenfield *et. al.* (1999), and Anthony and Larcombe, 2001). It is suggested, therefore, that the results of this study provide further understanding regarding the observed high sediment tolerance of these species, but also the high

frequency and abundance of these species along the turbid inshore reefs of the inner shelf of the GBR.

Coral Skeletal Growth

The sediment treatments employed in this study did not affect coral growth rates in either *T. mesenterina* or *M. digitata*, however, this may be more a function of the growth response and its susceptibility to environmental stress. That is, coral growth rates of *T. mesenterina* and *M. digitata* may not be as responsive to sub lethal stress from sediment or temperature conditions over short time periods as initially anticipated. This observation is supported by the work of Edinger *et. al.* (2000) who investigated coral growth rates at reefs subjected to combined eutrophication and sedimentation stress. Specifically, they reported that coral growth rates did not reliably predict rates of reef accretion and, in fact, measured normal to rapid coral growth rates whilst still observing net reef erosion (on polluted reefs). I suspect, however, that the lack of change in coral growth rates assessed in this study is more likely a result of insufficient strength in prescribed treatments to affect a significant response (*see also* Anthony, *et. al.*, 2002).

Through previous study, coral calcification and growth rates have been strongly correlated with light conditions (Grigg, 1981; Roth, *et. al.*, 1982; Hubbard and Scaturo, 1985; Barnes and Chalker, 1990; Baker, 2004). Here, I observed that the growth of *T. mesenterina* was unaffected by the prescribed light treatments, however, the growth rate of *M. digitata* was reduced with decreasing light irradiance. This suggests that *T. mesenterina* may be less sensitive to changes in light conditions than *M. digitata*. Additionally, this result indicates that *T. mesenterina* may be tolerant to light conditions within a wide range (<300-800 micro Einsteins m^{-2} s^{-1}). Interestingly, these results may provide further clarity on why *T. mesenterina* may dominate a variety of reef environments from deep-water slopes to the reef crest while colonies of *M. digitata* are more commonly found in shallow depth range and may be a dominant species of shallow reef flats/lagoons which are characterized by high sunlight irradiance and relatively low water turbulence (Veron, 2000; pers. obs.).

Coral Lipid Concentration

Lipid concentrations also showed no significant changes from sediment and water temperature treatments. Again, this suggests that the sediment and temperature treatments were below the threshold levels of these colonies and that sufficient light and

nutrient energy resources were available to maintain normal lipid concentrations. Similar to the effect of light on growth, light treatments again had an effect. This time, however, the effect was not observed on *M. digitata* but on *T. mesenterina* that significantly decreased in lipid concentration within the Unshaded treatments. This reduction in lipids suggests that light conditions within the Unshaded treatments were creating a stress in which stored energy resources (e.g. lipids) were being utilized in order to maintain the positive energy growth as observed in the buoyant weight results. It is hypothesized, therefore, that the light conditions within this treatment were at or above the threshold limit of *T. mesenterina* and that with time, lipid concentrations would have reduced to a level where coral growth would have been stunted, and possibly followed by colony mortality. Given the robust nature of this species, however, it is possible that a percentage of the population may have acclimatized to these conditions, balanced their energy resources, and continued to survive. It is therefore suggested that future experiments involving *T. mesenterina* be carried out for a period greater than two weeks so that any potential acclimatization and recovery behavior may be observed.

Given the dominance of *M. digitata* in the high light, shallow reef environments it is not surprising that no significant decrease in lipids were detected. Again, it is believed to be a function of colony morphology that enables tolerance to such extreme light conditions. Specifically, the vertical orientation of colony branches effectively minimizes the surface area exposed during the height of the day when irradiance is at its maximum.

It was noted in section 3.4.3 that the mean lipid concentrations of *T. mesenterina* were generally twice that of *M. digitata*. When considered with the observation that the growth rates of *T. mesenterina* were slightly less than that of *M. digitata*, it is interesting to speculate on the life history strategies of these two species, particularly in regard to energy resource allocation. Excess energy of *T. mesenterina* appears to be allocated toward storage while in *M. digitata* it is allocated to growth. This energy reserve of *T. mesenterina* may help in explaining why it appears to be such a robust species able to tolerate and survive through extreme environmental events (Anthony *et. al.*, 2004; pers obs.). Lipid storage may not be a luxury afforded to organisms that live along the reef flat where competition for space is a continuous pressure and the preparation for potential, future events, therefore becomes secondary priority.

Chlorophyll a Concentration

Of the three physiological responses measured, chlorophyll concentration proved to be the most sensitive. A significant change in chlorophyll concentration was observed in the light treatments of both *T. mesenterina* and *M. digitata*. In this, it is interesting to note that both species changed when subjected to conditions that differed from their original collection locations. *T. mesenterina*, collected from approximately four meters depth decreased in chlorophyll concentration when exposed to high light levels, indicating a bleaching response to that treatment. Alternatively, *M. digitata* collected from the comparatively warm and bright waters of the reef flat, increased in chlorophyll concentration within the Shaded and Unheated treatments, suggesting an acclimatization response to these new conditions. I hypothesize that in both cases modifications in chlorophyll concentration are a result of the symbiotic zooxanthellae adjusting to the new environmental conditions (Rowan, 2004; van Oppen, 2005). That is, reducing chlorophyll concentrations in response to high light availability and increasing in response to low light. In addition, the increase in chlorophyll of *M. digitata* as a result of decreasing water temperatures is an interesting observation. First, it suggests that the temperature treatments where of sufficient strength as to have an effect even though this effect was not reflected in the coral growth or lipid concentrations. It also suggests that the temperature sensitivity of *M. digitata* is greater than that of *T. mesenterina.* These findings may accounted by the work of Van Oppen (2005), who indicates that the initial uptake of the zooxanthellae is non-selective, suggesting an adaptive trait that allows the coral host to 'reshuffle' zooxanthellae strains and concentrations. She suggests, however, that this reshuffling may come at a cost in that coral growth rates may fluctuate depending on the strain types and concentrations utilized by the host at a given time. Van Oppen (2005) continues by reporting that scleractinian corals of the GBR are generally dominated by strains of zooxanthellae in the 'C' clad (or lineage) and suggests that a shift to increased concentrations of the more thermal tolerant 'D' clad may result in a reduced growth rate. Although zooxanthellae concentrations strain types were not quantified as part of this study, it is hypostasized that the observed differences physiological response may be more connected to differences in the utilization zooxanthellae than between the corals themselves (Redalje, 1976; Egana and DiSalvo, 1982).

It has been previously noted that *T. mesenterina* displayed a significant reduction in lipid concentration while *M. digitata* did not. However, this could simply be an expression of how each species was affected by the stress of fragmentation and collection (i.e. the relative size of the broken edge is greater for *T. mesenterina* than *M. digitata* and requires more energy diverted to the injury). Regardless, this difference does correspond nicely to the significant loss and gain in chlorophyll concentrations observed respectively. It is reported that in exchange for the essential nutrients supplied by the host coral, the symbiotic zooxanthellae will transfer up to 95% of their photosynthetic production (energy) to the coral (Muscatine, 1990). It is therefore intuitive that a decrease in lipid concentration, a secondary energy source, should be observed corresponding with a loss in a primary energy source. It is suggested, that *T. mesenterina* may be a good candidate for future, long-term studies regarding the energy pathways of scleractinian corals and how they change, particularly during periods of prolonged stress.

CHAPTER 4 EFFECTS OF SEDIMENTS APPLIED TO CORALS *IN SITU* USING A NEW EROSIONAL BLOCK TECHNIQUE.

4.1 Introduction

Sedimentation from both natural and anthropogenic sources, and its effects on coral reef systems, has been a major focus of marine research for more than fifty years (Nesteroff, 1955; Dodge and Vaisnys, 1977; Rogers, 1990). While some studies have been conducted *in situ* (Rogers, 1983; Hodgson, 1990; Stafford-Smith, 1992; Stafford-Smith and Ormond, 1992), most studies investigating the effects of sedimentation on corals have been conducted using experimental laboratory systems (Lasker, 1980; Dodge, 1982; Babcock & Davies, 1991; Riegl and Branch, 1995; Anthony, 1999; Anthony and Fabricius, 2000). The strength of experimental laboratory research is the ability to control environmental conditions and enable isolation of the effect of key variables. However, the tight control of environmental conditions may not necessarily be representative of the natural environment. I argue that there is a general lack of experimental field data, and that the development of manipulative research methods *in situ*, are necessary in order to fully understand how sediments affect corals and coral reefs in their natural environments.

To date, the most common approach used in the assessment of sediment effects on corals *in situ*, has been one of monitoring. That is, previous studies have been mainly mensurative, with local sedimentation rates measured against relative coral stress responses and correlations used to draw conclusions (Hubbard, 1986; Babcock and Davies, 1991; Stafford-Smith, 1992; Bernhard *et. al.*, 1996; McClanahan and Obura, 1997). The primary drawback of this approach is the general lack of ability to manipulate and control the variables, particularly the environmental conditions. Specifically, there is little to no control over the type of sediment (i.e. grain size, nutrient content), the strength and/or duration of sediment exposure, or the spatial distribution of the sediments. The dependency on ambient environmental conditions, may significantly limit our understanding of the sediment/coral relationship simply by limiting the number of scenarios that may be observed.

Only a few studies have attempted experimental manipulation of sediment regimes *in situ*. Rogers (1983), for example, conducted experiments at San Cristobal Reef, Puerto Rico to assess the sediment tolerance of four coral species. Sediment application (up to 800 mg cm^{-2} d^{-1}) was conducted daily for over two months (long-term). Results indicated an interspecies specific difference in sediment tolerance levels. Philip and Fabricius (2003) studied the effects of short-term sedimentation on 12 coral species on the GBR, Australia. Concentrations ranging from 79-234 mg cm^{-2} d^{-1} were applied *in situ*, for up to 36 hours. However, the sediment application in this study may not have been representative to a natural event as they were applied to surface and in single doses. Stafford-Smith and Ormond (1992) investigated the sediment rejection mechanisms of 42 species of scleractinian coral near Lizard Island, Australia. Four sediment sizes were defined and applied *in situ* up to 1000 mg cm^{-2} in some treatments. The type, intensity, and duration of the behavioral response of each species were observed. Similar to these studies, most previous manipulative studies are characterized by their focus on the short-term shock effects of sedimentation. Natural sediment regimes, however, are typically characterized by weeklong events of sedimentation and re-suspension cycles (Larcombe, *et. al.*, 1995; McCulloch, *et. al.*, 2003; Alongi and McKinnon, 2005). To date, there has been no method available for the continuous manipulation of turbidity/sedimentation regimes on reefs at the medium-term (week-long) scale.

The purpose of this study is two-fold: (1) to assess the biological response of three scleractinian coral species to a continuous, two week long, sediment event and (2) to develop and test a new method for continuous, *in situ*, sediment application.

The sediment dispensing technique that I develop here is based on the erosive plaster blocks principle (Jokiel and Morrissey, 1993) and the sediment brick principle of Babcock and Davies (1991). Specifically, I constructed sediment blocks composed of plaster of paris and silicate-based sediments that were suspended above coral assemblages, and through their gradual erosion dispense over the corals. By combining known erosion and sediment dilution rates and models on particle flux (Stokes Law,1851; Gibbs *et. al.*, 1971), I develop a model for predicting particle behavior, sedimentation rates, and turbidity concentrations over replicated patches of coral reef. Six sediment blocks were placed *in situ*, suspended above a fringing inshore reef, and the sediment response of three scleractinian coral species (*Acropora formosa, Montipora tuberculosa,* and *Porites* cylindrica) were examined. The method is the first feasible and cost effective way to produce an experimental sediment gradient on coral reefs *in situ*.

4.1.1 Description of Study Species

A. formosa, M. tuberculosa, and *P. cylindrica* were selected based on their high local abundance as well as the natural variability in their life history strategies (e.g. morphology, energy allocation strategies). These life history strategies are important, as they are likely to be critical in the coral's response to sedimentation ability to survive changing environmental conditions.

Acropora formosa (Dana, 1846) colonies are arborescent with cylindrical branches and can form monospecific stands on reef slopes, fringes, and in lagoons in various locations from turbid waters to those with strong waves and high currents; from areas where there is little light to being fully exposed to the sun (and the air) at low tide. (Veron, 2000; Lukan, 2006). Branches are often straight, but often form irregular patterns and can vary in size according to depth. That is, shallow water branches are shorter and more compact, while deeper water colonies tend to maintain longer and more open (Veron and Wallace, 1984). Axial corallites are exsert with tubular radial corallites. *A. formosa* is similar to *A. nobilis*, but can be distinguished by the larger and 'rasp-like' radial corallites that are found on *nobilis* (Veron, 1986; Veron, 2000).

Montipora tuberculosa (Lamarck, 1816), or the 'table coral', is widespread and commonly found over a wide range of habitats from turbid inshore reef lagoons to deep clear water reefs offshore (Kuhlmann, 1983; Craig *et. al.*, 2004). Morphology can vary between colonies, but are typically submassive or thick plate-like colonies. Corallites are small and separated by papillae/tuberculae. *M. tuberculosa* is similar to *M. monasteriata* but are distinguished in that the corallites of *M. tuberculosa* are much smaller (Veron, 1986).

Porites cylindrica (Dana, 1846), colonies are branching, often with an encrusting base and shallow corallites giving the branches a smooth surface. They are highly adaptive to a wide range of environmental conditions, from the turbid inshore reefs to the clear waters of offshore reefs, however, *P. cylindrica* is more likely to dominate lagoons or back reef margins where strong wave and current action is minimized (Veron, 2000).

4.1.2 Description of Study Area

This study was conducted on the coral reef along the southeast shore of Pelorus Island (18.56º S, 146.5º E). Pelorus Island is part of the Palm Island group approximately 15-20 km off the coast north Queensland (*Figure 4.1*). This site was selected due to its high coral cover and diversity. The site is also located on the eastern, exposed side of the island. Here sedimentation and turbidity regimes are less severe than on other typical inshore reefs and more similar to those of the mid- and outer- shelf reefs of the GBR. This was beneficial in that the corals of this area were not previously acclimatized to high sediment levels, and therefore, the community is not dominated by corals with high tolerance to sedimentation.

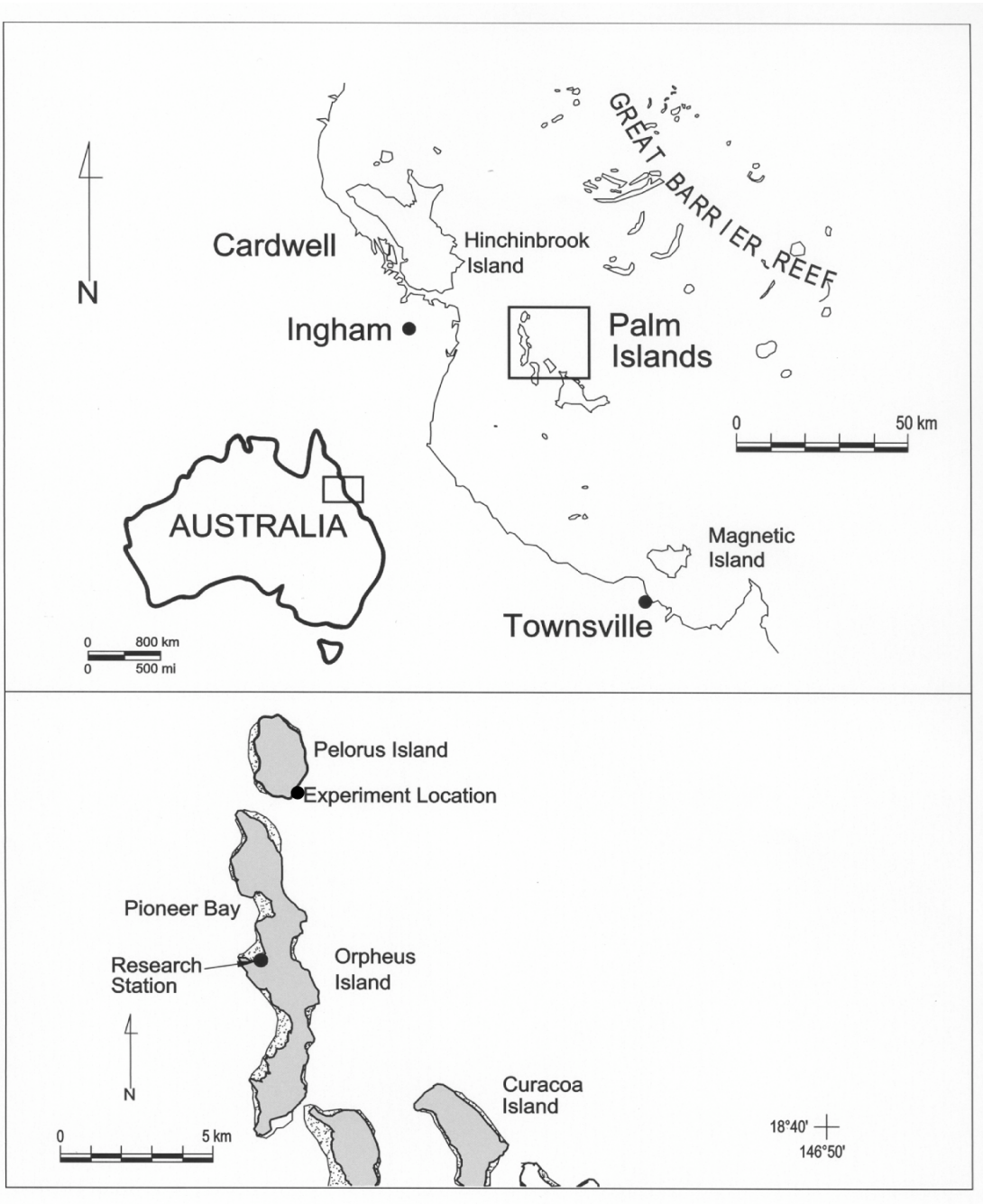


Figure 4.1: Map of Pelorus and Orpheus Islands illustrating the location for experimentation (18.56º S, 146.5º E), and base of operations (Orpheus Island Research Station) for this study.

4.2 Materials and Methods

4.2.1 Erosion Block Design & Calibration

In order to test the efficacy of the suspended erosion blocks as a method for manipulating *in situ* sediment regimes, a pilot study was conducted. Four blocks were constructed using various ratios of sediment and plaster of paris (*Table 4.1*). For each block, the mixture was thoroughly homogenized, quickly poured into a cylindrical PVC mold (1 m x 25 cm), placed into a 60º C oven, and allowed to dry for 96 hours. Each block was weighed, placed into a flow chamber (30 cm x 10 cm x 10 cm, 0-11 cm s^{-1}, 25º C, 35 ppm) for 72 hours, and then dried and reweighed. The erosion constant (Ø, cm g^{-1}) for each block was calculated using the formula:

$$Ø = U \Delta t / \Delta W$$

Where U (cm s^{-1}) is the flow velocity, Δt (s) is the duration of deployment, and ΔW (g) is the change in weight.

Table 4.1: Constants (Ø) calculated for experimental erosion blocks using various ratios of plaster to sediment. As sediment content increased there was a corresponding increase in erosion rates.

Plaster: Sediment	Erosion Constant Ø (cm g^{-1})
1:0	134745
1:1	14588
3:4	2874
1:2	533

In general these erosion block devices were designed to generate a sediment plume that would dissipate in concentration with increasing distance from the source. Furthermore, the erosion blocks were designed to concentrate the effectiveness of the block and minimize incidental impacts to surrounding reef areas. Experiments 1 and 2 demonstrated that reef corals such as *T. mesenterina* and *M. digitata* are able to tolerate sediment loads of up to 246 ± 47 mg cm^2 d^{-1} under controlled laboratory conditions. This experiment, however, was to be conducted on the exposed side of Pelorus Island where sedimentation and turbidity regimes are less severe and where corals may demonstrate a response to this level of sedimentation. Therefore, the erosion block was specifically designed such that sediment plume >200 mg cm^{-2} d^{-1} would be generated within the first 0.5 m and dissipate quickly thereafter to background levels within 2.0 m.

In order to achieve the desired sediment application, multiple physical and environmental factors were considered including sediment grain size, current velocity, and size of the erosion block. Particle behavior, that is, the horizontal and vertical movements of particles through the water column, was predicted using equations based on Stokes Law (1851) and the study of Gibbs *et. al.* (1971). Based on this information, I developed a model in which the downward settling velocity for particles ranging from 5–1000 µm was tested. In this model, the downward settling velocity for a given particle of sand (ω) was estimated using*:

$$\omega = \frac{-3\eta + \sqrt{(9\eta^2 + gr^2\rho_f(\rho_s - \rho_f)\,(0.015476 + 0.19841(r)))}}{\rho_f\,(0.011607 + 0.144881\,(r))}$$

* Non-turbid water is assumed

Where ρ_s (g cm^{-3}) is the density of the sediment particle, ρ_f (g cm^{-3}) is the density of the fluid through which it is traveling, g (cm s^{-2}) is the acceleration due to gravity, r (cm) is the radius of the particle, and η (g cm^{-1} s^{-1}) is the dynamic viscosity of the liquid.

The horizontal distance (X) that a particle may travel before settling is dependent on the water flow velocity (ν) and the particles vertical distance above the substrate (Y), and its downward settling velocity (ω).

$$X = \nu\,(Y / \omega)$$

Thus, given a specific sediment grain size and mean water velocity, the appropriate distance and height at which the erosion block should be placed from the target coral population can be estimated.

The mass of the erosion block required (M) to generate the desired sediment condition for the time required was determined using:

$$M = (\nu\,\Delta t) / Ø$$

The weight of sediment alone (Ms) can be calculated by using the ratio of plaster to sand and their specific densities. The portion of sand is then divided by the sum of the total:

$$Ms = \frac{\rho s\,(S-1)}{(\rho s\,(S-1)) + (\rho p\,(P-1))}$$

Where S is the number of parts of sand, P is the number of parts of plaster, ρs is the density of the sand and ρp is the density of the plaster.

In order to predict sedimentation rates, the area of coverage (A) must also be estimated. Here, A was calculated as a horizontal semicircle with a radius equal to the calculated horizontal distance (X) that the particle will travel before settling. The semicircle was used, as it is a simple and relatively natural geometric form, and accounts for 180° of sediment particle coverage.

$$A = \frac{\pi X^2}{2}$$

Sedimentation rates (U) were then estimated using:

$$U = (Ms / \Delta t) / A$$

4.2.2 Erosion Block Composition & Construction

Based on the results of the pilot study and calculations from sediment behavior modeling, erosion sediment blocks were created by mixing plaster of paris with silicate-based sediments (<500 μm) and water in a 3:4:3 ratio (*Figure 4.2*). To provide a means of attaching the mold to stands in the field, as well as adding strength and support to the erosion block, a 125 cm x 25 mm section of threaded steel rod was run longitudinally down the center of the mold. Two wooden caps were placed on the ends of the mold prevent loss of the sediment mixture and stabilize the threaded steel rod in the center of the mold (*Figure 4.3*). The entire mold was placed into an oven at 60º C and allowed to dry for 96 hours.

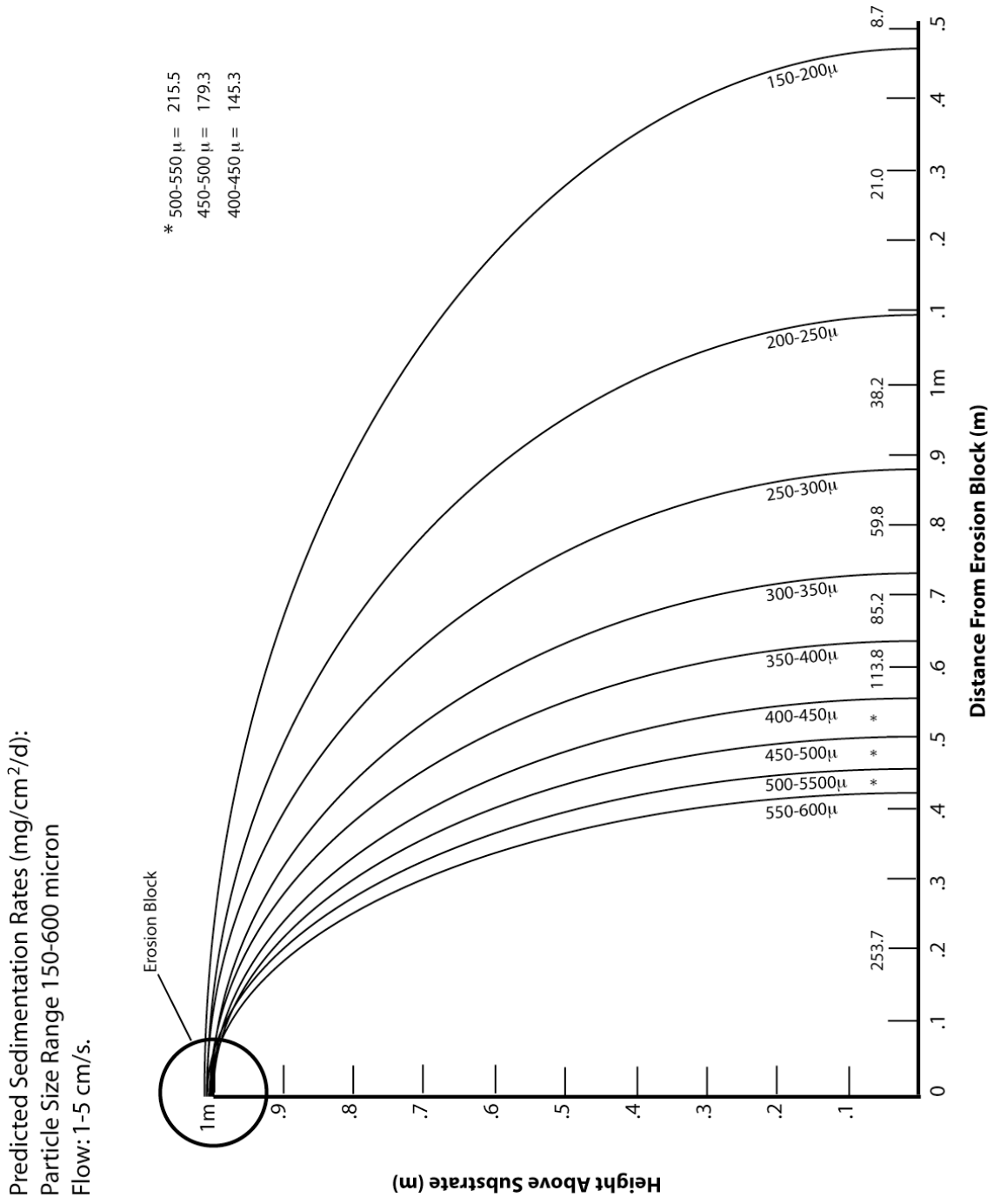


Figure 4.2: Predicted sedimentation rates as produced by the experimental erosion blocks with a plaster to sediment ratio of 3:4, particle sizes ranging from 150-600 µ, in flow conditions ranging from 1-5 cm s^{-1}.

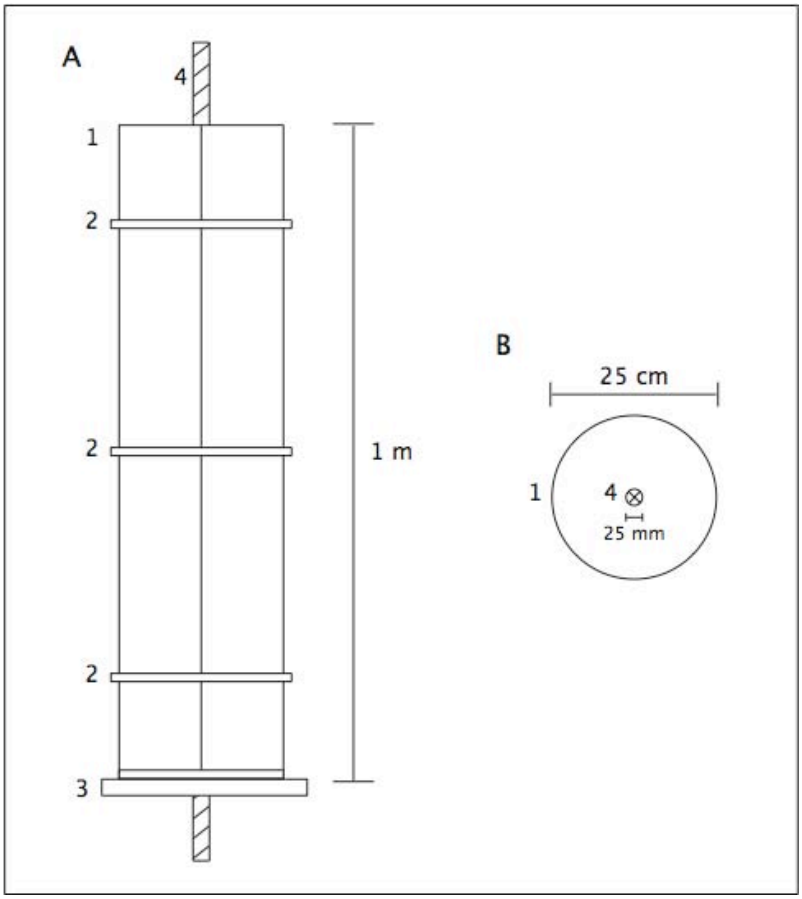


Figure 4.3: Side (A) and transverse (B) profiles of the mold used to form the experimental erosion block. A cylindrical PVC pipe, cut longitudinally (1), is held together by three (2 cm) hose clamps (2). A wooden cap (3) acts as a base, gives support to the mold, prevents the loss of the sediment mixture, and holds the 1.25 m section of 25 mm threaded steel rod (4) in the center of the mold.

4.2.3 Experimental Set-up

Six sites were selected at approximately 11 m below lowest astronomical tide (LAT) at the southeast part of Pelorus Island. At each site, an erosion block was suspended horizontally between two star pickets, and 1 m above the reef. To map the sedimentation rates at various distances from each block six cylindrical sediment traps (3.25 cm x 30 cm) were deployed around the erosion block at distances from 0-1.5 m. Colonies of *A. formosa, M. tuberculosa,* and *P. cylindrica* were identified, tagged, and mapped at varying distances from the sediment block ranging from 0-1.5 m (*Figure 4.4; map sketches provided in Appendix C*). Between the six sites, each species was represented by at least thirty-five individual colonies.

Figure 4.4: Photograph showing a typical experimental site setup. The sediment erosion block was suspended horizontally between two star pickets approximately 1 m above the reef. Six cylindrical sediment traps (3.25 cm x 30 cm) were deployed around the erosion block at distances from 0-1.5 m.

Multiple turbidity and sedimentation plume scenarios were tested prior to experimentation. Variables such as cylinder size, height above substrate, particle size and current velocity were tested and adjusted to determine an efficient and effective arrangement. In accordance to these calculated values, each site was positioned at least 20 m away from the next to ensure independence between sites. Calculations based on expected current velocities (0-10 cm s^{-1}) indicated that the turbidity generated, and sediment plume radius, should not exceed 15 m. Greater than 80% of the sediment was predicted to settle within the first 2m when using these anticipated current velocities.

4.2.4 Experimentation

Upon deployment of the erosion blocks and sediment traps, the approximate location of each colony was mapped with its location and distance relative to the center of the erosion block (*Appendix C*). Each colony was then visually assessed for percent mortality and photographed using a digital camera (Sony PC1). Visual assessment and digital photography was carried out on each colony every five days for the duration of the fifteen-day experiment.

On day fifteen, all sediment traps were collected and brought back to the laboratory. Sediment samples were filtered through pre-weighed, Whatman GF/C filters (~1 µm pore size), rinsed with distilled water, dried at 80º C, and then re-weighed.

4.2.5 Assessment of Stress Response

Coral response to sediment application was assessed by measuring the percentage of individual colony bleaching/tissue damage, as a function of distance between the colony and the sediment block. Underwater digital photos were taken of each colony prior to, during, and after exposure to applied sediments. To quantitatively assess the percent bleaching, each photo was analyzed using Image J image processing and analysis software (v. 1.32, Mac OSX, Wayne Rasband, Bethesda, Maryland, USA).

4.2.6 Data Analysis

The experimental design consisted of two fixed factors (Site and Coral Species) using at least thirty-five coral colonies per species. Replicate numbers were based on the data from the 1997 Darwin East Arm Port Development project where researchers were also attempting to detect a coral bleaching response from sedimentation. Based on the results of their statistical analysis (i.e. calculated standard error), thirty-five replicate colonies per species was determined to be of sufficient power ($1-\beta \geq 0.80$) at a precision level of $\alpha = 0.05$. Additionally, a replicate of thirty-five coral colonies per species was calculated as sufficient to reduce variation between measurements such that the maximum likely error (e) is ≤ 1.0% while effectively minimizing the required sampling effort (*Table 4.2*).

Table 4.2: Calculated maximum likely error (e) in measuring the percentage of coral bleaching with a given sample size (n). Based on data from the Darwin East Arm Port Development (1997), a sample size of n=35 was determined to reduce the maximum likely error to an acceptable level (e=1.00 %) while maintaining a practical sampling effort (105 coral colonies).

n	e	Total # Corals
5	2.66	15
10	1.88	30
15	1.53	45
20	1.33	60
25	1.19	75
30	1.09	90
35	1.00	105
50	0.84	150
75	0.68	225
100	0.59	300

The relationship between coral response and sediment rate was analyzed using linear regression for each species. The effects of site, species, and their potential interaction were tested using a univariate ANOVA. All assumptions were tested using histograms and the Levene's test for homogeneity of variances (p=0.05). All analyses were performed using Microsoft Excel (X) for Macintosh and the SPSS (v. 10.0) statistical packages.

4.3 Results

4.3.1 Erosion Block Performance

Sedimentation rates ranged from 1.2 to 371.7 mg cm^{-2} d^{-1} with a mean rate of 81.5 ± 17.7 mg cm^{-2} d^{-1}. In this, a trend was observed demonstrating a significant decrease in sediment concentration with increasing distance from the sediment source (Linear Regression: B= -0.517, t= -3.5, P=.001) (*Figure 4.5a*). In regard to sediment dispersal and area affected, the erosion block appeared to be limited to a distance no greater than 1.5 m. Specifically; sediment concentrations measured in traps beyond 1.5 m were not significantly higher than the measured natural background sedimentation rate (3.3 ± 0.4 mg cm^{-2} d^{-1}).

This information can be utilized to better understand how experimental coral colonies interacted with the sediment treatments. Based on the mean sediment concentrations at various distances from the erosion block, a sedimentation gradient was estimated by plotting an exponential trend line on the resulting data cluster (*Figure 4.5b*). This exponential trend line was used to estimate sediment rates at distances from 0.0 to 1.6 m and had an equation of: $y=282e^{-2.7x}$ (R^2=0.45). An exponential trend line was used because of the exponential relationship between particle size and the downward settling velocity of particles within the Gibbs *et. al.* (1971) equation. This is further supported in that the exponential pattern was determined to best match the sediment distribution pattern observed from sediment taps *in situ*. In general, results indicate that the mean sediment concentrations and the area of distribution observed were very close to those concentrations and application rates that were predicted using the pre-experiment modeling (*Table 4.3*).

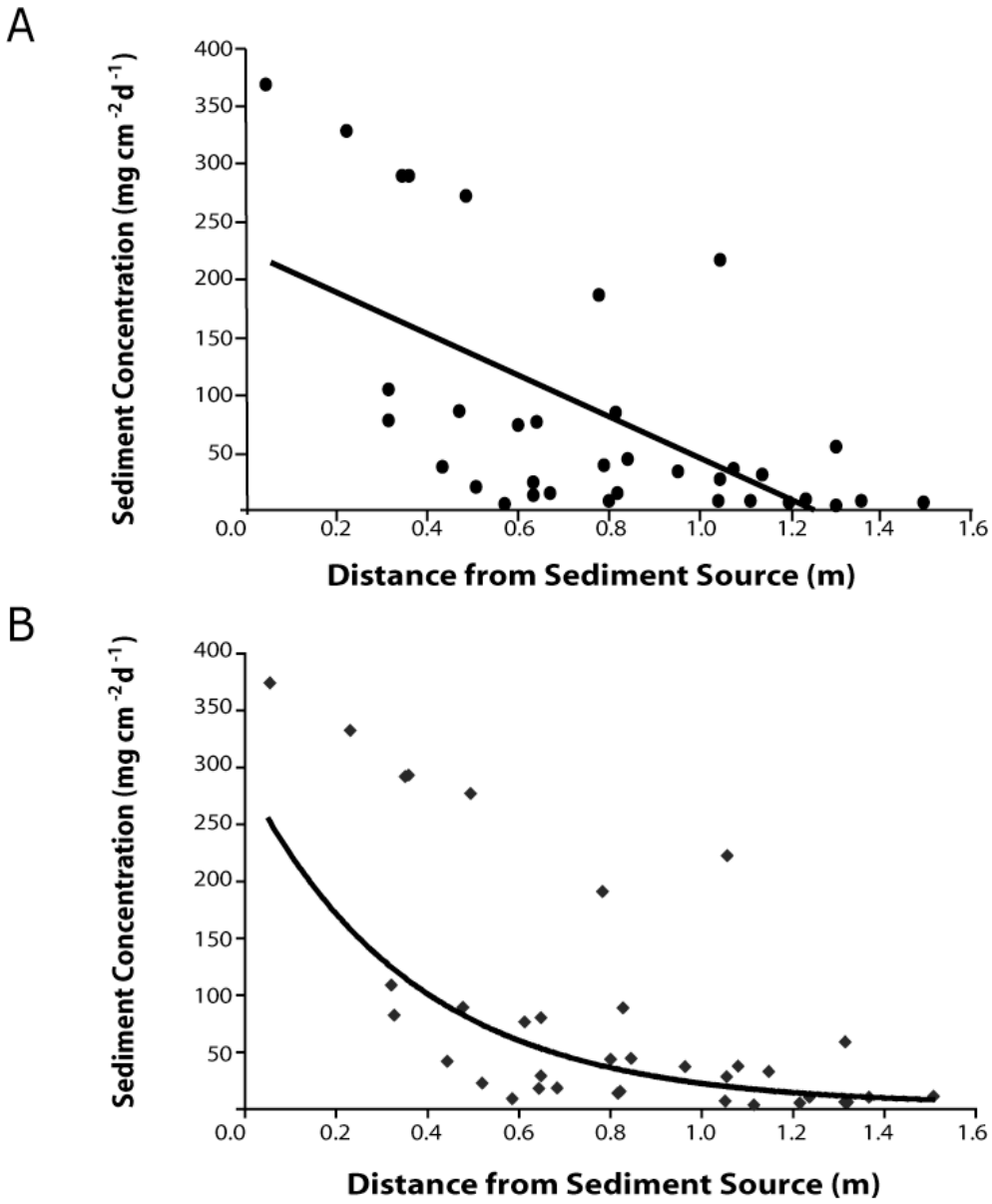


Figure 4.5: (A) Results of a Linear Regression show that sediment concentrations decreased significantly with increasing distance from the sediment source (y=-179X+224, R^2=0.39). (B) The exponential trend line used to estimate sediment rates at distances from 0.0 to 1.6 m from the experimental erosion block (y=282$e^{-2.7x}$, R^2=0.45). All assumptions were tested using histograms and the Levene's test for homogeneity of variances (p=0.05).

Table 4.3: Mean sediment concentrations from traps collected from all six experimental sites and the mean sedimentation rates predicted with pre-experiment sediment calculations. Distances were grouped into 0.5 m increments creating five separate zones. *NBS=Natural Background Sedimentation.

Distance from Erosion Block (m)	Predicted Sediment Concentration (mg cm^{-2} d^{-1})	Mean Sediment Trap Concentration (mg cm^{-2} d^{-1})	± S.E.
<0.5	216	215	51
0.5-1.0	88	65	19
1.0-1.5	21	31	15
>1.5	*NBS	3	1

4.3.2 Coral Stress Response

Coral stress response to the experimental sediment event varied between species. *M. tuberculosa* showed a significant increase in colony mortality with decreasing distance to the sediment source (Linear Regression: B = 29.0, t = 5.5, $P \leq 0.001$), while *A. formosa* and *P. cylindrica* showed no significant change (*Table 4.4; Appendix C*). In addition, the total mean percentage of individual *M. Tuberculosa* colonies that remained unbleached was 78.9 ± 2.9% while individual colonies of *A. formosa* and *P. cylindrical* showed high resistance to sediment treatments. The total mean unbleached area (per colony) measured at 97.4 ± 0.41% and 99.0 ± 0.13% respectively.

Table 4.4: Linear Regression results testing for significant relationship between the percentages of colony bleaching for *Acropora formosa*, *Montipora tuberculosa*, and *Porites cylindrica* in correlation to measured sediment concentration.

A. ***Acropora formosa***				
Model (1)	**B**	**SE**	**_**	**t**
(Constant)	96.0	1.24		77.4
Distance	1.57	1.36	0.189	1.15

Data were normally distributed and variances were homogeneous (p=0.177)

B. ***Montipora tuberculosa***				
Model (1)	**B**	**SE**	**_**	**t**
(Constant)	56.8	4.57		12.4
Distance	29.0	5.28	0.686	5.49

Data were normally distributed and variances were homogeneous (p=0.075)

C. ***Porites cylindrica***				
Model (1)	**B**	**SE**	**_**	**t**
(Constant)	98.9	0.285		347.7
Distance	0.110	0.338	0.056	0.324

Data were normally distributed and variances were homogeneous (p=0.348)

This variation in coral responses is also observed when the percentage of unbleached coral is compared to the estimated sedimentation rate (*Figure 4.6*). Specifically, the mean percentage of unbleached coral tissues within colonies of *A. formosa* ($y=-0.0134X+97.9$, $R^2=0.024$) and *P. cylindrica* ($y=0.0001X+99.1$, $R^2=0.0001$) remained relatively unchanged while those in *M. tuberculosa* ($y=-0.1731X+89.8$, $R^2=0.51$) demonstrated a significant decline with increasing sedimentation rates (Linear Regression: B = -0.173, t = -5.9, $P \leq 0.001$).

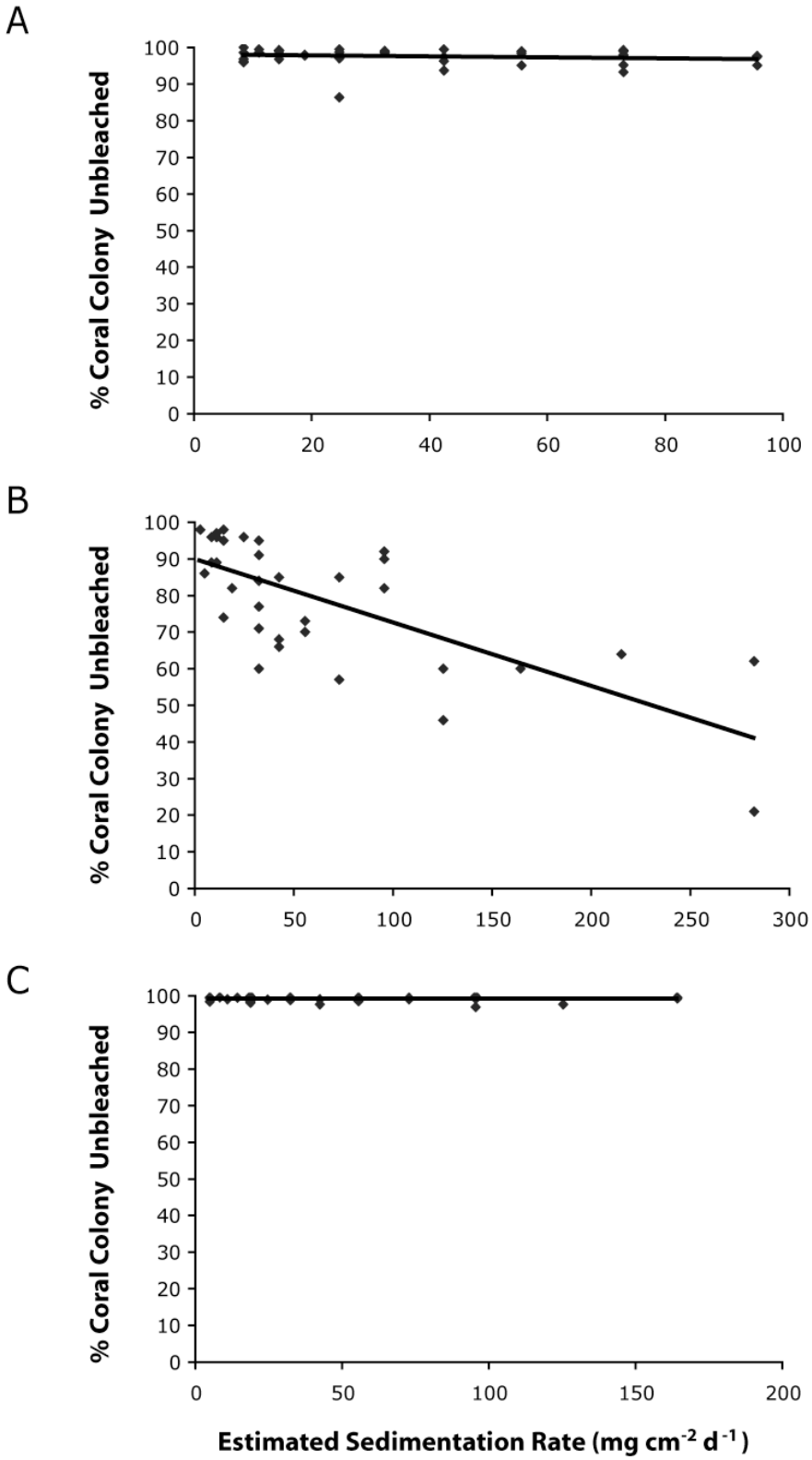


Figure 4.6: Coral colony unbleached (%) in relation to the sedimentation rate (mg cm^{-2} d^{-1}) estimated from the mean distance of the colony from the erosion block in (A) *Acropora formosa* (y=-0.0134X+97.9, R^2=0.024), (B) *Montipora tuberculosa* (y=-0.1731X+89.8, R^2=0.51), and (C) *Porites cylindrica* (y=0.0001X+99.1, R^2=0.0001).

4.4 Discussion

Coral Response to Sediment

Applied sediment treatments produced a significant bleaching (tissue damage) effect on colonies of *M. tuberculosa* while no effect was observed on colonies of *A. formosa* or *P. cylindrica*. Upon the commencement of sediment application, the plate-like colonies of *M. tuberculosa* were quickly covered with sediments and continued to accumulate this material throughout the duration of the experiment. Additionally, *M. tuberculosa* displayed no active sediment removal strategies (i.e. mucus excretion, tentacle movement) and as a result, tissue necrosis occurred beneath the overlying sediments (*Figure 4.7*). It is interesting to note that the perimeter of the colonies remained relatively clear of sediments and apparently unaffected by sediments, suggesting that the center of the colony may be sacrificed as part of some life history strategy to maintain colony growth and survival.

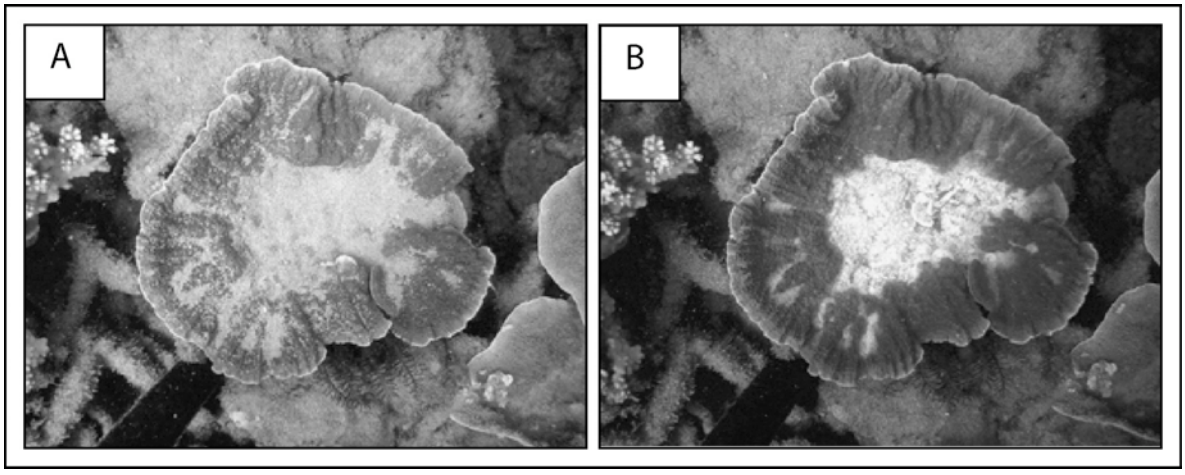


Figure 4.7: Photographs showing a colony of *M. tuberculosa* (A) covered with sediments and (B) the same colony with sediments wafted away revealing the necrosis of underlying tissues.

The variation in sediment tolerance observed between species is likely a result of colony morphology. The plate-like form of *M. tuberculosa* easily collects and accumulates sediment particles; where as the upright, cylindrical branches of *A. formosa* and *P. cylindrica* expose little horizontal surface area for sediments to collect. Additionally, the corallite structures on *M. tuberculosa* are relatively small when compared to other plating species such as *M. monasterata* or *T. mesenterina*, and the corallites are separated by papillae/tuberculae. These features may possibly inhibit the horizontal shedding of sediments by tentacle movement, mucus secretion, or water movement over the colony. These observations are supported by the similar observations of Riegl and Bloomer (1995) who also observed physiological variation

between corals in response to sedimentation. In this study, Riegl and Bloom reported that not all parts of the alcyonacean colonies were equally effected by tissue damage and bleaching. Specifically noted lack of damage and bleaching on the 'elevated lobes and finger-like projections' compared to the 'flat parts' of the colonies. Again, similar to this study, it was concluded that this morphological difference affected the intra-colony response as these elevated areas facilitated passive sediment resistance and were reportedly never covered by sediment for long periods.

Sediment as a Mechanism for Community Change

The variation in sediment tolerance observed in this project supports the hypothesis that sedimentation is a mechanism for structuring coral communities. Sedimentation and/or other environmental conditions changing the structure or inhibiting the development of coral reefs have been the focus of numerous studies (Roy and Smith, 1971; Acevedo *et. al.*, 1989; Sakai and Nishihira, 1991; Aronson and Precht, 1995; Hunter and Evans, 1995; Ostrander *et. al.*, 2000). The most common observation reported is a reduction in coral abundance and diversity due to coral bleaching induced from sediment stress or direct smothering. However, phase shifts between coral and algal dominance on the reef are also reported. For example, Coutinho *et. al.* (1993) studied the effects of coastal deforestation on the coral ecosystem located in the Abrolhos region, Bahia state, Brazil. Here the increases in sedimentation rates from local deforestation were cited as the catalyst for change. Furthermore, a predominance of algal over coral communities was observed in the most deteriorated zones. This process appears to go both ways. Hunter and Evans (1995) describe the effects of diverting two large sewage outfalls, after twenty-five years of input into Kaneohe Bay, Hawaii and the rapid and dramatic decreases in nutrient levels, turbidity, phytoplankton abundance and the subsequent change in community structure.

Previous studies such as that conducted by Szmat (2002) and by Fabricius and McCorry (2006) have investigated species shift on coral reef communities relative to changes in water quality parameters including sedimentation and turbidity. Both studies, however, primarily focused on excess nutrient enrichment of coral reefs and discussed the potential for primary benthic dominance to shift from coral-to-algal based communities. Brown (2000), on the other hand, discusses the potential for delay (or haulting) of recovery and/or potential to cause a coral-to-coral species shift in those coral communities recovering from bleaching induced mortality. In this, Brown focuses on the post-stress recovery of coral communities that are exposed to elevated pollution

levels such as heavy metals. Specifically, it is suggested that branching coral species could be replaced by more 'physically rigorous' massive corals; resulting in a net loss of ecosystem biodiversity. I propose here a similar argument in that a coral-to-coral shift may also result following sediment-induced mortality resulting in a reef community dominated by sediment specialist species (e.g. *T. mesenterina* in Cockle Bay, Magnetic Island). Following on from Brown's conclusions, I submit that this coral-to-coral shift may be further exaggerated if the effecting sediments contain pollutant elements such as heavy metals. Further study in this area could benefit by incorporating the effects pollutants on the sediment response of coral species, particularly those identified as sediment specialist.

Erosion Block Performance

The new method described and tested here allows future studies to perform long-term sediment application experiments and observe changes in community dynamics (e.g. mortality, acclimatization, recovery) *in situ* against natural background conditions. Results clearly demonstrate that this new erosion block is a good technique that has great potential to transform the way that sediments are applied to coral reefs during scientific research. It is the first method described thus far that can apply sediments to a coral reef *in situ*, in a predictable, continuous, and sustained way.

The shape and size of each plume varied between sites. I hypothesize that this is a result of small differences in local current direction and strength between sites (influenced primarily by local benthic topography) and therefore an influential factor in the performance of individual erosion blocks. These small differences between sites may be very difficult to predict and have the potential to significantly alter the actual sediment distribution that is initially calculated or expected. Furthermore, factors such as water turbulence (from waves), which are not included in the predictive models, may exacerbate the discrepancy between predicted and actual sediment concentrations. These influences may be accounted for by testing the effect of sediment at each site with a separate regression if a sufficient number of replicate colonies and sediment traps are present at each site to achieve the power and precision required in the statistical design.

The method described in this study allows for the creation of a sediment gradient (decreasing loads with distance from the source), a new development in the manipulation of sediment regimes *in situ*. I believe that his is important, as it will enable the testing of new hypothesis of sediment effects, along the sediment gradient, directly in the field. The bleaching effect and tissue death caused by sedimentation observed on *M. tuberculosa* in this study is likely to be a stress factor that could ultimately remove this and other sediment-sensitive species from the reef if treatments were sustained. Long-term effects could include transitions in species morphology, lower species diversity and abundance, or even a phase shift to an algal-dominated system as previously reported in other studies (Roy and Smith, 1971; Acevedo *et. al.*, 1989; Sakai and Nishihira, 1991; Coutinho *et. al.*, 1993Aronson and Precht, 1995; Hunter and Evans, 1995; Brown, 2000; Ostrander *et. al.* 2000; Szmat, 2002; Fabricius and McCorry 2006).

CHAPTER 5 GENERAL DISCUSSION

5.1 General Conclusions

McClanahan and Obura (1997) have argued that reefs exposed to high sediment regimes are dominated by sediment tolerant coral genera, while reefs exposed to low sediment influence are dominated by sediment-intolerant genera. This argument has been repeatedly supported by evidence presented in the primary scientific literature. Acevedo *et. al.* (1989) for example, discusses the modification of coral reef zonation through sediment stress. Babcock and Davies (1991) illustrate how sedimentation can effect coral recruitment while Hubbard (1996) provides example of how sediments may control reef development (*see also* Roy and Smith, 1971). Sediments have been demonstrated to influence colony morphology (Bernhard *et. al.*, 1996), effect photophysiology of algal symbiotic algae (Phillips and Fabricius, 2003) and alter coral energy resource allocation (Riegl and Branch, 1995). Species existing within these high sediment environments may therefore, be considered 'sediment specialists', and perhaps representing a life history strategy in which high sediment environments are tolerated and exploited to minimize competition (niche differentiation).

In the first experiment, *T. mesenterina* not only demonstrated a very high tolerance to sediment (>100 mg cm^{-2} d^{-1}), it did so for an extended period (>30 days), and without assistance from passive removal strategies such as water flow or vertical orientation. The ability to tolerate this level of sediment loading under these conditions establishes this species as a true sediment specialist. Furthermore, results such as these demonstrate that not all corals are negatively impacted by direct sedimentation (other than by complete smothering) and lends support to the view that sedimentation does not necessarily impact this species to the magnitude previously perceived for coral reefs in general (Dodge and Vaisnys, 1977; Cortès and Risk, 1985; *reviewed by* Rogers, 1990).

In the second study, both *T. mesenterina* and *M. digitata* demonstrated sediment specialist characteristics by handling very high levels (≅ 250 mg cm^{-2} d^{-1}) of sediment, for 15 days, without any detectable physiological response in coral growth (buoyant weight), lipid content, or chlorophyll concentrations. It is not surprising, therefore, that both *T. mesenterina* and *M. digitata* can often dominate reefs along the turbid inshore waters of the GBR (Osborne, *et. al.*, 1997; pers. obs.). Both species, however, did show physiological sensitivity to changes in irradiance and water temperature treatments. Based on these results, I hypothesize that the abundance of these species is significantly

less along the clear water reefs of the mid- and outer-shelf of the GBR where irradiance is often significantly greater (assuming equivalent depth ranges at areas of comparison) and the advantages of utilizing sediment specialist strategies are reduced. I believe that it would be beneficial for future studies in this area to investigate the relative abundance of these species in connection to the environmental conditions in which they are located. The information collected in such a study could further the current understanding of these species and the niche they fill, and the role that they play in the function of reef ecosystems on both local and geographic scales. Furthermore, I believe that this increased understanding may prove critical to further enable management agencies and other interested stakeholders to more accurately predict the future of coral reef change in response to local, regional, and global environmental stressors (e.g. coastal development to global climate change).

In the third portion of this study, the plating species, *M. tuberculosa*, showed a biological response to the sediment treatments (up to ≅ 215 mg cm^{-2} d^{-1} for 15 days), including colony bleaching and tissue necrosis. Interestingly, a significant trend was observed where the percentage of colony bleached increased in direct correspondence to increasing sediment concentrations. No increased bleaching response, however, was detected for colonies of *A. formosa* or *P. cylindrica* that were exposed to the same sediment concentrations along the same gradient. This illustrates the susceptibility of this particular species to increased sedimentation and provides further support for the hypothesis that sedimentation acts as a mechanism for community change on coral reefs (Roy and Smith, 1971; Acevedo *et. al.*, 1989; Babcock and Davies, 1991; Riegl and Bloomer, 1995; Hubbard, 1996; Brown, 2000). More specifically, I propose that sedimentation acted as a negative selective pressure against the *M. tuberculosa* and that with time, this species would have decreased in abundance and/or have been removed from the reef all together. Thus, more sediment tolerant species such as the *A. formosa* or *P. cylindrica* could then exploit these new conditions to become more dominant along the reef. This issue is complicated, however, by the potential for acclimatization in corals, particularly if a colony only suffers partial mortality. Although unlikely, this does create a potential for individual colonies and populations to acclimatize to new conditions and recover to (or near) pre-event abundance and distribution along the reef.

A new method for the application of sediments to coral reefs *in situ* was also described and has shown to be an effective means for manipulating sediment conditions along coral reefs. Although there was some variation between the predicted and actual

sedimentation rates, it can be accounted for and minimized by accounting for turbid water flow within the predictive model. Carefully studying and understanding local water flow conditions prior to the installation can facilitate optimal positioning and can also improve the performance of the erosion block. I believe that the erosion block technique described has great potential to stimulate new research into this field and facilitate long-term sediment application studies with significantly lower cost and effort than previously practicable.

Ultimately, this study has indicated that not all corals are created equal in regard to sedimentation, that there are some corals that may be considered 'sediment specialists', and that this group should includes *T. mesenterina* and *M. digitata* from the inshore reefs of the GBR. Furthermore, this study underlines the point that the effects of sedimentation on coral reefs are not clearly defined. Indeed, coral tolerance to sedimentation may be dependent on multiple factors including the:

- environmental and biological history of the area;
- species composition of the reef;
- degree, severity, and duration of the changing of environmental conditions;
- life history strategies of the individual corals on the reef and their ability to tolerate and/or acclimatize to changing environmental conditions; and
- degree and severity of the changing of environmental conditions

Through investigation of the effect of irradiance and water temperature on the sediment tolerance of these sediment specialist species, as well as the application of sediment *in situ*, results from this study have also provided additional incite into the future of community structure. Specifically, the potential for sediment to act as a negative selection agent that I observed within the *in situ* sediment experiment (Brown 1997; Brown 2000; Fabricius and McCorry, 2006) in combination with the lack of physiological stress response of *T. mesenterina* and *M. digitata* to high sediment treatments under increased environmental stressors (Lasker, 1980; Rogers, 1990; Pittock, 1999; Pockley, 2000; Berkelmans, 2002; Pandolfi *et. al.*, 2003; Baker *et. al.*, 2004; Lesser and Farrel, 2004) suggest that that the biological role and function of these sediment specialist may become increasingly important as environmental conditions on coral reefs globally decline (Pandolfi et. al., 2003) from what are normally considered ideal (Coles, *et. al.*, 1976; Gleason and Wellington, 1993; Grigg *et. al.*, 1984; Grigg and Dollar, 1990; Berkelmans and Willis, 1999; Lirman *et. al.*, 2003).

Finally, I believe that the new method for sediment application *in situ* presented here has considerable potential to prompt additional study in the field of sedimentation on corals and coral reefs and it is my hope that this new method, and results presented in this study, may eventually serve to enhance the management and protection of these valuable ecosystems.

REFERENCES

Acevedo, R., J. Morelock, and J.A. Olivieri. 1989. Modification of coral reef zonation by terrigenous sediment stress. PALAIOS. 4:92-100.

Alongi, D.M. and A.D. McKinnon. 2005. The cycling and fate of terrestrially-derived sediments and nutrients in the coastal zone of the Great Barrier Reef. Marine Pollution Bulletin. 51(1-4):239-252.

Anthony. K. R. N. 1999. Sediment stress factor or food source for reef corals. PhD thesis, James Cook University, Townsville, Australia.

Anthony, K.R.N. 1999 (a). A tank system for studying benthic aquatic organisms at predictable levels of turbidity and sedimentation: Case study examining coral growth. Limnology and Oceanography. 44(6):1415-1422.

Anthony, K.R.N. 1999 (b). Coral suspension feeding on fine particulate matter. Journal of Experimental Marine Biology and Ecology. 232:85-106.

Anthony, K.R.N. 2000. Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). Coral Reefs. 19:59-67.

Anthony, K.R.N., and S.R. Connolly. 2004. Environmental limits to growth: physiological niche boundaries of corals along turbidity-light gradients. Oecologia. 141:373-384.

Anthony K.R.N., S.R. Connolly, and B.L. Willis. 2002. Comparative analysis of tissue and skeletal growth in corals. Limnology and Oceanography. 47:1417-1429.

Anthony, K.R.N. and K.E. Fabricius. 2000. Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. Journal of Experimental Marine Biology and Ecology. 252:221-253.

Anthony, K.R.N., P.V. Ridd, A. Orpin, P. Larcombe, and J.M. Lough. 2004. Temporal variation in light availability in coastal benthic habitats: effects of clouds, turbidity and tides. Limnology and Oceanography. 49:2201-2211.

Anthony, K.R.N. and P. Larcombe. 2001. Coral reefs in turbid waters: sediment-induced stresses in corals and likely mechanisms of adaptation. Proceedings of the 9th International Coral Reef Symposium, Bali. October 23-27. (2):239-244.

Aronson, R.B. and W.F. Precht. 1995. Community change on a coral reef: First time in 3400 years. Twenty-Third Benthic Ecology Meeting, New Brunswick, NJ (USA), 17-19 Mar 1995.

Atkinson, M.I., E. Kotler, and P. Newton. 1994. Effects of water velocity on respiration, calcification, and ammonium uptake of a *Porites compressa* community. Pacific Science. 48(3):296-303.

Babcock, R. and P. Davies. 1991. Effects of sedimentation on settlement of *Acropora millepora*. Coral Reefs. 9:205-208.

Baker, A.C., C.J. Starger, T.R. McClanahan, and P.W. Glynn. 2004. Coral Reefs: Coral's Adaptive Response to Climate Change. Nature. 430(7001):741.

Barnes, D.J. and B.E. Chalker. 1990. Calcification and photosynthesis in reef-building corals and algae. In *Coral Reefs* (ed Dubinsky Z). Ecosystems of the World 25, Elsevier, Amsterdam. 109-131.

Beardall, J. and J.A. Raven. 2004. The Potential Effects of Global Climate Change on Microalgal Photosynthesis, growth and ecology. Phycologia. 43(1):26-40.

Berkelmans, R. 2002. Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. Marine Ecology Progress Series. 229:73-82.

Berkelmans, R. and B.L. Willis. 1999. Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef. Coral Reefs. 18:219-228.

Bernhard, R.C., C. Heine, and G.M. Branch. 1996. Function of funnel-shaped coral growth in a high-sediment environment. Marine Ecology Progress Series. 145:87-93.

Brown, B.E. 1997. Disturbances to reefs in recent times. Birkeland C (ed.) Life and dealth of coral reefs. Chapman and Hall Inc, New York. 354-385.

Brown, B.E. 2000. The significance of pollution in eliciting the 'bleaching' response in symbiotic cnidarians. International Journal of Environment and Plllution. 13(1-6):392-415.

Brown, B.E. and L.S. Howard. 1985. Assessing the effects of 'stress' on reef corals. Advances in Marine Biology. 22:1-63.

Brown, B.E. and J.C. Ogden. 1993. Coral bleaching. Scientific American. 268:64-70.

Bruno, J.F. and P.J. Edmunds. 1998. Metabolic consequences of phenotypic plasticity in the coral *Madracis mirabilis* (Duchassaing and Michelotti): the effect of morphology and water flow on aggregate respiration. Journal of Experimental Marine Biology and Ecology. 229:187-195.

Buddemier, R.W. and D.G. Fautin. 1993. Coral bleaching relative to elevated seawater temperature in the Andaman Sea (Indian Ocean) over the last 50 years. Coral Reefs. 15:151-152.

Chalker, B.E. and W.C. Dunlap. 1981. Extraction and quantitation of endosymbiotic algal pigments from reef-building corals. Proceedings of the 4th International Coral Reef Symposium, Manila. 2:45-50.

Chappone, M., K. Sullivan-Sealey., G. Bustamante, and J. Tschirky. 1999. A rapid assessment of coral reef community structure and diversity patterns at a naval station in Guantanamo Bay Cuba. International Conference on Scientific Aspects of Coral Reef Assessment, Monitoring, and Restoration. Ft. Lauderdale, Florida (USA), 1999.

Coles, S.L., P.L. Jokiel, and C.R. Lewis. 1976. Thermal tolerance in tropical versus subtropical pacific reef corals. Pacific Science. 30(2):159-166.

Cortès, J.N., and M.J. Risk. 1985. A Reef Under Siltation Stress: Cahuita, Costa Rica. Bulletin of Marine Science. 36(2):339-356.

Costanza, R., R. d' Arge, R. de Groot, S. Farbar, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neilll, J. Parnero, R.G. Raskin, P. Sutton, M. Van den Belt. 1997. The value of the wold's ecosystems services. Nature. 387:253-260.

Coutinho, R., R.C. Villaca, C.A. Magalhaes, M.A. Guimaraens, M. Apolinario, and G. Muricy. 1993. Man-Made effects on the coraline ecosystems of the Abrolhos region, Bahia Brazil. Acta Biol. Leopold. 15(1):133-144.

Craig, P., C. Birkeland, and S. Belliveau. 2004. High temperatures tolerated by a diverse assemblage of shallow-water corals in American Samoa. Coral Reefs. 20(2):185-189.

Davies, P.S. 1989. Short-term growth measurements of corals using an accurate buoyant weighing technique. Marine Biology. 101:389-395.

Davies, P.S. 1990. A rapid method for assessing growth rates of corals in relation to water pollution. Marine Pollution Bulletin. 21(7):346-348.

Dennison, W.C. and D.J. Barnes. 1998. Effect of water motion on coral photosynthesis and calcification. Journal of Experimental Marine Biology and Ecology. 115:66-77.

Devlin, M., J. Waterhouse, and J. Brodie. 2000. Terrestrial discharge into the Great Barrier Reef: Distribution of riverwaters and pollutant concentrations during flood plumes. Proceedings of the 9th International Coral Reef Symposium, Bali, Indonesia, October 23-27. 2:1205-1211.

Dodge, R.E. 1982. Effects of drilling mud on the reef-building coral *Montastrea annularis*. Marine Biology. 71:141-147.

Dodge, R.E. and J.R. Vaisnys. 1977. Coral populations and growth patterns: Responses to sedimentation and turbidity associated with dredging. Journal of Marine Research. 35(4):715-730.

Done, T.J. 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs. 1(2):95-107.

Edinger, E.N., G.V. Limmon, J. Jompa, W. Widjatmoko, J.M. Heikoop, and M.J. Risk. 2000. Normal growth rates on dying coral reefs: Are coral growth rates good indicators of reef health? Marine Pollution Bulletin. (5):404-425.

Egana, A.C. and L.H. DiSalvo. 1982. Mass expulsion of zooxanthellae by Easter Island corals. Pacific Science. 36:61-63.

Fabricius, K.E. and D. McCorry. 2006. Changes in octocoral communities and benthic cover along a water quality gradient in the reefs of Hong Kong. Marine Pollution Bulletin. 52(1):22-33.

Fitt, W.K. and M.E. Warner. 1995. Bleaching patterns of four species of Caribbean reef corals. Biological Bulletin, Marine Biological Laborator, Woods Hole. 189(3):298-307.

Folch, J., M. Lees, and G.H. Sloane Stanley. 1957. A simple method for the isolation and purification of total lipidses from animal tissues. Journal of Biological Chemistry. 226: 497-509.

Foster, A.B. 1980. Environmental variation in skeletal morphology within the Caribbean reef corals *Montastrea annularis* and *Siderastrea sidereal*. Bulletin of Marine Science, 30(3), 678-709

Furnas M. 2003. Catchments and corals: terrestrial runoff to the Great Barrier Reef. Australian Institute of Marine Science.

Gleason, D.F. and G.M. Wellington. 1993. Ultraviolet radiation and coral bleaching. Nature. 365:835-838.

Glynn, P.W. 1996. Coral reef bleaching: facts, hypotheses and implications. Global Change Biology. 2:495-509.

Gibbs, R.J., M.D. Matthews, and D.A. Link. 1971. The relationship between sphere size and settling velocity. Journal of Sedimentary Petrology. 41(1):7-18.

Graus, R.R. and I.G. Macintyre. 1989. The zonation patterns of Caribbean coral reefs as controlled by wave and light energy input, bathymetric setting and reef morphology: Computer simulation experiments. Coral Reefs. 8(1):1-12.

Grigg, R.W. 1981. Coral reef development at high latitudes in Hawaii. The Reef and Man. Proceedings of the 4th International Coral Reef Symposium, Manila. 1:687-694.

Grigg, R.W., J.J. Polovina, and M.J. Atkinson. 1984. Model of a coral reef ecosystem III. Resource limitation, community regulation, fisheries yield and resource management. Coral Reefs. 3(1):439-452.

Grigg, R.W. and S.J. Dollar. 1990. Natural and anthropogenic disturbance on coral reefs. In *Coral Reefs* (ed Dubinsky Z). Ecosystems of the World 25, Elsevier, Amsterdam. :109-131.

Harland, A.D., P.S., Davies, and L.M. Fixter. 1992. Lipid content of some Caribbean corals in relation to depth and light. Marine Biology. 113:357-361.

Harmelin-Vivien, M.L. 1994. The effects of storms and cyclones on coral reefs: A review. Journal of Coastal Research, Special Issue 12:211-231.

Helmuth, B.S.T., K.P. Sebens, T.L. Daniel. (a). 1997. Morpological variation in coral aggregations: Branch spacing and mass flux to coral tissues. Journal of Experimental Marine Biology and Ecology. 2(1-2):233-259.

Helmuth, B.S.T., B.E.H. Timmerman, K.P. Sebens. (b). 1997. Interplay of host morphology and symbiont microhabitat in coral aggregations. Marine Biology. 130(1):1-10.

Hodgson, D. 1990. Tetracycline reduces sedimentation damage to corals. Marine Biology. 104:493-496.

Hoegh-Guldberg, O. and R.J. Jones. 1999. Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. Marine Ecology Progress Series. 183:73-86.

Hubbard, D.K. 1986. Sedimentation as a control of reef development St. Croix, U.S.V.I. Coral Reefs. 5:117-125.

Hubbard, D.K. and D. Scaturo. 1985. Growth rates of seven species of scleractinian corals from Cane Bay and Salt River, St. Croix, USVI. Bulletin of Marine Science. 36(2):325-338.

Hunter, C.L. and C.W. Evans. 1995. Coral reefs in Kaneohe Bay, Hawaii: Two centuries of western influence and two decades of data. Bulletin of Marine Science. 57(2):501-515.

Hudson, M.A. 1985. Patterns of species diversity on coral reefs. Annual Review of Ecology and Systematics. 16:149-177.

Jameson, S.C., J.W. McManus and M.D. Spalding. 1995. State of the Reefs: Regional and Global Perspectives. United States Department of State. Washington, DC.

Jeffrey, S.W. and G.F. Humphrey. 1975. New spectrophotometric equations for determining chlorophyll a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochemistry Physiology Pfranzen. 167:191-194.

Jokiel, P.L., J.E. Margos, and L. Franzisket. 1978. Coral growth: buoyant weight technique. Monogr. Oceanogr. Methodol. 5:529-542.

Jokiel P.L. and S.L. Coles. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs. 8:155-162.

Jokiel, P.L., and J.I. Morrissey. 1993. Water motion on coral reefs: Evaluation of the “clod card” technique. Marine Ecology Progress Series. 93(1-2):175-181.

Johns, G.M., V.R. Leeworthy, F.W. Bell, and M.A. Bonn. 2001. Socioeconomic study of reefs in southeast Florida. Florida Fish and Wildlife Conservation Commission and National Oceanic and Atmospheric Administration, final Report for Broward County, Palm Beach County, Miami-Dade County and Monroe County.

Jones, R.J., O. Hoegh-Guldberg, A.W.D. Larkum, and U. Schreiber. 1998. Temperature-induced bleaching of corals begins with impairment of the CO2 fixation mechanism in zooxanthellae. Plant Cell and Environment. 21:1219-1230.

Jones, R.J, T. Kildea, and O. Hoegh-Guldberg. 1999. PAM Chlorophyll Fluorometry: A New *in situ* Technique for Stress Assessment in Scleractinian Corals, used to Examine the Effects of Cyanide from Cyanide Fishing. Marine Pollution Bulletin. 38(10):864-874.

Jurg B. 1996. Towards a new generation of sediment traps and a better measurement/understanding of settling particle flux in lakes and oceans: A hydrodynamical protocol. Aquatic Sciences 58: 283-296

Kleypas, J.A. 1996. Coral reef development under naturally turbid conditions: fringing reefs near Broad Sound, Australia. Coral Reefs. 15:153-167.

Kuffner, I.B. 2001. Effects of ultraviolet radiation and water motion on the reef coral *Porites compressa* (Dana): A flume experiment. Marine Biology. 138(3):467-476.

Kuhlmann, D.H.H. 1983. Composition and ecology of deep water coral associations. Helgoland Marine Research. 36(2):183-204.

Larcombe, P., P.V. Ridd, A. Prytz, and B. Wilson. 1995. Factors controlling suspended sediment on inner-shelf coral reefs, Townsville, Australia. Coral Reefs. 14:163-171.

Larcombe, P., A. Costen, and K.J. Woolfe. 2001. The hydrodynamic and sedimentary setting of nearshore coral reefs, central Great Barrier Reef shelf, Australia: Paluma Shoals, a case study. Sedimentology. 48(4):811-835.

Lasker, H.R. 1980. Sediment rejection by reef corals: The roles of behavior and morphology in *Montastrea cavernosa* (Linnaeus). Journal of Experimental Marine Biology and Ecology. 47:77-87.

Lesser, M.P., V. M. Weis, M.B. Patterson, and P. Jokiel. 1994. Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): diffusion barriers, inorganic carbon limitation, and biochemical plasticity. Journal of Experimental Marine Biology and Ecology. 178:153-179.

Lesser, M.P. and J.H. Farrell. 2004. Exposure to Solar Radiation Increases Damage to Both Host Tissues and Algal Symbionts of Corals During Thermal Stress. Coral Reefs. 24(3):367-377.

Lirman, D., B. Orlando, S. Marcia, D. Manzello, L. Kaufman, P. Biber, and T. Jones. 2003. Coral communities of Biscayne Bay, Florida and adjacent offshore areas: diversity, abundance, distribution, and environmental correlates. Aquatic Conservation: Marine and Freshwater Ecosystems. 13(2):121-135.

Lucan, E.M. 2006. Acropora formosa, Staghorn Acropora. Dr. Jungle's Animial World, Coral Reefs Library. Web Reference: http://animal-world.com/encyclo/reef/sm_stony/AcroporaFormosa.php

Lough, J.M. 2000. 1997-1998: Unprecedented themal stress to coral reefs? Geophysical Resesearch Letters. 27(23):3901-3904.

Marshall, P.A. and A.H. Barid. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs. 19(2):155-163.

Marubini, F. and B. Thake.1999. Bicarbonate addition promotes coral growth. Limnology and Oceanography. 44(3):716-720.

McClanahan, T.R. and D. Obura. 1997. Sedimentation effects on shallow coral communities in Kenya. Journal of Experimental Marine Biolgoy and Ecology. 209:103-122.

McCulloch, M., C. Pailles, P. Moody, and C.E. Martin. 2003. Tracing the source of sediment and phosphorus into the Great Barrier Reef lagoon. Earth and Planetary Science Letters. 210(1-2):249-258.

Meesters, E.H., G. Nieuwland, G.C.A. Duineveld, A. Kok, R.P.M. Bak. 2002. RNA/DNA ratios of scleractinian corals suggests acclimatisation / adaptation in relation to light gradients and turbidity regimes. Marine Ecology Progress Series. 227:233-239.

Montebon, A.R.F. and H.T. Yap. 1992. Metabolic responses of *Porites cylindrica* (Dana) to water motion. Proceedings of the 7th International Coral Reef Symposium, Guam. 1:381-382.

Mumby, P.J., J. Chisholm, A.J. Edwards, S Andrefouet, and J. Jaubert. 2001. Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. Marine Ecology Progress Series. 222: 209-216.

Muscatine, L. 1990. The role of symbiotic algae in carbon and energy flux in reef corals. In Dubinsky Z (ed) *Coral Reefs*: Ecosystems of the World, Volume 25. Elsevier Science, Amsterdam. :75-87

Nesteroff, W.D. 1955. Some geological results from the Calypso cruise to the Red Sea. Deep-Sea Research. 2(4):274-283.

Norse, E. 1993. Global Marine Biodiversity. Norway (UNEP) Expert Conference on Biodiversity Directorate for Nature Management, Trondheim (Norway). :41-43.

Nyström, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance & resilience in human dominated environment. Trends in Ecology and Evolution. 15:413-447.

Osborne, K., R. Ninio, and H. Sweatman. 1997. The current status of sessile benthic organisms on the Great Barrier Reef. Australian Institute of Marine Science. PMB No. 3. Townsville, Queensland Australia.

Ostrander, G.K., K.M. Armstrong, E.T. Knobbe, D. Gerace, and E.P. Scully. 2000. Rapid transition in the structure of a coral reef community: the effects of coral bleaching and physical disturbance. Proceedings of the National Academy of Sciences, USA. 97(10):5297-5302.

Pandolfi, J.M., R.H. Bradbury, E. Sala, T.P. Hughes, K.A. Bjorndal, R.G. Cooke, D. McArdle, L. McClenachan, M.J.H. Newman, G. Paredes, R. Warner, and J. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science. 301:955-958.

Pastorok, R.A. and G.R. Bilyard. 1985. Effects of sewage pollution on coral-reef communities. Marine Ecology Progress Series. 21:175-189.

Patterson, M.R., K.P. Sebens, and R. Randolph Olson. 1991. *In situ* measurements of flow effects on primary production and dark respiration in reef corals. Limnology and Oceanography. 36:936-48.

Phillip, E. and K. Fabricius. 2003. Photophysiological stress in scleractinian corals in response to short-term sedimentation. Journal of Experimental Marine Biology and Ecology. 287(1):57-78.

Pittock, A.B. 1999. Coral reefs and environmental change: Adaptation fo what? American Zoologist. (1):10-29.

Pockley, P. 2000. Global warming identified as main threat to coral reefs. Nature. 407(6807):932.

Ralph, P.J., R.J. Gademann, A.W.D. Larkum, and U. Schreiber. 1999. *In situ* underwater measurements of photosynthetic activity of coral zooxanthellae and other reef-dwelling dinoflagellate endosymbionts. Marine Ecology Progress Series. 180:139-147.

Reaka-Kudla, M.L., D.E. Wilson, E.O. Wilson. 1997. The Global Biodiversity of Coral Reefs: A Comparison with Rain Forests. Biodiversity II. Eds. (Joseph Henry Press, Washington, DC). :83-108.

Redalje, R. 1976. Light adaptation strategies of hermatypic corals. Pacific Science. 30(3):212.

Riegl, B. and J.P. Bloomer. 1995. Tissue damage in scleractinian and alcyonacean corals due to experimental exposure to sedimentation. Beits Palaont. 20:51-63.
Riegl, B. and G.M. Branch. 1995. Effects of sediment on the energy budgets of four scleractinian and five alcyonacean corals. Journal of Experimental Marine Biology and Ecology. 186(2):259.

Richmond, R.H. 1993. Coral Reefs: Present Problems and Future Concerns Resulting from Anthropogenic Disturbance. American Zoology. 33:524-536.

Rogers, C.S. 1979. The effect of shading on coral reef structure and function. Journal of Experimental Marine Biology and Ecology. 41(3):269-288.

Rogers, C.S. 1983. Sublethal and lethal effects of sediments applied to common Caribbean reef corals in the field. Marine Pollution Bulletin. 14(10):378-382.

Rogers, C.S. 1990. Responses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series. 62:185-202.

Rosenfeld M, V. Bresler, and A Abelson. 1999. Sediment as a possible source of food for corals. Ecology Letters. 2:345-348.

Roth, A.A., C.D. Clausen, P.Y. Yahiku, V.E. Clausen, and W.W. Cox. 1982. Some effects of light on coral growth. Pacific Science. 36(1):65-82.

Rowan, R. 2004. Coral Bleaching: Thermal Adaptation in Reef Coral Symbionts. Nature. 430(7001):742.

Roy, K.J. and S.V. Smith. 1971. Sedimentation and coral reef development in turbid water: Fanning Lagoon. Pacific Science. 25(2):234-248.

Sakai, K. and M. Nishihira. 1991. Immediate effect of terrestrial runoff on a coral community near a river mouth in Okinawa. Galaxea. 10(2):125-134.

Schrage, J. and C.A. Clayson. 2003. Precipitation and freshwater lens formation in the tropical western pacific (2003-12ISA). In: *Abstract Volume, 83rd AMS Annual Meeting,* 9-13 February 2003. Long Beach CA., American Meteorological Society., Boston, MA. 12:309-310.

Sebens, K.P., I. Witting, and B. Helmuth. 1997. Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). Journal of Experimental Marine Biology and Ecology. 211(1):1-28.

Stafford-Smith, M.G. 1992. Mortality of the hard coral *Leptoria phrygia* under persistent sediment influx. Proceedings of the 7th International Coral Reef Symposium, 22-26 June 2006. Guam. 1:289-299.

Stafford-Smith, M.G. and R.F.G. Ormond. 1992. Sediment-rejection mechanisms of 42 species of Australian Scleractinian Corals. Marine and Freshwater Resources. 43:683-705.

Stokes, G. G. 1851. On the effect of the internal friction on the motion of pendulums. Cambridge Philo. Trans. 9(2):8-106.

Szmat, A.M. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries. 25(4B):743-766.

Teleki, K. 2000. Coral Grief? Coral bleaching and climate change. FOCUS archive, CERNet Newsletter.
24 November 2000.

V an Oppen, M. 2005. Molecular ecology of the coral-algal symbiosis. Australian Frontiers of Science, Walter and Elizabeth Hall Institute of Medical Research, Melbourne Australia, April 12 – 13, 2005.

Veron, J.E.N. and C.C. Wallace. 1984. Scleractinia of Eastern Australia. Australian Institute of Marine Scienc. Monograph Series. Townsville, Australia.

Veron, J.E.N. 1986 Corals of Australia and the Indo-Pacific . Angus & Robertson, Sydney.

Veron, J.E.N. 2000. Corals of the World. Australian Institute of Marine Science, Townsville.

Willis, B.L. 1985. Phenotypic plasticity versus phenotypic stability in the reef corals *Turbinaria mesenterina* and *Pavona cactus* Proceedings of the 5th International Coral Reef Congress, 27 May – 1 June, 1985, Tahiti. :107-112.

Woolfe, K.J., and P. Larcombe. 1998. Terrigenous sediment accumulation as a regional control on the distribution of reef carbonates. Special Publications of the International Association of Sedimentologists. 25:295-310.

APPENDIX A

Results of the mean growth rates, lipid concentrations, and PAM yields of Turbinaria under the various water flow and sediment treatments as described in Chapter 2.

Table A1: Means for the growth (g d^{-1}) of *T. mesenterina* under the water flow and sediments as described in Chapter 2.

Flow	Sediment	Mean	Std. Deviation	N	S.E.
Low	**Control**	1.7	0.4	12	0.1
	Low	1.7	0.6	11	0.2
	High	1.6	0.5	12	0.1
	Total	1.7	0.5	35	0.1
High	**Control**	1.6	0.6	11	0.2
	Low	1.9	0.4	11	0.1
	High	2.3	1.0	12	0.3
	Total	1.9	0.7	34	0.1
Total	**Control**	1.6	0.5	23	0.1
	Low	1.8	0.5	22	0.1
	High	2.0	0.8	24	0.2
	Total	1.8	0.6	69	0.1

Table A2: Means for the lipid concentrations (mg cm^{-2}) of *T. mesenterina* under the water flow and sediments as described in Chapter 2.

Flow	Sediment	Mean	Std. Deviation	N	S.E.
Low	**Control**	7.7	2.0	11	0.6
	Low	8.1	2.4	12	0.7
	High	7.2	2.3	11	0.7
	Total	7.7	2.2	34	0.4
High	**Control**	6.9	2.2	11	0.7
	Low	8.0	2.1	11	0.6
	High	7.0	1.8	11	0.5
	Total	7.3	2.0	33	0.4
Total	**Control**	7.3	2.1	22	0.4
	Low	8.0	2.2	23	0.5
	High	7.1	2.0	22	0.4
	Total	7.5	2.1	67	0.3

Table A3: Means for the PAM yields (Fv/Fm) of *T. mesenterina* under the water flow and sediments as described in Chapter 2.

Flow	Sediment	Mean	Std. Deviation	N	S.E.
Low	**Control**	0.585	0.043	12	0.012
	Low	0.603	0.045	12	0.013
	High	0.604	0.056	12	0.016
	Total	0.597	0.048	36	0.008
High	**Control**	0.609	0.040	11	0.012
	Low	0.590	0.063	11	0.019
	High	0.631	0.032	12	0.009
	Total	0.610	0.048	34	0.008
Total	**Control**	0.597	0.042	23	0.009
	Low	0.596	0.053	23	0.011
	High	0.618	0.046	24	0.009
	Total	0.604	0.048	70	0.006

APPENDIX B

Results of the mean growth rates, lipid concentrations, and chlorophyll concentrations of Turbinaria mesenterina and Montipora digitata under the various light, temperature, and sediment treatments as described in Chapter 3.

Table B1: Means for the growth (g d^{-1}) of *T. mesenterina* under the various light, temperature, and sediments as described in Chapter 3.

Light	Tem	Sed	Mean	Std. Deviation	N	S.E.
Unshaded	**Unheated**	**Control**	1.8	0.2	3	0.1
		High	0.7	0.5	3	0.3
		Very High	0.7	1.0	3	0.6
		Total	1.1	0.8	9	0.3
	Heated	**Control**	1.3	1.2	3	0.7
		High	1.3	1.2	3	0.7
		Very High	0.7	0.5	3	0.3
		Total	1.1	0.9	9	0.3
	Total	**Control**	1.6	0.8	6	0.3
		High	1.0	0.9	6	0.4
		Very High	0.7	0.7	6	0.3
		Total	1.1	0.8	18	0.2
Shaded	**Unheated**	**Control**	0.9	0.4	3	0.2
		High	0.7	0.1	3	0.1
		Very High	0.9	0.3	3	0.2
		Total	0.8	0.3	9	0.1
	Heated	**Constrol**	1.3	0.1	3	0.0
		High	0.9	0.1	3	0.1
		Very High	1.0	0.5	3	0.3
		Total	1.1	0.3	9	0.1
	Total	**Constrol**	1.1	0.4	6	0.1
		High	0.8	0.2	6	0.1
		Very High	1.0	0.4	6	0.2
		Total	1.0	0.3	18	0.1
Total	**Unheated**	**Constrol**	1.3	0.6	6	0.2
		High	0.7	0.3	6	0.1
		Very High	0.8	0.7	6	0.3
		Total	0.9	0.6	18	0.1
	Heated	**Control**	1.3	0.8	6	0.3
		High	1.1	0.8	6	0.3
		Very High	0.9	0.5	6	0.2
		Total	1.1	0.7	18	0.2
	Total	**Control**	1.3	0.6	12	0.2
		High	0.9	0.6	12	0.2
		Very High	0.8	0.5	12	0.2

Table B2: Means for the growth (g d^{-1}) of *M. digitata* under the various light, temperature, and sediments as described in Chapter 3.

Light	Tem	Sed	Mean	Std. Deviation	N	S.E.
Unshaded	**Unheated**	**Control**	2.0	0.7	3	0.4
		High	1.7	0.4	3	0.2
		Very High	0.7	1.2	3	0.7
		Total	1.5	0.9	9	0.3
	Heated	**Control**	2.3	0.6	3	0.4
		High	1.7	0.7	3	0.4
		Very High	2.0	0.6	3	0.3
		Total	2.0	0.6	9	0.2
	Total	**Control**	2.2	0.6	6	0.3
		High	1.7	0.5	6	0.2
		Very High	1.3	1.1	6	0.4
		Total	1.7	0.8	18	0.2
Shaded	**Unheated**	**Control**	1.1	0.5	3	0.3
		High	1.0	0.5	3	0.3
		Very High	1.6	0.6	3	0.4
		Total	1.2	0.5	9	0.2
	Heated	**Control**	1.5	0.4	3	0.2
		High	1.0	0.3	3	0.2
		Very High	1.3	0.9	3	0.5
		Total	1.3	0.6	9	0.2
	Total	**Control**	1.3	0.5	6	0.2
		High	1.0	0.3	6	0.1
		Very High	1.5	0.7	6	0.3
		Total	1.3	0.5	18	0.1
Total	**Unheated**	**Constrol**	1.6	0.7	6	0.3
		High	1.3	0.5	6	0.2
		Very High	1.1	1.0	6	0.4
		Total	1.3	0.8	18	0.2
	Heated	**Constrol**	1.9	0.6	6	0.3
		High	1.4	0.6	6	0.3
		Very High	1.7	0.8	6	0.3
		Total	1.7	0.7	18	0.2
	Total	**Constrol**	1.8	0.7	12	0.2
		High	1.4	0.5	12	0.2
		Very High	1.4	0.9	12	0.3

Table B3: Means for the lipid concentration (mg cm^{-2}) of *T. mesenterina* under the various light, temperature, and sediments as described in Chapter 3.

Light	Tem	Sed	Mean	Std. Deviation	N	S.E.
Unshaded	**Unheated**	**Control**	9.3	0.6	3	0.3
		High	8.1	1.2	3	0.7
		Very High	8.7	0.6	3	0.4
		Total	8.7	0.9	9	0.3
	Heated	**Control**	9.5	1.2	3	0.7
		High	9.7	3.2	3	1.8
		Very High	9.2	0.4	3	0.2
		Total	9.5	1.7	9	0.6
	Total	**Control**	9.4	0.8	6	0.3
		High	8.9	2.3	6	1.0
		Very High	9.0	0.5	6	0.2
		Total	9.1	1.4	18	0.3
Shaded	**Unheated**	**Control**	13.0	4.0	3	2.3
		High	11.3	1.5	3	0.9
		Very High	12.5	0.8	3	0.4
		Total	12.3	2.3	9	0.8
	Heated	**Control**	14.5	1.9	3	1.1
		High	14.0	1.5	3	0.9
		Very High	13.9	2.1	3	1.2
		Total	14.2	1.6	9	0.5
	Total	**Control**	13.8	2.9	6	1.2
		High	12.7	2.0	6	0.8
		Very High	13.2	1.6	6	0.7
		Total	13.2	2.2	18	0.5
Total	**Unheated**	**Control**	11.2	3.3	6	1.3
		High	9.7	2.1	6	0.9
		Very High	10.6	2.2	6	0.9
		Total	10.5	2.5	18	0.6
	Heated	**Control**	12.0	3.1	6	1.2
		High	11.9	3.3	6	1.3
		Very High	11.6	2.9	6	1.2
		Total	11.8	2.9	18	0.7
	Total	**Control**	11.6	3.1	12	0.9
		High	10.8	2.9	12	0.8
		Very High	11.1	2.5	12	0.7

Table B4: Means for the lipid concentration (mg cm^{-2}) of *M. digitata* under the various light, temperature, and sediments as described in Chapter 3.

Light	Tem	Sed	Mean	Std. Deviation	N	S.E.
Unshaded	**Unheated**	**Control**	4.8	1.5	3	0.8
		High	5.6	2.7	3	1.5
		Very High	5.5	1.6	3	0.9
		Total	5.3	1.8	9	0.6
	Heated	**Control**	4.7	1.9	3	1.1
		High	4.4	0.5	3	0.3
		Very High	4.2	0.1	3	0.1
		Total	4.4	1.0	9	0.3
	Total	**Control**	4.7	1.5	6	0.6
		High	5.0	1.8	6	0.8
		Very High	4.9	1.3	6	0.5
		Total	4.9	1.5	18	0.3
Shaded	**Unheated**	**Control**	5.1	1.3	3	0.8
		High	7.1	1.8	3	1.0
		Very High	6.4	3.0	3	1.8
		Total	6.2	2.1	9	0.7
	Heated	**Control**	6.0	1.0	3	0.6
		High	5.9	2.2	3	1.2
		Very High	5.7	1.7	3	1.0
		Total	5.9	1.5	9	0.5
	Total	**Control**	5.6	1.1	6	0.5
		High	6.5	1.9	6	0.8
		Very High	6.1	2.2	6	0.9
		Total	6.0	1.7	18	0.4
Total	**Unheated**	**Control**	5.0	1.3	6	0.5
		High	6.4	2.2	6	0.9
		Very High	6.0	2.2	6	0.9
		Total	5.8	1.9	18	0.5
	Heated	**Control**	5.4	1.5	6	0.6
		High	5.1	1.6	6	0.7
		Very High	5.0	1.4	6	0.6
		Total	5.1	1.4	18	0.3
	Total	**Control**	5.2	1.4	12	0.4
		High	5.7	1.9	12	0.6
		Very High	5.5	1.8	12	0.5

Table B5: Means for the chlorophyll concentration (mg cm^{-2}) of *T. mesenterina* under the various light, temperature, and sediments as described in Chapter 3.

Light	Tem	Sed	Mean	Std. Deviation	N	S.E.
Unshaded	**Unheated**	**Control**	128.0	15.7	3	9.1
		High	115.6	26.4	3	15.2
		Very High	102.4	19.2	3	11.1
		Total	115.4	21.2	9	7.1
	Heated	**Control**	101.4	16.8	3	9.7
		High	136.4	57.6	3	33.3
		Very High	117.2	10.3	3	6.0
		Total	118.4	34.0	9	11.3
	Total	**Control**	114.7	20.6	6	8.4
		High	126.0	41.7	6	17.0
		Very High	109.8	16.0	6	6.5
		Total	116.9	27.6	18	6.5
Shaded	**Unheated**	**Control**	200.1	28.5	3	16.5
		High	189.8	38.4	3	22.2
		Very High	173.4	31.4	3	18.2
		Total	187.8	30.9	9	10.3
	Heated	**Control**	172.3	20.5	3	11.8
		High	187.4	25.0	3	14.4
		Very High	164.5	53.0	3	30.6
		Total	174.7	32.6	9	10.9
	Total	**Control**	186.2	26.9	6	11.0
		High	188.6	29.0	6	11.8
		Very High	169.0	39.3	6	16.0
		Total	181.2	31.6	18	7.4
Total	**Unheated**	**Control**	164.1	44.5	6	18.2
		High	152.7	50.2	6	20.5
		Very High	137.9	45.3	6	18.5
		Total	151.6	45.3	18	10.7
	Heated	**Control**	136.9	42.3	6	17.3
		High	161.9	48.5	6	19.8
		Very High	140.9	42.9	6	17.5
		Total	146.5	43.4	18	10.2
	Total	**Control**	150.5	43.8	12	12.6
		High	157.3	47.3	12	13.7
		Very High	139.4	42.1	12	12.1

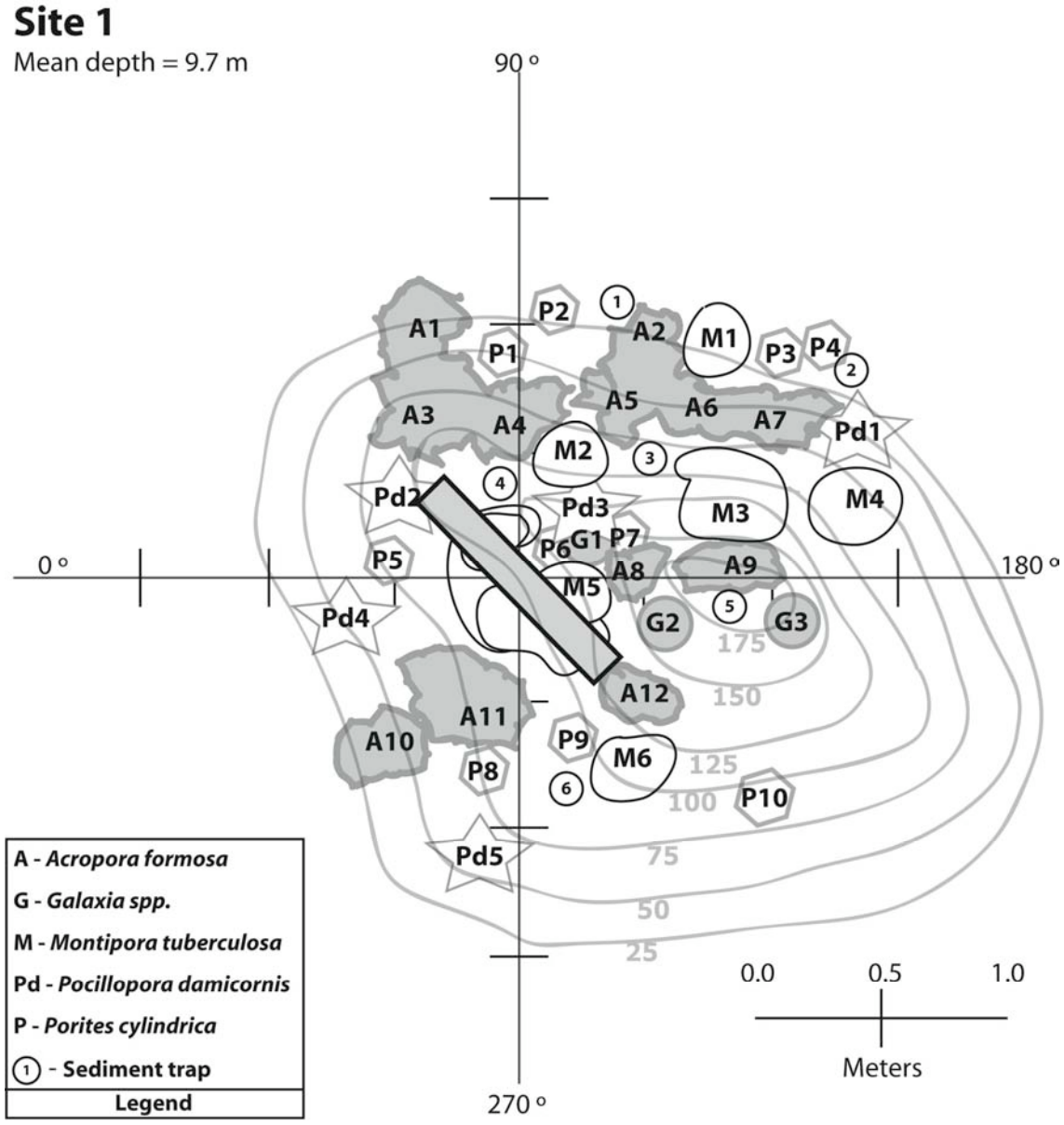
Table B6: Means for the chlorophyll concentration (mg cm^{-2}) of *M. digitata* under the various light, temperature, and sediments as described in Chapter 3.

Light	Tem	Sed	Mean	Std. Deviation	N	S.E.
Unshaded	**Unheated**	**Control**	82.0	30.6	3	17.7
		High	66.5	19.0	3	11.0
		Very High	79.9	21.8	3	12.6
		Total	76.1	22.3	9	7.4
	Heated	**Control**	33.6	9.0	3	5.2
		High	27.5	3.0	3	1.7
		Very High	33.3	2.2	3	1.3
		Total	31.4	5.7	9	1.9
	Total	**Control**	57.8	33.3	6	13.6
		High	47.0	24.6	6	10.1
		Very High	56.6	29.0	6	11.9
		Total	53.8	27.9	18	6.6
Shaded	**Unheated**	**Control**	63.5	18.6	3	10.8
		High	71.6	12.5	3	7.2
		Very High	70.1	26.9	3	15.6
		Total	68.4	17.9	9	6.0
	Heated	**Control**	81.5	10.3	3	6.0
		High	74.5	15.5	3	9.0
		Very High	53.6	4.5	3	2.6
		Total	69.9	15.8	9	5.3
	Total	**Control**	72.5	16.7	6	6.8
		High	73.0	12.7	6	5.2
		Very High	61.8	19.5	6	8.0
		Total	69.1	16.4	18	3.9
Total	**Unheated**	**Control**	72.8	24.8	6	10.1
		High	69.1	14.7	6	6.0
		Very High	75.0	22.6	6	9.2
		Total	72.3	20.0	18	4.7
	Heated	**Control**	57.5	27.7	6	11.3
		High	51.0	27.6	6	11.3
		Very High	43.4	11.5	6	4.7
		Total	50.6	22.9	18	5.4
	Total	**Control**	65.2	26.3	12	7.6
		High	60.0	23.1	12	6.7
		Very High	59.2	23.7	12	6.9

APPENDIX C

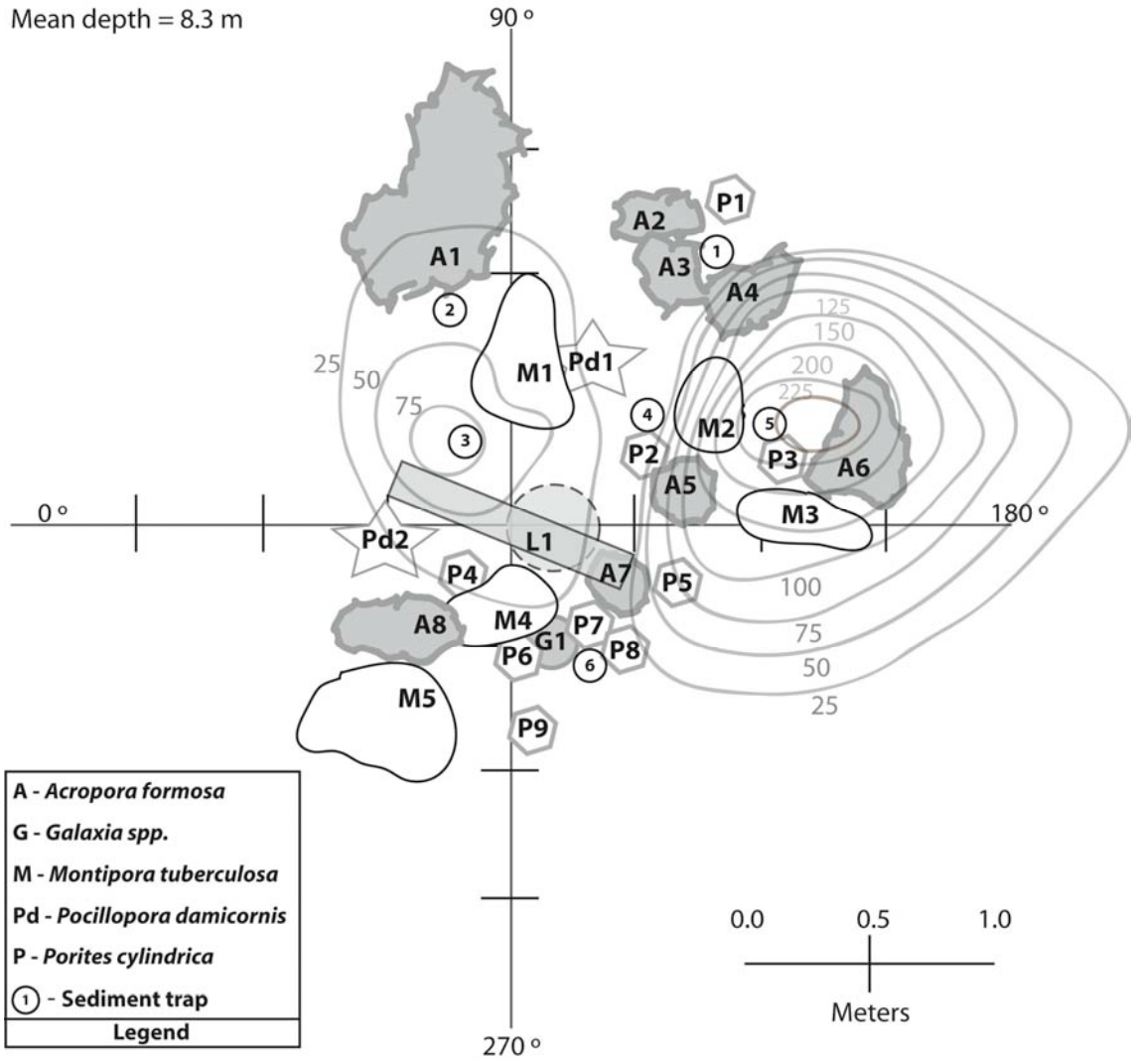
Figures showing the approximate coral colony locations and estimated sediment plumes (mg cm^{-2} d^{-1}) generated from the erosive sediment blocks at each of the 6 experimental sites.

Note that sediment plume contour lines were estimated 'by hand' based on sedimentation rate data collected. No findings or conclusions drawn in this thesis were based on these images. These figures are provided as an illustration of the 'mud-maps' created for each site only and are not necessarily representative of actual field conditions.



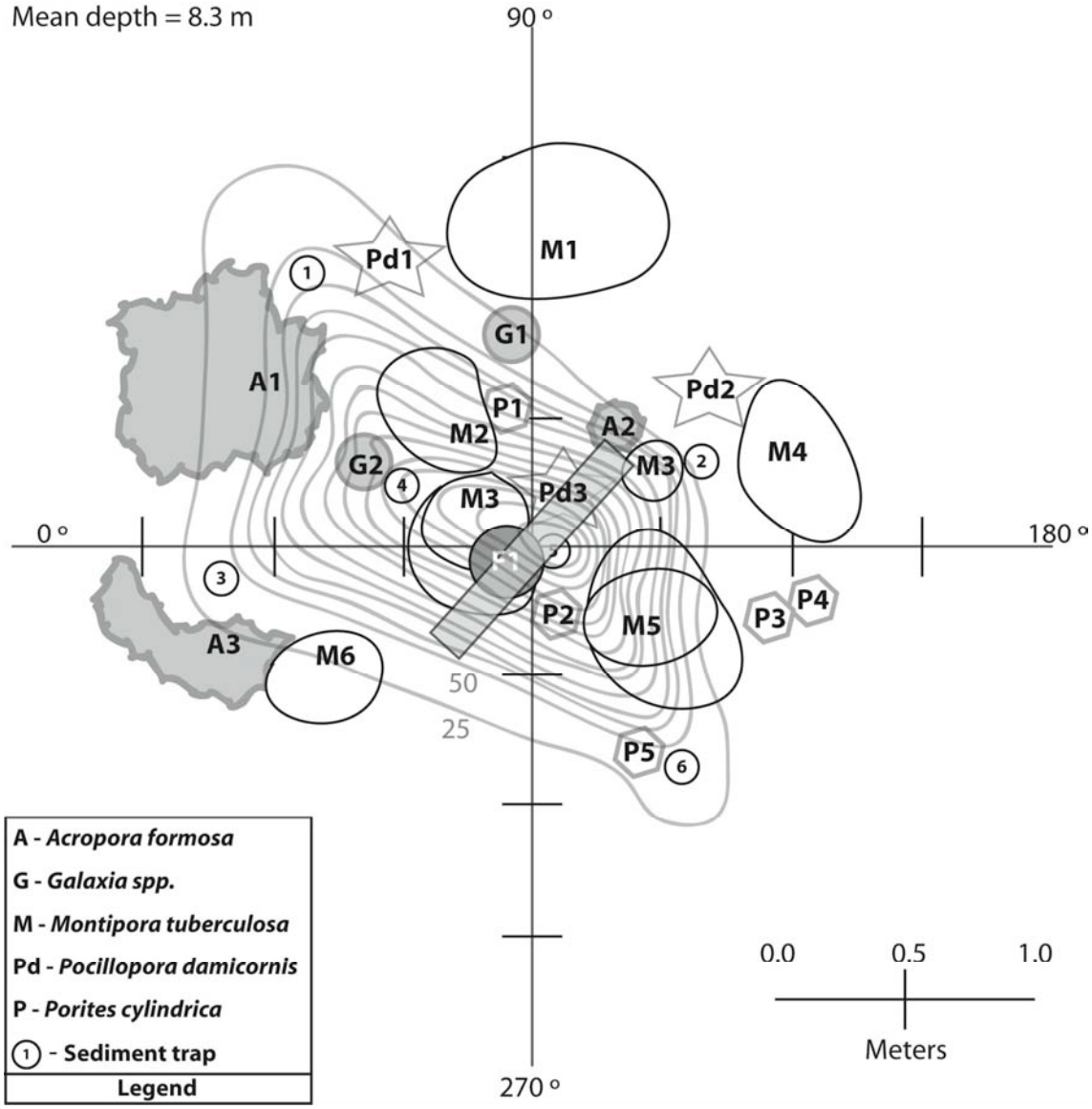
Site 2

Mean depth = 8.3 m



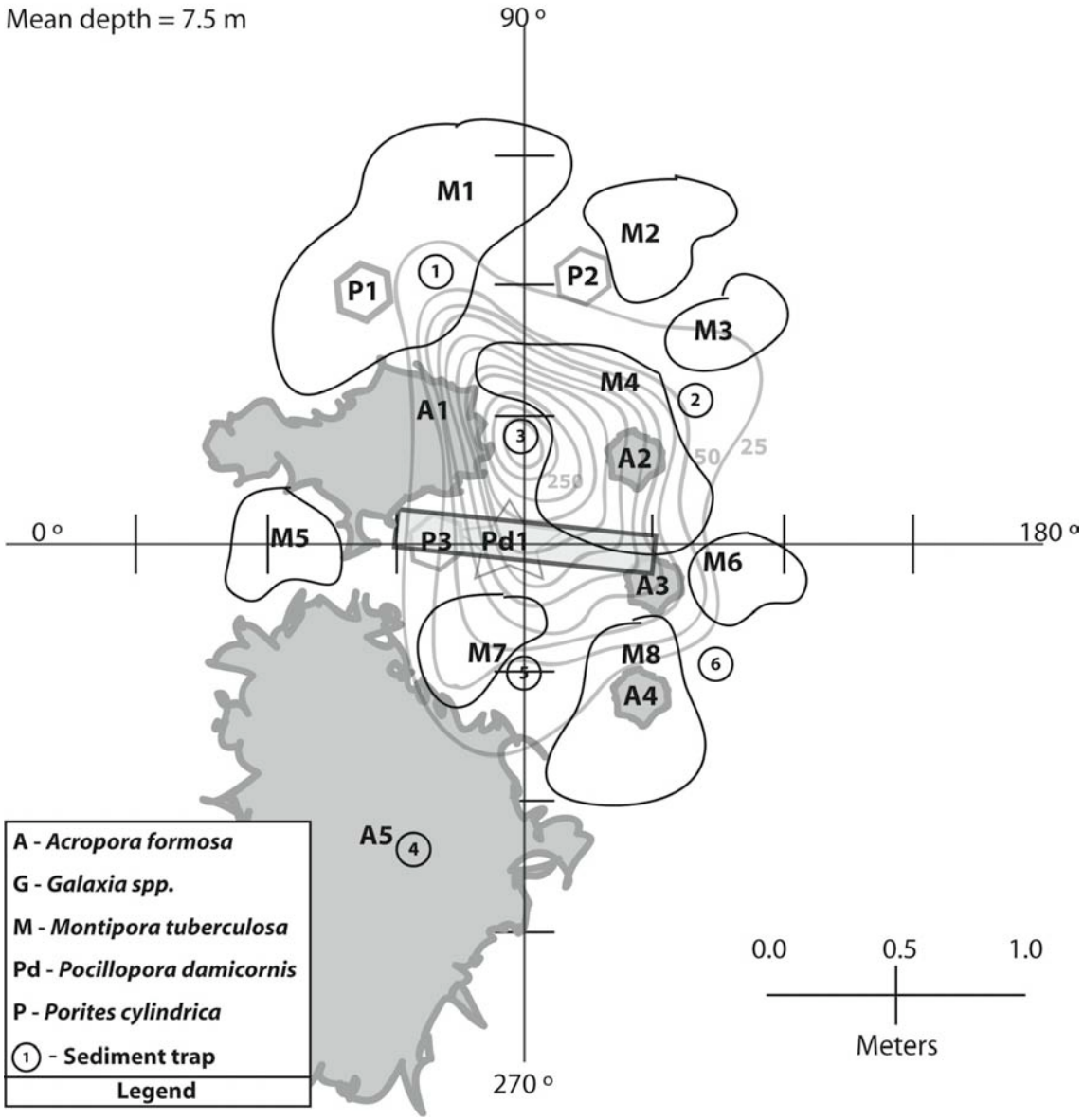
Site 3

Mean depth = 8.3 m



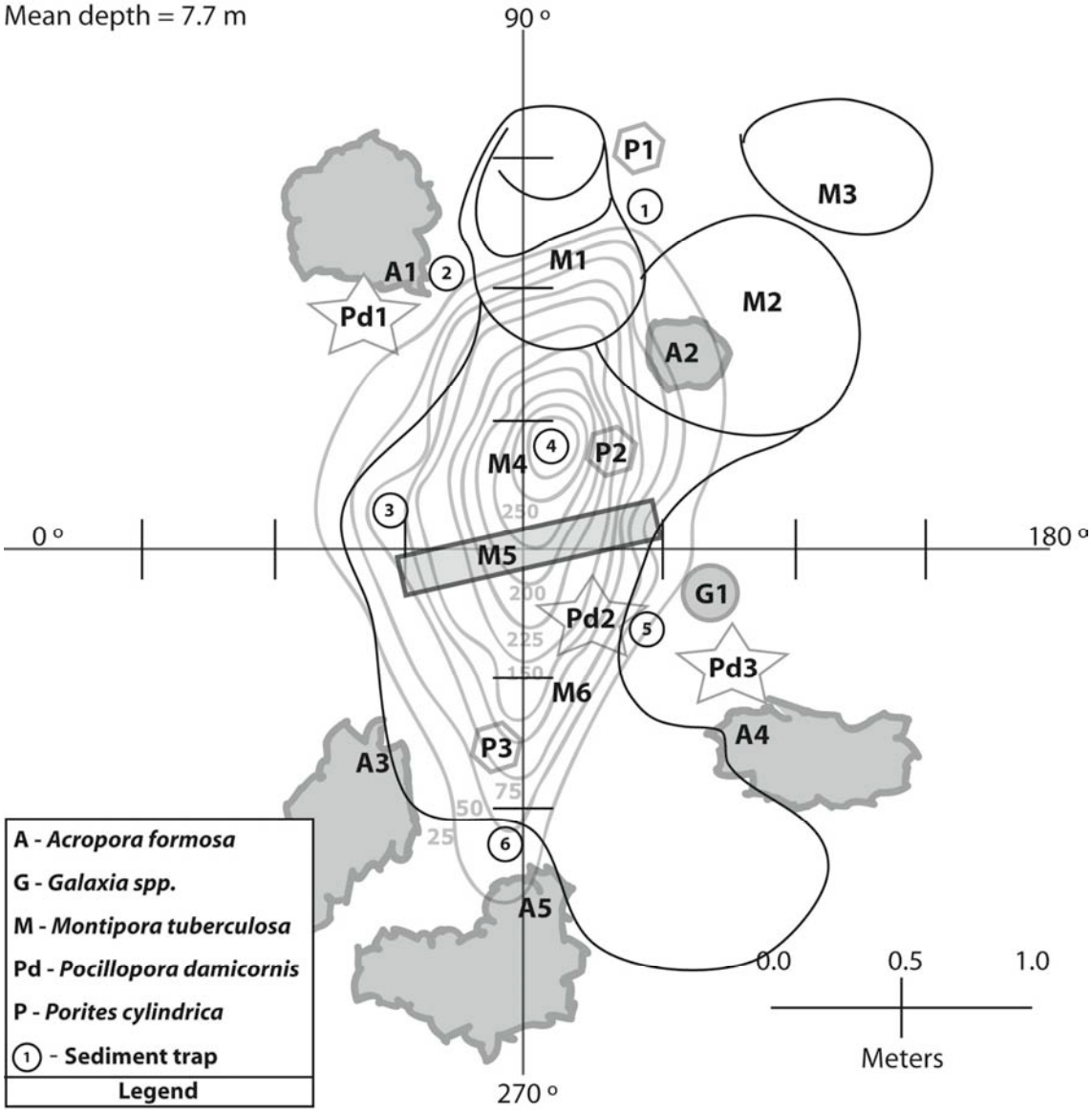
Site 4

Mean depth = 7.5 m



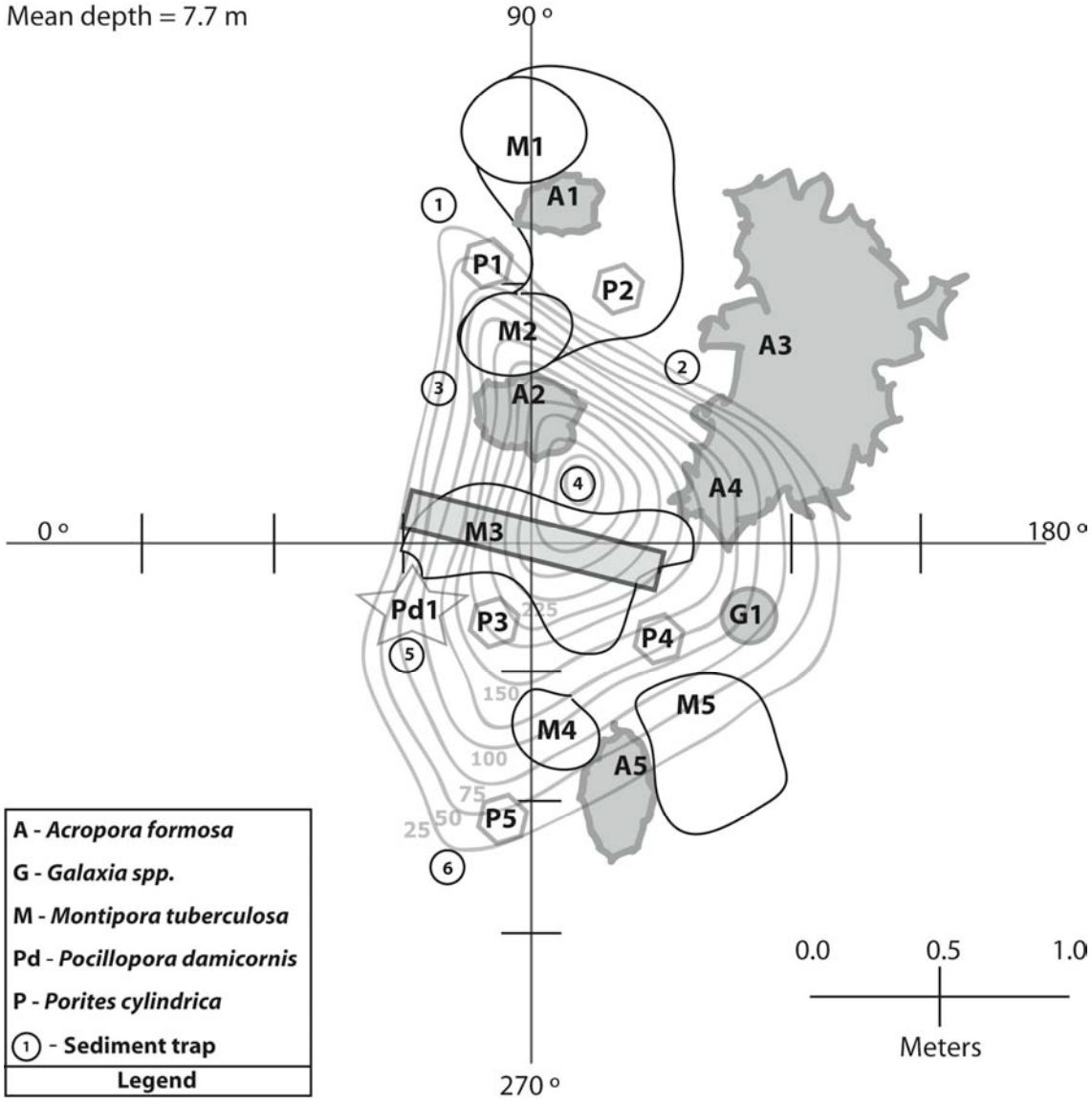
Site 5

Mean depth = 7.7 m



Site 6

Mean depth = 7.7 m



Results of the mean percentage of Acropora formosa, Montipora tuberculosa, and Porites cylindrica that was unbleached after subjection to sediment treatments as described in Chapter 4.

Table C1: Mean percentage of *A. formosa* that remained unbleached in sediment treatments as described in Chapter 4.

	N	Minimum	Maximum	Mean	Std. Deviation
% non- bleached coral	38	86	100	97.3947	2.53131
Valid N (listwise)	38				

Table C2: Mean percentage of *M. tuberculosa* that remained unbleached in sediment treatments as described in Chapter 4.

	N	Minimum	Maximum	Mean	Std. Deviation
% non- bleached coral	36	21	98	78.9444	17.47642
Valid N (listwise)	36				

Table C3: Mean percentage of *P. cylindrica* that remained unbleached in sediment treatments as described in Chapter 4.

	N	Minimum	Maximum	Mean	Std. Deviation
% non- bleached coral	35	97	100	99.0286	0.74698
Valid N (listwise)	35				