# TISSUE THICKNESS AS A TOOL TO MONITOR THE STRESS RESPONSE OF MASSIVE *PORITES* CORALS TO TURBIDITY IMPACT ON LIHIR ISLAND, PAPUA NEW GUINEA

Thesis submitted by

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*Death is not an option.*

# ABSTRACT

In massive *Porites* colonies, living tissue invests only a thin layer on the outer perimeter of the skeleton, normally around 25-50% of an annual growth increment in healthy colonies. The depth to which skeleton is occupied by tissue is referred to as 'tissue thickness'. Tissue thickness has been argued to be a sensitive bioindicator that may be potentially used to monitor changes in coral health *prior* to collapse and mortality. The primary goal of this study was to assess the response of tissue thickness in massive *Porites* colonies at Lihir Island ($3^0$05'S $152^0$38'E) to an anthropogenically increased turbidity regime associated with mining activities. In order to achieve this goal it was also necessary to identify possible sources of natural variability in tissue thickness, both spatial and temporal, and to quantify their influence. Possible sources of tissue thickness variability identified through both literature review and observation included: i) changes in thickness through the lunar month as a function of skeletal growth patterns; ii) change in thickness due to differences in local environmental conditions; iii) change in tissue thickness with differences in colony size and shape. Where possible, the influence of all of these factors was examined in both shallow (<11 m) and deep (>14 m) habitats, across sites around Lihir Island and between years (sampling took place in 2001, 2002, and 2003).

Tissue thickness in massive *Porites* changes over a lunar month as part of skeletal growth processes. This study looked for ways in which allowance could be made and procedures devised for sampling at different times of

the lunar month. Tissue thickness decreased, on average, by 20% on the day after the full moon. Tissue thickness increased, on average, by 0.3 µm per day during the lunar month. These patterns of variation were consistently observed between study sites, at different depths, and in different sampling years. The only exception appeared to be when tissue thickness became critically thin (below 2.2 mm), which was only found at a site heavily affected by turbidity. Hence, growth processes in massive *Porites* were reduced or halted when limited energy reserves were available under stressful conditions. Monthly tissue uplift in the same colonies was resumed when an increase in tissue thickness above the minimum threshold of 2.2 mm was achieved. The consistency of tissue variations throughout the lunar month in all but these very few extremely stressed individuals allowed measurements taken from individuals at different times of the lunar month to be easily adjusted for comparison.

In the second study, changes in tissue thickness in response to increased turbidity were examined by measuring tissue thickness in massive *Porites* colonies along an anthropogenic turbidity gradient in 2001, 2002 and 2003. Tissue thickness was significantly less where turbidity levels reached 15-30mg $l^{-1}$. This was the maximum turbidity encountered near coral reefs in this study. Tissue thickness was not significantly reduced by lower turbidity levels, but it was always less in colonies in deeper water than in colonies in shallow water. Some variability of tissue thickness was also observed between study sites and years. However, neither spatial nor temporal variability masked the general pattern of decreasing tissue thickness with increasing turbidity.

The final study examined differences in tissue thickness with colony size and shape and looked at environmentally-induced changes in tissue thickness in colonies with different morphologies. Massive *Porites* corals on Lihir Island were found to occur in six distinct growth forms, namely rounded, round-encrusting, pyramidical, pyramid-encrusting, encrusting and vertical encrusting. Some of these shapes could be described quantitatively by height/circumference ratios. However, the angle of substrata slope was found to be a better indicator for changes in shapes with study sites and water depth. Allowing for changes in tissue thickness with depth, colony morphology did not affect tissue thickness. Hence, colony morphology was not a significant factor in sampling for tissue thickness. Similar-sized colonies were selected for sampling. The effects of colony size on tissue thickness were tested and colony size could also be excluded as a factor which significantly affected tissue thickness.

Patterns of change in tissue thickness in *Porites* colonies at Lihir Island indicated that mining activities had affected, and were affecting, corals and coral communities over a much more restricted area than predicted by the mine's environmental impact statement. Tissue thickness patterns corresponded closely with indices of live coral cover and turbidity measurements. Tissue thickness was found to be a simple and reliable bioindicator for turbidity stress on corals on Lihir Island. Changes in tissue thickness indicate when corals are being adversely affected by anthropogenic activities. This gives tissue thickness a huge advantage over other monitoring techniques, because these mostly detect change after it has occurred - and not while it is occurring.

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*Für meine Großeltern, die ich über alles liebe und immer vermissen werde.*
*Oma und Opa, ich hab's geschafft!*

# 1.0 GENERAL INTRODUCTION

1.1 BACKGROUND: Coral reefs are amongst the most diverse ecosystems on earth and also among the most productive (Pomerance *et al.*, 1999). They are often perceived as being fragile and vulnerable to changes in their environment, however, they have proven to be very capable of adapting and acclimatizing to major and sometimes relatively swift environmental changes over several million years (Buddemeier and Smith, 1999). In recent years, much concern has been raised that coral reefs around the world are degrading, mostly due to chronic, anthropogenic disturbances (e.g. Wilkinson, 1992; Roberts, 1993; Hoegh-Guldberg, 1999; McCulloch *et al.*, 2003; Bellwood *et al.*, 2004). Consequently, effective management of coral reefs requires appropriate regulation of damaging human activities. Assessment of whether a particular reef is exposed to potentially damaging human activities must be based on verifiable estimates of the intensity and extent of stress and its significance for reef 'health'. Coral and reef stress are defined and discussed in detail in Chapter 2, but may briefly be described as the condition where coral and reef growth rates are reduced to one or more environmental parameters being near tolerance limits of the individual or system (e.g. Tomascik and Sander, 1987a). Reef 'health' is a term which is often used loosely, and which is rarely quantified. One study separates coral reef 'health' into three categories: critical, threatened and stable, the latter describing 'reefs with no imminent threat of collapse through anthropogenic damage, which should remain healthy in the immediate future' (Wilkinson, 1992). In this last case, 'healthy' seems to mean mainly unaffected by anthropogenic interference. Done (1992)

assessed 30 coral-dominated communities on the Great Barrier Reef (GBR) over the period of 1980-85 and described reefs as ‘very unhealthy’ based on the absence or presence of significant net increase or decrease in percent coral cover (Done, 1992). Coral growth rate is often quoted as a measure of reef health (Edinger and Risk, 2000), as are e.g. species diversity and live coral cover. Edinger and Risk (2000) point out that coral growth rate may not be a useful measure of reef ‘health’ since it is possible for coral growth rates to be high while reef ‘health’ is poor because destruction (erosion) rates exceed construction rates.

A wide range of techniques have been employed to measure stress in, or the ‘health’ of, reef corals, reef communities and whole reefs (see Chapter 2). These techniques do not always give clear results. This is due to several factors including the following:

(1) High natural variability in coral response to stress (e.g. Peters and Pilson, 1985);

(2) A time lag between impact and response (Risk, 1999);

(3) Previous impacts, which make it difficult to distinguish the effects of a single impact from the effects of multiple impacts (Hughes and Connell, 1999);

(4) Limited understanding of coral physiology and histology leading to problems distinguishing effects of unnatural disturbances from natural long-term fluctuations on the reef (Brown and Howard, 1985);

(5) A general unwillingness, to date, of coral reef ecologists to acknowledge and integrate in their assessments of coral and reef

health the valuable longer-term histories and records of past conditions and responses yielded by geological and geochemical investigations (Risk, 1999).

Moreover, techniques for measuring stress in reef organisms and systems often involve expensive and sophisticated equipment and are, therefore, of limited use in remote locations or developing countries, where 90% of the world's reefs are situated (Brown and Howard, 1985; Burke *et al.*, 1998; Risk, 1999).

One of the most promising techniques for monitoring reef 'health' involves the use of bioindicator organisms. These are organisms that change visibly or measurably in response to changes in reef 'health' at the levels of individuals, populations and assemblages. 'Biomarkers' can also indicate a change in environmental conditions, but these are restricted to cellular, biochemical, molecular or intra-cellular physiological changes in the bioindicator organism and require sophisticated technologies to analyse (Lam and Gray, 2003). Bioindicators are useful because they are direct indicators of stress upon an ecosystem (Erdmann and Caldwell, 1997). The best bioindicators respond to environmental stressors in known, predictable ways. Hence, they can be used to undertake rapid surveys over wide areas (Risk and Risk, 1997). A good bioindicator species is representative of other species in the ecosystem (Underwood and Peterson, 1988). They should be abundant, easy to identify and sample, and show a graduated response to increasing stress (Erdmann and Caldwell, 1997). In addition, bioindicator species should not be subject to human exploitation to avoid

potentially amplifying or distorting the organism's response to a particular stress factor (unless, of course, the stressor studied is human exploitation). The indicator should also provide an early warning of sublethal stresses to the primary habitat-structuring organisms, like reef corals (Erdmann and Caldwell, 1997). Where bioindicator organisms occur they may present a reliable, inexpensive way to monitor reef health, and can be utilised by local communities in developing countries (Erdmann and Caldwell, 1997).

The tissue thickness of massive *Porites* corals, described as the depth of skeleton occupied by tissue, is used as a bioindicator of sediment stress in work described here. Tissue thickness fulfils all the criteria listed above for a bioindicator and has previously been found to identify the impact of sediment stress from a point-source better than any other growth parameters studied (Barnes and Lough, 1999). Tissue thickness was first mentioned by Darke (1991) and described in detail by Barnes and Lough (1992). Although these authors proposed that tissue thickness might be a measure of coral and reef health, the validity of tissue thickness as a bioindicator has not yet been fully established (e.g., True, 1995).

The object of this study was to assess in detail the possibility that tissue thickness could be applied as bioindicator for monitoring reef response to increased turbidity stress. Towards that end, work was carried out to establish natural variability in tissue thickness so that unnatural change could be identified against a background of natural change.

1.2 MASSIVE *PORITES*: There are seven species of massive *Porites* corals in the Indo-Pacific (Veron, 1986). These species are: *P. lutea, P. lobata* and *P. australensis,* which are the most abundant, *P. solida* which is common, *P. mayeri* and *P. myrmidonensis,* which are relatively rare and *P. stephensoni,* which is rare and does not attain large size (Veron, 1986). Massive *Porites* species are very common in the Indo-Pacific (Done and Potts, 1992), but no *Porites* form large, massive colonies in the Atlantic. The morphology of massive *Porites* is extremely plastic, with colony shape ranging from hemispherical to pyramidical to flattened-encrusting (see detailed descriptions in Chapter 5). Massive *Porites* can be easily identified *in situ* by their characteristically small polyp diameter (~1 mm). Massive *Porites* species can colonise a wide range of reef habitats (Done and Potts, 1992) and their widespread distribution makes them ideal bioindicators of coral health (True, 1995).

*Porites* is commonly used in laboratory and field research, especially in the assessment of how environmental change affects corals. Published examples of factors affecting reefs that were assessed using *Porites* include:

- Eutrophication (Tomascik and Sander, 1987b).
- Damage caused by anchors (Rogers and Garrison, 2001).
- Petroleum hydrocarbons (Readman *et al.*, 1996).
- Fungi (Ravindran *et al.*, 2001).
- Riverine metal content (Bastidas and Garcia, 1999).
- Water depth (Custodio and Yap, 1997).
- Ultraviolet radiation (Bessat *et al.*, 1997).

- Water motion (Montebon and Yap, 1997).
- Climate changes (Lough *et al.*, 1997).
- Shading (True, 1995).
- Bioerosion (Liu and Hsieh, 2000).
- Copper and reduced salinity (Alutoin *et al.*, 2001).
- Salinity and temperature changes (Kato, 1987).
- Cyanide (Jones and Steven, 1997).
- Nuclear testing (Hudson, 1985).
- Volcanic activity (Heikoop *et al.*, 1996).
- Changes in sea surface temperature and El Niño Southern Oscillation (Alibert and McCulloch, 1997).
- Reduced light levels (Heikoop *et al.*, 1998).
- Increased sedimentation (Gleason, 1998).
- Mining (Fallon *et al.*, 2002).
- Sea-level changes (Smithers and Woodroffe, 2000).

Variables measured in such studies include reproductive state (e.g. Tomascik and Sander, 1987b), recruitment (Rogers and Garrison, 2001), skeletal extension (e.g. Custodio and Yap, 1997), annual density banding (e.g. Hudson, 1985), abundance and distribution of different colonial morphs (Gleason, 1998) and the incorporation of various trace elements (Fallon *et al.*, 2002) and skeletal isotope ratios (e.g. Alibert and McCullough, 1997). *Porites* skeletons contain ‘annual’ density bands, which can be displayed by X-radiography of skeletal slices taken along a colony’s growth axis. A year’s growth usually results in a high and low density band, together referred to as a density band couplet (Buddemeier and Maragos,

1974). It is possible to recover annual growth and annual calcification rates from such banding (Chalker *et al.*, 1985; Lough *et al.*, 1997). Further, the banding allows dating of environmental records associated with changes in the chemistry of coral skeletons, such as stable isotope ratios and trace inclusions (Lough *et al.*, 1996).

Coral growth can be defined as an increase in colony size due to linear extension, or as an increase in colony mass due to calcification. Buddemeier (1974) observed fine density bands within the annual density banding pattern of certain types of massive coral. It was speculated that fine bands formed under lunar control because there was a maximum of 12-13 fine bands within a year's growth (Buddemeier, 1974; Buddemeier and Kinzie III, 1975; Buddemeier and Kinzie III, 1976; Houck *et al.*, 1977). Barnes and Lough (1989) suggested that annual density bands in massive *Porites* are made up from fine density bands. They suggested that fine density bands are not usually seen because they are only apparent on X-radiographs when the fine bands are parallel to the X-ray beam. Barnes and Lough (1989) also identified an apparent link between the spacing of fine bands and the spacing of dissepiments but were unable, at that time, to provide an explanation for this link. Dissepiments are very thin, horizontal skeletal bridges formed between vertical skeletal elements. They serve to isolate coral tissues from skeleton vacated by coral tissues (e.g. Plate 1, Barnes and Lough, 1992). These authors later provided an explanation for the link between spacing of fine bands and spacing of dissepiments (Barnes and Lough, 1993) by relating periodic, probably lunar monthly uplift of the base of the tissue layer, and consequent formation of

new dissepiments, with thickening of skeletal elements throughout the depth of the tissue layer (see below). This explanation arose out of a conceptual model (Barnes and Lough, 1993) and mathematical models (Taylor *et al.*, 1993) for the formation of annual density bands in coral skeletons. In both the conceptual model and the mathematical models, the formation of fine density bands is superimposed over the annual cycle in skeletal density, rather than the annual cycle being made up of fine density bands as earlier believed (Barnes and Lough, 1989).

According to the conceptual model developed by Barnes and Lough (1993), three growth processes are involved in annual density band formation in massive Porites (Plate 1):

1) Extension of skeletal elements at the outer surface of a colony;
2) Thickening of skeletal elements throughout the depth of the tissue layer;
3) Periodic and abrupt uplift of the lower margin of the tissue layer.

Extension of the skeleton increases the thickness of the tissue layer and the tissue layer remains more or less the same thickness because of periodic uplift of its lower margin. These ideas were not new. It was obvious the corals increased in size by extension of skeletal elements at the outer surface of a colony. Moreover, it was generally accepted that that uplift of the basal regions of tissue was a discontinuous process marked by formation of dissepiments (see Wells, 1969 for review). The new suggestion made by Barnes and Lough (1993) was that skeletal elements are thickened through the depth of the tissue layer. Evidence of such

thickening came from weekly staining of growing colonies with Alizarin and from increasing robustness of spines and synapticulae from the surface of a colony to the most recent dissepiment visible in Scanning Electron Microprobe analysis (Barnes and Lough, 1993).

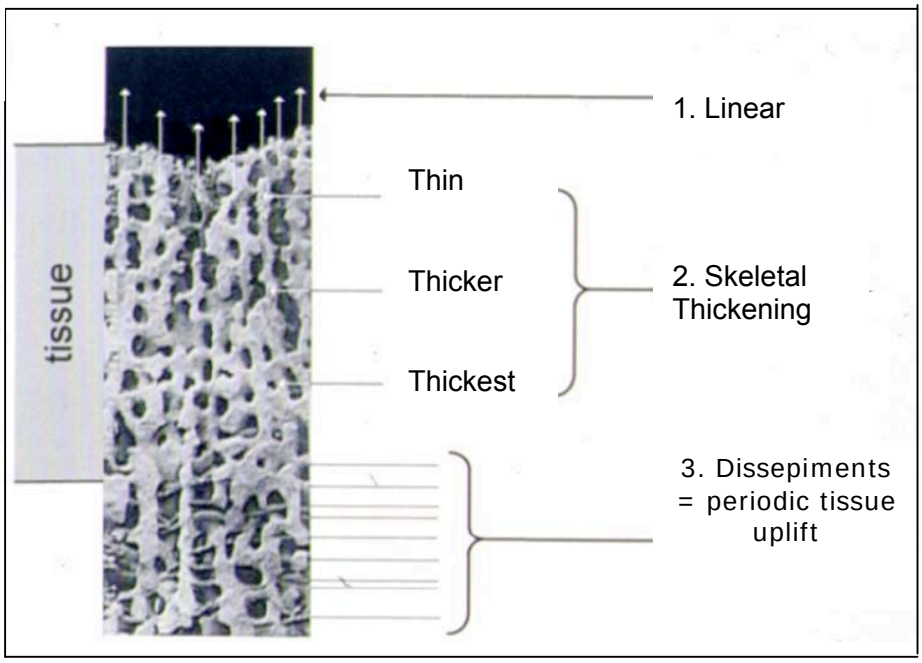



Plate 1. Three major growth processes involved in density band formation indicated on SEM of *Porites* skeleton (courtesy D.J. Barnes)

According to Barnes and Lough (1993; see also Taylor *et al.*, 1993), annual density bands arise because of annual variations in calcification rate, which alters the amount of thickening added to the skeletal scaffolding that was created by extension of skeletal elements at the outer surface of the coral. Tissue thickness is usually considerably less (between 25 and 50%) than the distance a coral skeleton extends in a year. Thus, within one year's skeletal growth, one region of the skeleton would have been covered by tissue more during summer and another region would have been covered more during winter. Thus, since calcification is likely to have been fastest in summer, one region of skeleton would have been thickened more than the

other. Of course, the processes involved are continuous and tissue is likely to cover skeleton that took about 6 months to extend (Barnes and Lough, 1992). Thus, in midsummer, when calcification is fastest, the tissue would have been covering skeleton that initially formed from midsummer (current outer surface of colony) to midwinter. In midwinter, the tissue would have been covering skeleton that initially formed in midwinter (current outer surface of colony) to midsummer. Barnes and Lough (1993) likened this process to a “running mean” and suggested that the amount of thickening added to any point on a skeletal element would be a running mean of the calcification rates that were obtained over the time that tissue covered the point. As a result, skeletal elements would show an annual variation in their amount of thickening brought about by an annual variation in their calcification rate. Barnes and Devereux (1988) showed that annual density bands result from variations in the amount of thickening of skeletal elements. Consequently, an annual variation in the amount of thickening added to skeletal elements would appear in X-radiographs as annual density variations. One important consequence is that the timing of the cycle in skeletal density will not be the same as the time provided by dating from the outer surface of the colony - the usual method of dating coral growth (Lough and Barnes, 1990). Taylor *et al*. (1993) used computer modelling of density band formation based upon the ideas of Barnes and Lough (1993) to examine how various factors would interact in the formation of density bands. They found that differences in tissue thickness over the range observed in massive *Porites*, combined with annual variations in extension rate, could account for the considerable difference in descriptions of the appearance of density band patterns in the literature.

Barnes and Lough (1992) suggested that tissue thickness and changes in tissue thickness might provide a powerful environmental monitoring tool, as it is simpler and more straightforward than other techniques for monitoring coral “health”. Tissue thickness can be measured non-destructively in the field by taking small cores of each colony. Environmental changes may be seen as unusual tissue thicknesses at one location compared with surrounding locations or as changes in tissue thickness over time (True, 1995). Tissue thickness was found to be inversely related to water depth (True, 1995), to be higher at inshore reefs than at offshore reefs and to be higher at reefs in the northern GBR than at reefs in the southern GBR (Barnes and Lough, 1992). True (*in review*) showed that tissue thickness exhibits an annual cycle, and that it decreased rapidly when large colonies were shaded. Barnes and Lough (1999) found that tissue thickness decreased with increasing proximity to a mine site, where vast amounts of sediment were released to the marine environment. Tissue thickness was also found to vary over the surface of a colony, being highest on summits and decreasing down the sides (Barnes and Lough, 1992).

## 1.3. AIMS AND OBJECTIVES:

Work described here assessed the feasibility of using variations in tissue thickness of massive *Porites* corals as a bioindicator for turbidity stress created by the operation of a gold mine at Lihir Island, Papua New Guinea. The work also examined natural variability of tissue thickness to determine if unnatural change could be detected against a background of natural change. Changes in tissue thickness with water depth, locations, substrata

slope, colony growth form and colony size were examined, as were changes within colonies and with time of the lunar month and time of year. The aim here was to develop sampling protocols, which minimised natural variability and maximised the potential management use of tissue thickness as a cheap, simple and reliable tool to assess sediment stress on corals on Lihir Island. It also formed a basis for establishing similar monitoring programs for coral stress in other locations.

1.4. STUDY SITE: The Lihir Island Group is located approximately 50 km northeast of New Ireland in Papua New Guinea ($3^0$05'S $152^0$38'E). The group consists of five islands: Lihir, Sanambiet, Mali, Masahet and Mahur Islands (Fig. 1). The Lihir Management Company (LMC), for and on behalf of, Lihir Gold Limited, began operating an open-pit gold mine in Luise Harbour, on the east coast of Lihir Island in 1997. The plant site is located at PutPut Point where mine tailings are discharged to the deep-sea marine environment via a pipe outlet at 125 m below sealevel (Fig. 1). As this depth is below the thermocline, sediments discharged from this outlet are not re-entrained to the surface and do not harm the nearby reef (NSR Draft Environmental Plan, 1989). However, mine construction and operations increased sediment-loaded run-off to the nearby sea, mainly due to vegetation clearing; road, airport and operational infrastructure construction; and the accumulation of low-grade ore stock piles exposed to a wet climate. Approximately 60 Mt of low-grade ore will remain in stockpiles until after extraction operations are completed. The stockpiles create acid runoffs when combined with rainfall, which is high and regular on Lihir Island. The disposal of hard and soft rock waste on Lihir Island is

through ocean dumping. This method was assessed as the most environmentally and financially feasible method of waste disposal due to the island's steep submarine slopes and deep surrounding ocean (1600 m; NSR Draft Environmental Plan, 1989). By the time the mine stops open pit mining (projected to be in 2022, low grade ore will be processed for approximately another 20 years), approximately 600 Mt (340 Mt hard rock and 260 Mt soft rock, 98% of which is comprised of argillic soil and coloured oxide clays) will have been disposed by using split-hopper barges operating 24 hours a day, 365 days of the year (see Plate 2).

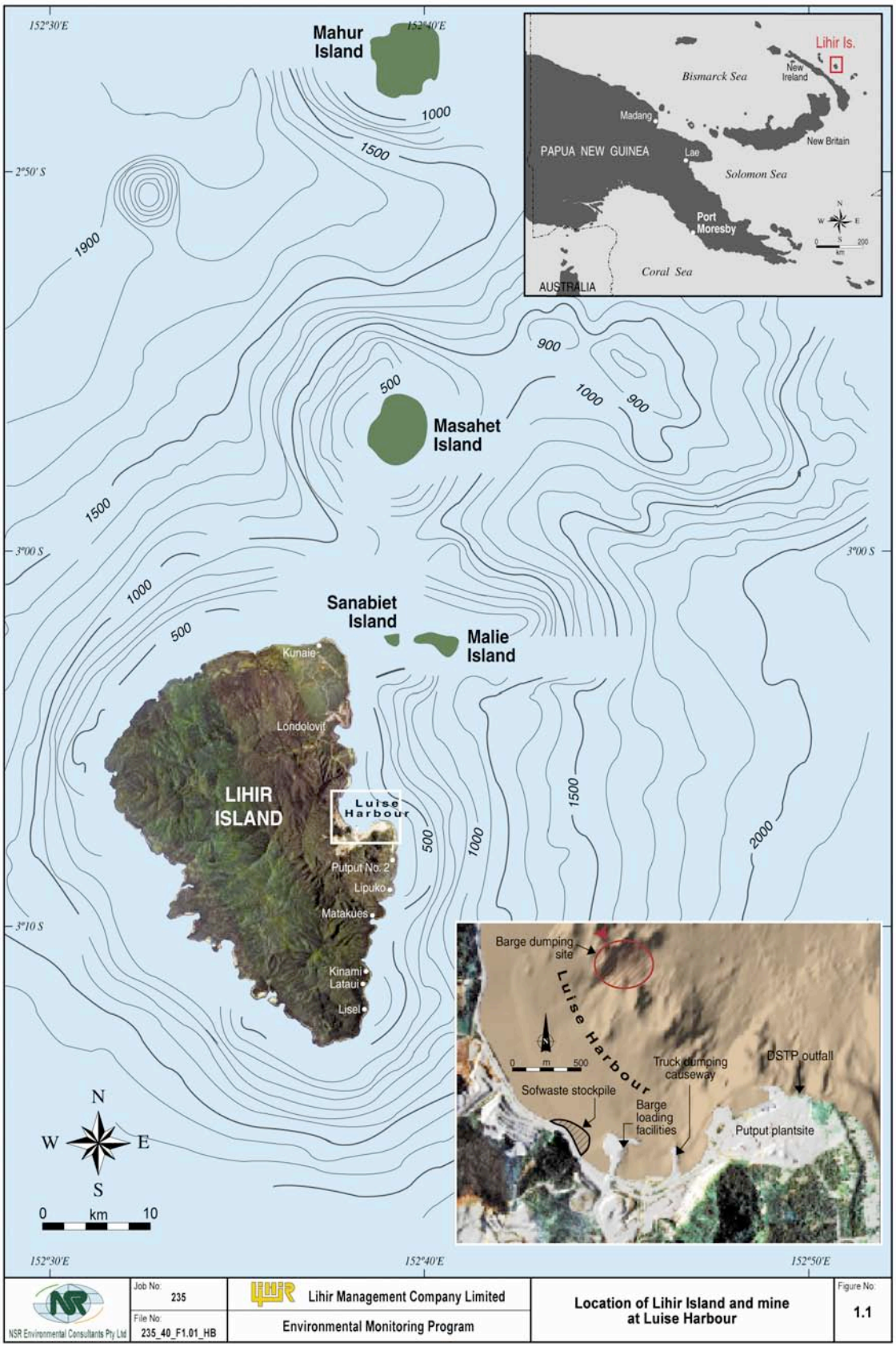



Figure 1. Location of Lihir Island and gold mine in Luise Harbour (courtesy NSR).

Plate 2. Photo of waste rock on split-hopper barge at dumping site (note the brown colour of the sediment plume in surrounding waters from the previous barge-load)

Terrestrial run-off and waste dumping from barges creates a surface sediment plume that affects some of the fringing reefs in Luise Harbour. The likely effects of the gold mine on the coral reefs were predicted in a baseline study (NSR, 1989). A regularly revised three-yearly Environmental Management and Monitoring Program (EMMP) is undertaken by LMC Environment Department and includes studies on 'nearshore sedimentation rates and turbidity' and 'fringing coral reefs'. Natural System Resources (NSR) has been contracted to monitor the fringing coral reefs with photo and video transects since 1994 (NSR, 2000). NSR has proposed four zones of biological impact from long-term exposure of the fringing coral reef to the combined effects of sediment deposition, suspended sediments, turbidity and diminished water quality (NSR, 1989). These were: 'severe', 'transitional', 'minor' and 'control'. These predictions were made using 50% exceedence probability values of total suspended solid (TSS) concentrations. The median TSS concentrations were *predicted* to be >100 mg $l^{-1}$ in severe impact zones, >25 mg $l^{-1}$ in transitional impact zones, >10

mg $l^{-1}$ in minor impact zones (twice the oceanic concentration) and control zones with <10 mg $l^{-1}$ TSS concentrations. NSR (1989) warned that these predicted effects were first approximations only, but continued to use these impact zone delineations for their coral reef monitoring assessments (e.g. NSR Coral Reef Monitoring Report, 2000; 2002). The extent of surface plumes were modelled for the different wind seasons on Lihir Island and water samples were taken for turbidity measurements during the sampling of sediment traps, which are located at 22 sites on Lihir Island (NSR, 1996). However, neither of these sampling regimes provided a detailed, quantitative account of the sedimentary plume dynamics nor its possible impact on the coral reefs at Lihir Island. To remedy this shortcoming, LMC has supported two Ph.D projects that examine the interactions between mining activities and the marine environment, especially coral reefs. The first study was undertaken by Severine Thomas (2003) and included extensive surveys of sedimentation rates, turbidity levels and light levels along Lihir's east coast. Work described here constitutes the second project, which assessed the response of corals to mine-related activities.

A narrow fringing reef surrounds much of Lihir Island. It generally consists of a reef flat, extending 20-100 m from the shore. The volcanic basement on which the reef grows slopes steeply, and the fringing reefs typically terminate to seaward with a steep drop-off into very deep water. Strong wave action restricts the growth of all but the hardiest corals to depths below 3 m, that is, below the most vigorous wave activity. The major species on Lihir Island are branching acroporids, massive *Porites,* and *Millepora*, a hydrozoan coral. A more detailed description of Lihir Island,

oceanic and climatic characteristics, mine operations and the LMC monitoring program can be found in NSR (1989) and Thomas (2003). Thomas (2003) monitored oceanographic and climatic events to determine their potential impact on the sediment plume around Luise Harbour. However, she found no distinctive links between major environmental factors such as wind, rainfall, wave action and currents and plume behaviour. Photographs and detailed descriptions of study sites sampled in this study are provided in Appendix A.

1.5. METHODOLOGY: Study sites with the following features were identified on the reefs surrounding Lihir Island:

1. Occurrence of sufficient numbers of suitable massive *Porites* colonies (see below);
2. Closeness to the NSR coral reef monitoring sites and sediment traps and/or;
3. Proximity to nephelometer stations used in parallel research (Thomas, 2003).

Twenty potential work locations were assessed and eight were chosen for work in 2001. This increased to 13 sites in 2002 to enable higher density sampling along the eastern coast, where the response gradient of tissue thickness to turbidity appeared steep based on the 2001 results. At each site ten living, apparently healthy massive *Porites* colonies were selected for tissue thickness sampling using the following criteria:

a) Colonies must be of similar size (mean height: 250 mm, mean diameter: 440 mm; see Chapter 5 for variability in size classes);

b) Colonies must show less than 50% tissue mortality at the time of selection;

c) Colonies must be collected from similar water depths, representing shallow (<10 m depth) and deep (24-14 m) locations at each study site.

Selected colonies were marked with a stainless steel tag numbered between 0 and 9 and attached by fishing wire to the base of each colony. This identified colonies for later measurements. Short lengths of black PVC pipe were pushed over the tags to protect them from fouling. Cores of skeletal material 25 mm long were removed from a point on the uppermost one third of each colony (see Barnes and Lough, 1992) using a manually operated brace-and-bit fitted with a 29 mm diameter hole saw without a central drill bit. The brace-and-bit was positioned between the stomach of the diver and the coral colony to stabilise the diver. One hand gripped the colony and the other hand turned the brace-and-bit (see Plate 3).

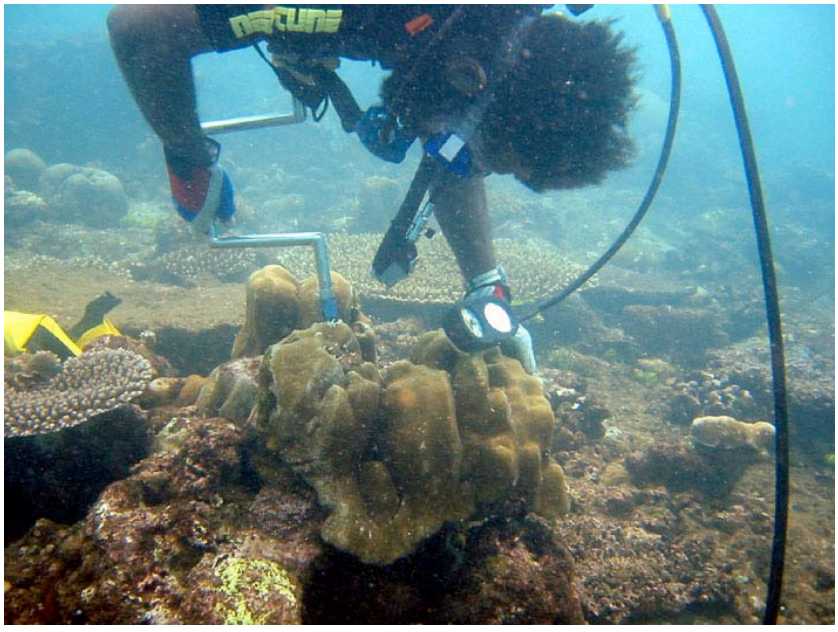


Plate 3. Diver drilling core into coral summit using brace-and-bit and holesaw.

Cores were taken normally to the growing surface to minimise sampling error (see Chapter 5, Section 5.4.1.4). Extracted cores were placed in a specially constructed and pre-labelled container for transport back to the boat (see Plate 4). Once out of the water, collected samples were put in labelled plastic vials before being sun-dried and chiselled in half along the growth axis normal to the skeletal surface. Tissue thickness was measured on the cut surfaces to the nearest 0.1 mm using digital callipers.

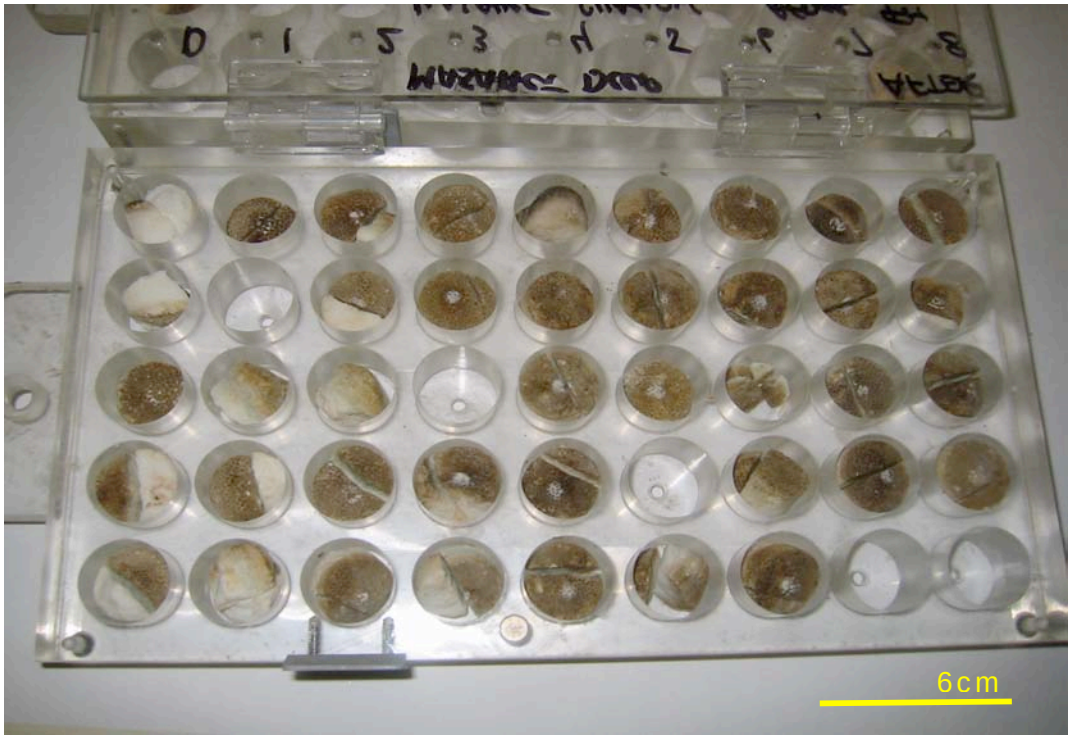



Plate 4. Perspex box used to collect coral cores underwater. Cores have been chiselled in half.

To avoid fouling and possible erosion of the skeletal surfaces exposed by coring, pre-made concrete plugs were inserted in each core hole immediately following core extraction. Tissue quickly grew across the surface of the plug and skeletal growth was resumed. Sections later cut through some colonies showed the limited impact of coring upon colony growth (Plate 5).

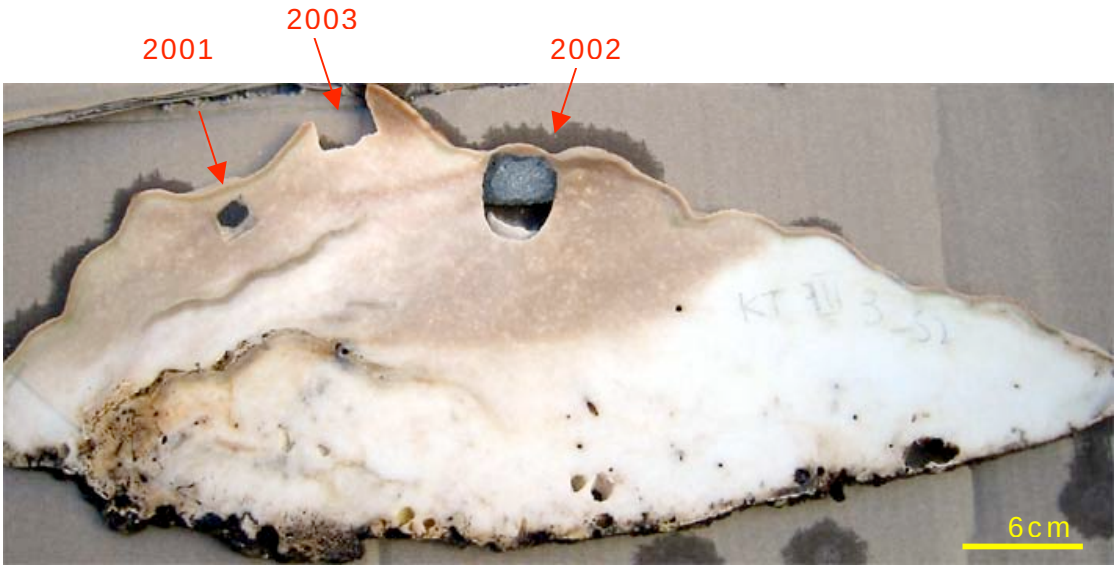



Plate 5. Slice through coral skeleton from a colony from deep water at an impact site. Arrows indicate cores taken in respective years. The overgrown concrete plug from 2002 is obvious. Tissue thickness can be seen as the thin brown band on the surface of the colony.

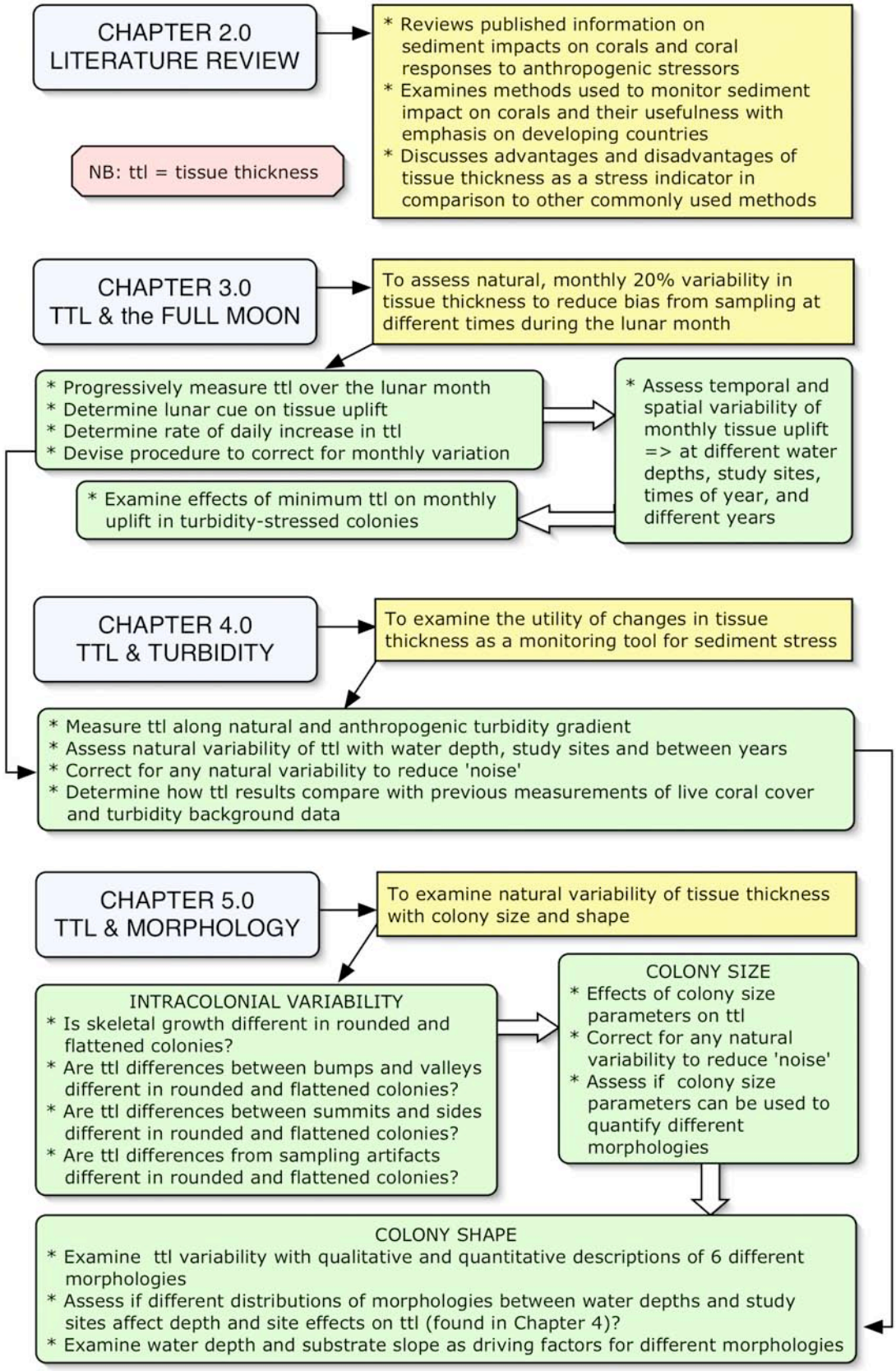
Several whole colonies were collected in 2000 and 2003 to examine skeletal growth rates in rounded and flattened colonies from a control site and a site heavily affected by sediment. In 2000, eleven rounded and 16 flattened colonies were collected at Masahet Island from shallow and deep water, respectively. These colonies were chosen to determine skeletal extension rates at a control site and for morphological measurements (Chapter 5, Section 5.4.1.). In 2003, five colonies were collected at Kapit III, a site with high turbidity impact. Four of five colonies at this site were previously examined in tissue thickness studies. These colonies were chosen because of their relatively small size (< 500 mm diameter) and rudimentary basal attachment, which made it possible to manually extract them from the field. All colonies were used to examine if tissue thickness patterns found in Chapter 3 were also apparent in skeletal extension rates. The colonies were sun-dried for several weeks and shipped back to the

Australian Institute of Marine Science (AIMS). They were cut in half along their assumed growth axis with a circular saw fitted with a masonry blade, and 7 mm thick slices were cut from one half of the colony for X-radiography and γ-densitometry analysis (descriptions of circular saw set-ups and slicing methodology are given in Barnes and Lough, 1989; also see Plate 6). Detailed descriptions of skeletal analyses are given in Barnes and Lough (1989) for X-radiography measurements and in Chalker and Barnes (1988) for γ-densitometry. Annual linear extension rates were obtained from X-radiograph positives, density was determined from the attenuation of a beam of gamma photons by a known thickness of coral skeleton (Chalker and Barnes, 1990). Annual calcification rates were determined as the mass of $CaCO_3$ deposited per unit area per year ($g.cm^{-2}$ $year^{-1}$) – the product of annual average density ($g\ cm^{-3}$) and annual extension rate ($cm\ year^{-1}$; Chalker and Barnes, 1990).

Plate 6. Circular saw with masonry blade cutting coral colony at AIMS.

1.6. STATISTICAL PROCEDURES: In this study, univariate split-plot ANOVAs were used to examine significant differences of datasets with more than one variable. Repeated measures multivariate designs were undertaken when the same individual colonies were measured over time (e.g. Chapter 3, Study 1). To establish the significance of the difference between two means, independent or paired (for comparisons between the same individuals) t-tests were used. Linear regressions were undertaken to assess the nature of the relationship between two variables. The statistical approach was decided in consultation with statistical advisors provided by AIMS and the Faculty of Mathematics, James Cook University. SPSS 11.0.2 for Mac OS X (SPSS Inc., Chicago) was used to analyse all data. Assumption testing for all analyses was undertaken as follows: studentised residuals were plotted with q-q plots in order to assess normality of the data. Levene's test and homogeneity plots of residuals versus predicted were used to assess homogeneity of variances. Natural log or square-root transformations were undertaken where assumptions of normality or homogeneity of variances proved invalid. In some cases, more than one ANOVA were to assess the data due to an unbalanced design (e.g., when comparing study sites with shallow and deep water habitats with sites having only shallow water habitats). Bonferroni's corrections were used to avoid the risk of committing a Type I error. This involved dividing the $\alpha$-value of 0.05 by the number of tests undertaken (e.g. if two tests were used $\alpha$=0.025). After an analysis was completed, all non-significant factors and interactions were removed and the test repeated (Y. Everingham, *pers. comm.*). The results of the new tests were only shown if they were significantly different from the original analyses.

## 1.7. OUTLINE OF THESIS:



# 2.0 LITERATURE REVIEW

2.1. BACKGROUND: Coral reefs are thought to be changing at local to global scales because of anthropogenic activities (e.g. Hallock *et al.*, 1993; Sebens, 1994). There are many techniques for assessing and measuring change on coral reefs, but most of these techniques detect change only after it has occurred (e.g. Edinger *et al.*, 1998). At present, there exists no simple and universally accepted technique for assessing the "health" of reefs, reef communities and reef organisms. This is unfortunate given the number and variety of natural and anthropogenic threats to reefs. Brown and Howard (1985) provided an early review of stress factors that may possibly threaten reef health. These factors and others identified in the literature since 1985 are presented in Table I. A review of the literature reveals that anthropogenically increased sedimentation and turbidity are commonly reported to be significant stress factors for many reefs. The deleterious effects of anthropogenic sediment impact on corals and coral reefs is the focus of this review.

2.1.1. What is stress and disturbance on coral reefs? Definitions, controversies and suggestions. The term "*stress"* has been applied to coral reefs and other biological communities with a variety of meanings (Richmond, 1993). One difficulty arises because stress can be seen as both a cause and an effect (Stebbing, 1981). Cause is the exogenous stimulus impacting an organism or community and effect is the response of an organism or community to that stimulus. Hughes and Connell (1999, p 932)consider stress as a "sublethal effect on the physiology of an organism,

such as a decline in feeding, growth or fecundity". Here, stress is a response. They also use the term to mean a disturbance (see definition below) that causes a decline in abundance of organisms in a community. Here stress is a cause. Stebbing (1981, p 326) uses stress to mean "the external force or stimulus that elicits generalised adaptive responses of organisms". Brown and Howard (1985, p 2) view stress as a "gradient between ideal conditions and the ultimate limit of survival", using it like Stebbing (1981) as an exogenous factor (also accepted by Tomascik and Sander, 1987a). Richmond (1993) states that he will adhere to Brown and Howard's (1985) exogenous definition, but then goes on to describe stress as an endogenous physiological condition that results from adverse or excessive environmental factors. Inherent in all definitions is the notion that stress will place any system upon which it is acting at a disadvantage by being energetically costly, thereby interfering with the normal functions of the system (Tomascik and Sander, 1987a). The impact of stress on a system will be influenced by its type, intensity and duration (Rogers, 1979). To prevent confusion related to different uses of the word "stress", it is here proposed to call the exogenous cause a *stressor* or *stress factor* and the endogenous affect a *stress response*.

Another problem applies to the distinction between "*coral stress response"* and "*reef stress response"*, which is not always straightforward (e.g., when changes in a population of a species on a reef are studied, are such changes classed as individual or community response?). Here, coral response will relate to any methodology that assesses individual coral colonies for their stress response, regardless of whether more than one

species is involved. Reef response is applied to methodologies used to assess broadscale community patterns, largely ignoring the individual coral colonies.

From an ecological point of view, a *disturbance* is “an event that damages or kills residents on a given site” (Connell, 1997, p 101) or “an ecological phenomenon which includes departures from a routine set of conditions” (Richmond, 1993, p 525). A disturbance can be classified as being of *acute* or *chronic* duration; acute disturbances generally last for a short time (minutes to days) but are often catastrophic (for example a cyclone). Chronic disturbances are long-term (weeks to years) and often have low magnitude, but persistent impact (for example terrestrial run-off). Acute stressors often kill major groups of reef organisms quite quickly, but as the stressor is removed affected reefs usually recover rapidly (Connell, 1997). A reef may be able to withstand chronic stressors, but chronic stressors can prevent full recovery following impact by an acute stressor (Kinsey, 1988; Green *et al.*, 1997a; Edinger *et al.*, 1998). If an acute disturbance occurs so frequently that there is little time for recovery, it is defined by Connell (1997) as a chronic disturbance. It then follows that the time available for recovery following a disturbance determines if the stressor is classed as acute or chronic.

Disturbances can also have either *direct* or *indirect* effects on the environment. For example, breakage during severe storms have direct acute effects while sediment runoff slowly smothering corals over a longer period following the storm would be a direct chronic effect. On the other

hand, sea urchin (*Diadema*) die-off might have an indirect acute effect since algal grazing could be greatly reduced resulting in overgrowth of corals by algae (Hughes, 1994). Eutrophication can promote an indirect chronic effect by causing increased algal growth, which can smother and kill corals (e.g. McCook, 1999). Connell (1997) found that reefs affected by anthropogenic and natural stressors recovered at similar rates and that recovery rates following direct and indirect impacts did not differ. Coral reefs are frequently disturbed by physical and biological stressors, the temporal and spatial scales of which are often too large or too small and hard to identify. Examples are storms, crown-of-thorn starfish (*Acanthaster planci*) outbreaks and coral bleaching events, some of which may be related to long-term changes in global climate (e.g. Hoegh-Guldberg, 1999). Stressors may not have direct acute or direct chronic effects but may affect recruitment and regeneration and affect communities over long time scales (Hughes and Connell, 1999). Anthropogenic stressors may be difficult to detect when they are superimposed on natural stressors, especially where the natural stress factor has the greater effect (Hughes and Connell, 1999). This is particularly true with the potentially large-scale, long-term effects of global climate change. For example, it may become more difficult to differentiate the coral bleaching stress response to anthropogenic stressors such as increased pollution from terrestrial run-off from the coral bleaching response to chronically rising sea surface temperatures.

Corals are well adapted to surviving natural environmental change and acute, natural disturbances are critical to maintenance of diversity of reefs

(Richmond, 1993). As two authors (Kinzie and Buddemeier, 1996, p 489) state: “Corals do not simply tolerate environmental changes, but react with an impressive array of acclimations in the short term, adaptations at the population level in the longer term and even changes in the community composition over even longer time periods”. Human activities, however, can transform natural disturbances into persistent and chronic disturbances. For example, the clearing of coastal forests increases natural suspended sediments and nutrients in terrestrial runoff causing direct and indirect effects on algal and coral growth and competition (Nystrom *et al.*, 2000). It is, therefore, important to identify natural environmental variability in coral reef systems before it is possible to identify changes due to unnatural stress factors. It is generally agreed that cumulative anthropogenic stressors are the most important threat to corals and reefs (e.g. Wilkinson, 1992; Hughes and Connell, 1999; Wilkinson, 1999; Nystrom *et al.*, 2000).

2.1.2. What are the most common anthropogenically-induced stress factors? A multitude of anthropogenic stressors affect corals and coral reefs around the world. These can be summarised into six major categories: sediment stressors, pollution, eutrophication, direct structural damage, exploitation of reef-associated fauna and flora and climate change (Fig. 2). Anthropogenically-induced stress factors do not always fall into just one of these major stress categories. For example, blast-fishing kills fish and other reef organisms and causes structural damage. Similarly, ship groundings cause structural damage but may also affect reefs through spillage of toxic

materials. The categories in Fig. 2 were chosen with regards to the most obvious effects on reefs from anthropogenically-induced stressors.

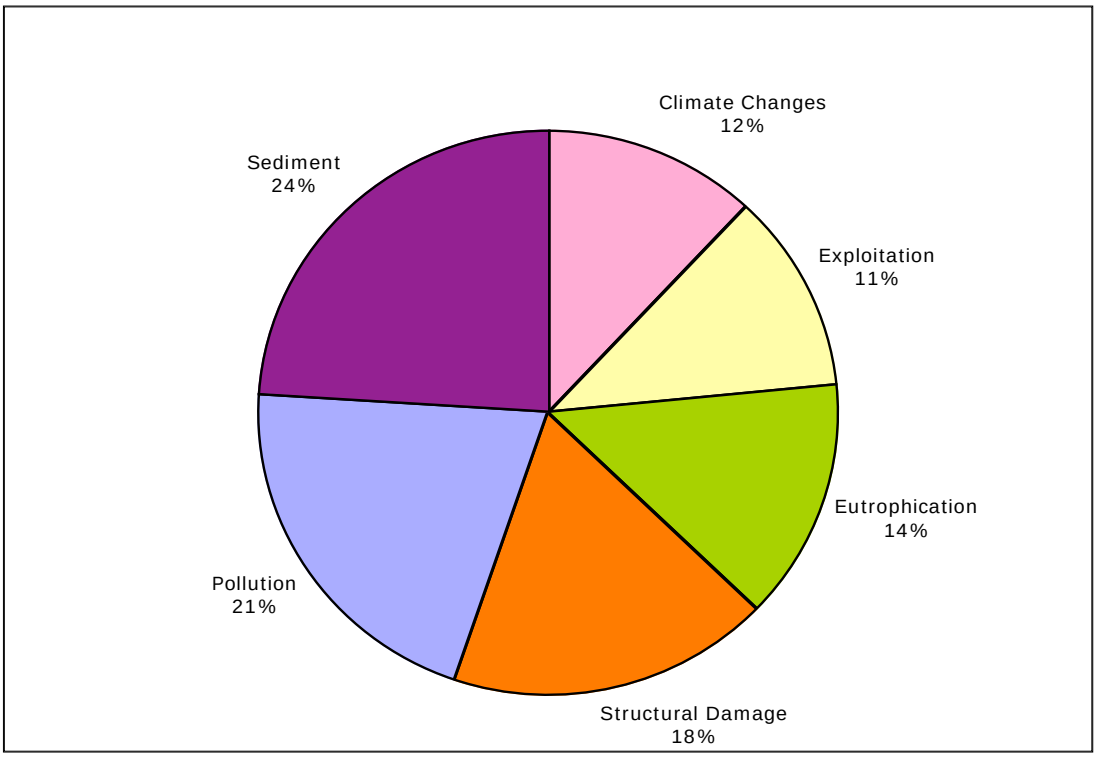



Figure 2. Human impacts on coral reefs mentioned in 357 scientific papers on coral reef ecology since 1985 (in %). See text for problems with generalizations of impact categories.

In the 357 publications reviewed, considerably more research has been devoted to sediment impacts, pollution and structural changes to reefs than to climate change, exploitation and eutrophication. Burke *et al.* (2002) found much the same distribution of research effort for anthropogenic impacts on southeast Asian reefs. Research on the effects of eutrophication on corals and coral reefs appears to have declined in recent years, possibly due to difficulties in identifying definite long-term stressors associated with elevated nutrient levels (e.g. Rawlins *et al.*, 1998; Koop *et al.*, 2001). Climate-change research has increased over the last 10 years, mostly because of research into mass coral bleaching, which is thought to be increasing with global warming (e.g. Hoegh-Guldberg, 1999). A number of

anthropogenic activities are commonly associated with each of the major stress categories depicted in Figure 2. These are listed and summarised in Table I below.

Table I. Major categories of anthropogenic impacts on coral reefs, their causes, comments and examples from the literature.

| Major stress category | Cause | Comments | Examples in literature |
|---|---|---|---|
| SEDIMENT (sedimentation and turbidity) | Deforestation | Leads to destabilised soil, increases run-off | (Ingram, 1994) |
| | Mine Tailing and Dumping | Either submarine tailing disposal or direct dumping into harbours | (Barnes and Lough, 1999) |
| | Dredging and Filling | Often for shipping channels | (Brown *et al.*, 1990) |
| | Land Reclamation | Particularly in countries with high population densities | (Hilton and Manning, 1995) |
| POLLUTION (chemicals, metals, radioactive waste, oil, toxic waste) | Shipping, Dumping at Sea | Problem in all major reef areas | (Al-Awadhi, 1999) |
| | Oil Mining, Production, Spills | Petroleum hydrocarbons bind with sediment, reduce coral growth and fertility | (Acuna *et al.*, 1997) |
| | Herbicide and Pesticide | Toxic effects on corals, land run-off | (Glynn *et al.*, 1989) |
| | Litter | Can smother or bury colonies | (Evans *et al.*, 1995) |
| | Desalination Effluents | Increases salinity near outfall | (Ferrier-Pages *et al.*, 1999) |
| | Thermal Effluents | Increases water temperature near outfall | (Coles, 1985) |
| | Nuclear Testing/Outfalls | Corals can incorporate radioactive materials from water column into skeletons | (Hudson, 1985) |
| | Mining and Smelting | Uptake of heavy metals into coral skeletons | (Fallon *et al.*, 2002) |
| STRUCTURAL CHANGES (destruction or destabilization of reef structure) | Coral Mining | Use of limestone for building materials | (Sluka and Miller, 1998) |
| | Aquaculture | Displacement of reefs by aquacultural facilities | (Maragos, 1993) |

| | | | |
|---|---|---|---|
| STRUCTURAL CHANGES (destruction or destabilization of reef structure) cont'd | Anchor Damage | Physical destruction of coral | (Rotmann, 1998) |
| | Urbanization and Coastal Development | Increased reclamation of reef areas for extending cities and industries | (Zann, 1994) |
| | Tourism | Impact from diving, snorkelling, reef walking, hotels | (Hawkins and Roberts, 1994) |
| | Ship Grounding | Destruction of reef area | (Smith, 1985) |
| | Engineering Modifications | Blasting, dredging of channels etc | (Kaly and Jones, 1994) |
| EUTROPHICATION (nutrients, mainly Phosphate and Nitrogen) | Sewage Effluents | Often untreated, near major urban centres, particularly in developing countries | (Hunter and Evans, 1995) |
| | Agricultural Run-Off | Often due to deforestation for agricultural purposes | (Carpenter *et al.*, 1998) |
| | Fertilisers | Agriculture, mainly N and P | (Rawlins *et al.*, 1998) |
| | Phosphate Mining & Shipping | Particularly relevant in Red Sea | (Abuhilal, 1994) |
| EXPLOITATION (removal of coral or reef associated fauna) | Fisheries | Destructive use of cyanide, blasting and nets, change in community structure | (Jennings and Polunin, 1996) |
| | Curio Trade and Collection of Reef Elements | Usually small scale, local fisheries | (Wells and Wood, 1991) |
| CLIMATE CHANGE (global phenomenon) | Sea Surface Temperature | Increases in SST harmful | (Lough, 2000) |
| | Sea Water Chemistry | Resulting in reduced calcification | (Wilkinson, 1999) |
| | El Niño Southern Oscillation | Global weather change | (Carriquiry *et al.*, 2001) |
| | UV Radiation | Increases in UV A and B harmful | (Anderson *et al.*, 2001) |
| | Storms | Increased frequency physical destruction | (Done, 1999) |

This study examines the impact of mining activities on coral reefs at Lihir Island, PNG. Mining activities have increased turbidity and reduced light levels on some coral reefs at Lihir Island (Thomas, 2003). Thus, this review focuses on the effects of anthropogenically increased sedimentation and

turbidity on coral reefs. There is little agreement on the extent and severity of sediment impact on corals and coral reefs in the literature (see below). This is mainly related to the confusion in terminology describing the stressors (see Section 2.1.3); to using greatly differing methods measuring both the stressors (Section 2.1.4) and the stress responses (Sections 2.1.5 and 2.2); and to the large range of coral stress responses (Section 2.1.3).

2.1.3. Sedimentation and turbidity effects on corals. A wide range of time scales and physical, geological and chemical processes are covered by the terms “sediment accumulation”, “sediment deposition” and “sedimentation” (Thomas, 2003). Thomas (2003, p 15) described the process of sediment accumulation as 'particles settling under gravity through the water column and reaching the bottom of the water body, which is defined as the water/sediment interface'. Sedimentation is the process of sediment accumulated over time. Sedimentation can affect corals by 1) reducing coral performance through redirection of energy and energy reserves to sediment rejection mechanism (Stafford-Smith and Ormond, 1992); 2) smothering and burial (Fabricius and Wolanski, 2000); 3) abrasion of soft tissues (Stafford-Smith, 1993); 4) inhibiting larval settlement on unstable substratas (Gilmour, 1999); 5) interference with coral respiration and photosynthesis (Peters and Pilson, 1985) and 6) modified exchange and/or supply of nutrients and other chemicals from deposited sediment (Woolfe and Larcombe, 1999).

Rogers (1990) reviewed the major responses of corals and coral reefs to sediment stress. She found that increased sedimentation rates resulted in

fewer coral species, reduced live coral cover, lower coral growth and lower calcification rates, increased coral bleaching, increased abundance of branching forms, changes in colony morphology, increased abundance of smaller colonies (due to their greater efficiency at sediment rejection) or population shifts to larger colonies (due to reduced larval recruitment and slower rates of reef accretion). The effects of sedimentation described by Rogers (1990) were related to high sedimentation rates (>10mg $cm^{-2}$ $d^{-1}$). Several studies have found that moderate sedimentation scarcely affects coral colonies (e.g. Peters and Pilson, 1985; Riegl, 1995; McClanahan and Obura, 1997) and can have beneficial effects through nutrients associated with the sediment (Anthony, 1999c; Rosenfeld *et al.*, 1999). Rates and impacts of sedimentation on coral reefs were also found to differ between locations, making comparisons difficult (Pastorok and Bilyard, 1985). Corals adopt a variety of strategies to cope with excessive sedimentation. These strategies include the use of their tentacles and cilia to physically disperse sediments, stomodeal distension through uptake of water and subsequent deflation through water expulsion to dislodge settled particles, and the entanglement of sediments in mucus, which later sloughs off the colony surface (Stafford-Smith and Ormond, 1992). Corals exhibit both active and passive removal of sediment particles. Where currents are strong, water movement will help prevent sediment particles from settling on colony surfaces. Different species also differ in their ability to reject sediment, with colony and calyx morphology playing an important role (Rogers, 1990). It is very difficult to compare the stress response of corals and coral reefs to sedimentation due to the large variety of strategies adopted by various coral species and colony morphologies. In addition, the hydrodynamic

environment and topography of a reef, as well as the source and type of sediment particles also affect the extent of sedimentation impacts on corals and coral reefs. To alleviate these issues, detailed descriptions of the source and type of sediment and the extent and geological time frame of sediment accumulation have to be given (e.g. Thomas, 2003). Also, the physical characteristics of the location and the type of stress response assessed in particular species or assemblages of corals have to be provided.

The term “sedimentation” has sometimes been confused to include suspended particles in the water column (e.g. Walker and Ormond, 1982; Gilmour, 1999). However, the amount of solid particles that are suspended in the water column and that cause light rays shining through the water to scatter are termed ‘turbidity’ (Parker, 2004). Turbidity reduces illumination of photosynthetic reef organisms by absorbing (Anthony and Fabricius, 2000) and scattering light (Dodge and Vaisnys, 1977). The most common impact of high turbidity on reef corals is a decrease in photosynthesis and an increase in respiration (e.g. Telesnicki and Goldberg, 1995b; Te, 1997). Increased turbidity may result in decreased coral species diversity and abundance in corals (van Woesik, 1993), increased coral bleaching (True, in review), changes in coral morphology and metabolism (Meesters *et al.*, 2002) and a shift in coral zonation towards shallow depths (Acevedo *et al.*, 1989). Corals adapt to increased turbidity by photoadaptive mechanisms similar to those by which they adapt to increased depth, including changes at the cellular level and behavioral and morphological variations (Meesters *et al.*, 2002). As with sedimentation, some studies have found no

significant impact from elevated turbidity (e.g. Yamazato, 1987) and increased turbidity can be beneficial by supplying food (Anthony, 2000). It is important to recognise that clear evidence exists to demonstrate that increased sedimentation and turbidity are not always detrimental to coral and reef health.

2.1.4. Methods of measuring sediment impact. In order to quantify the stress response of corals to sedimentation or turbidity impact and compare it with other studies, the extent and type of the stressor will have to be assessed first. Instruments to record data associated with sedimentation and turbidity were, until recently, complex and expensive (Moore, 1999). Even though many oceanographic parameters can now be continuously logged cheaply, the continuous logging of light intensity, is still problematic (e.g. McField, 1999). This means that a range of techniques and procedures has been used to monitor sedimentation and turbidity on coral reefs, often making it difficult to compare results obtained by different researchers. Methods of measuring sediment accumulation are described in detail by Thomas (2003). Sediment traps are simple, commonly used instruments (Rogers, 1990) that provide an excellent example of difficulties that arise in trying to compare results obtained by different researchers. The amount of sediment captured by traps depends upon their height to aperture ratio because this affects re-suspension of trapped sediments by water currents. Also, more sediment is collected by traps placed on or just above the substrata than by traps place higher in the water column (Rogers, 1990; Meesters *et al.*, 1998). Furthermore, it is important to recognise that sediment traps effectively collect all sediment passing over

the area covered by the trap and are not designed to release sediments that would normally be re-entrained and transported elsewhere. As a result, sediment traps do not measure the net rate of sedimentation that would naturally occur as a result of flux rate over the area covered by the trap and instead may yield a relatively high accumulation rate that is not a true reflection of the sedimentation rate (NSR, 1989). Nevertheless, sediment traps are simple, hardy, inexpensive and applicable from intertidal areas to deep water. More sophisticated sensors, such as sediment accumulation sensors (SAS, described by Thomas *et al.*, 2002) and optical backscatter sensors (OBS, Ridd and Larcombe, 1994) also have their problems and are frequently plagued by equipment failure and low reliability (Thomas, 2003; Orpin *et al.*, in press).

Nephelometers are instruments used to measure turbidity. Telesnicki and Goldberg (1995a) and Te (1997) review problems associated with nephelometry. Nephelometry can underestimate turbidity in the field by as much as 50% (Telesnicki and Goldberg, 1995a). Scattering properties also vary non-linearly through the water column (e.g. Orpin *et al.*, in press), with different conditions at the surface and near the bottom, which is a problem when instruments are located at fixed, preselected depths. Turbidity data is not easily converted into sediment accumulation rates and vice versa, but some studies have used turbidity data inappropriately as a proxy for instantaneous sediment accumulation rates or have related sediment trap data to water turbidity (see Woolfe and Larcombe, 1999). Care has to be taken when comparing studies examining sediment impact on corals due to the large range of measurements used to quantify this

stress factor and the logistical problems inherent in measuring sediment impact in a large body of water. Continuous logging of underwater light levels at various depths through the water column may be the most useful method in determining turbidity stress on reef corals.

2.1.5. Field versus laboratory experiments. When chosing to undertake a study on the stress response of corals to a known stress factor, two possible approaches can be taken – a field study or a laboratory experiment. Underwood and Peterson (1988) described problems and differences associated with assessing responses to impacts from stressors in the field and the laboratory. They were mostly concerned with the effects of pollution. According to Underwood and Peterson (1988), the aim of a laboratory experiment is to hold constant as many confounding variables as possible and then to vary those of interest. A field experiment, on the other hand, permits uncontrolled natural variations in all variables except the one that is being manipulated (see also Brown and Howard, 1985 for a discussion of these issues). For studies of sustained or chronic stressors, including sediment impact, field experiments are best used when comparing amongst different sites subject to different levels of impacts (Rogers, 1990). Rees *et al.* (1999) suggest that it is important to measure the performance of stressed organisms in the natural environment. This is because organisms may be subject to considerable strain from being kept under laboratory conditions and it may be difficult to separate this stressor from that being artificially imposed, even between controls and treated groups (Hedgpeth, 1973). Indeed, several studies found apparent contradictions between results obtained in laboratory and in field studies

(e.g. Hedgpeth, 1973; Bak, 1987; Stimson, 1997). Field studies offer advantages over laboratory studies where increase in sediment impact is due to industrial, agricultural or urban development, largely because field studies investigate the actual responses to such human activities. This is especially the case where environmental data is available for a site before impacts began, as it was the case in this study on Lihir Island.

2.1.6. Developed versus developing nations. The methodology used to assess reef and coral health must be adapted to the different needs and resources of a particular country. Several factors restrict the easy implementation of research programs on coral reefs. These include: difficulties associated with working in a shallow marine environment, the multinational distribution between countries, which often have different legislations and the fact that 90% of countries with reefs can be classified as developing nations. These nations usually have limited funds, widespread poverty, ineffectual law enforcement and populations dependent on exploiting reefs for their day-to-day survival (Rajasuriya *et al.*, 1995; Goreau, 1997; Ross and Delorenzo, 1997; Risk, 1999; Munday, 2000). Global centres of high reef coral diversity coincide with human population centres, especially in southeast Asia and the Caribbean, which have the greatest potential for species loss (Wilkinson, 1992; Chadwick-Furman, 1996). Most reef research has been carried out on a few hundred reefs which are either convenient to access, that is, near the surface or surface-breaking, or especially significant due to their size or historical activities (Eakin *et al.*, 1997, see Figure 2). Almost 75% of all sediment impact research has been focussed on reefs off Florida and the Caribbean

and on Australia's Great Barrier Reef (GBR; Fig. 3). Developing nations have limited access to research funds, equipment and qualified environmental scientists to carry out regular monitoring programs (Machiwa, 1992) and generally have little use for the sophisticated techniques developed by western scientists (Risk *et al.*, 1993).

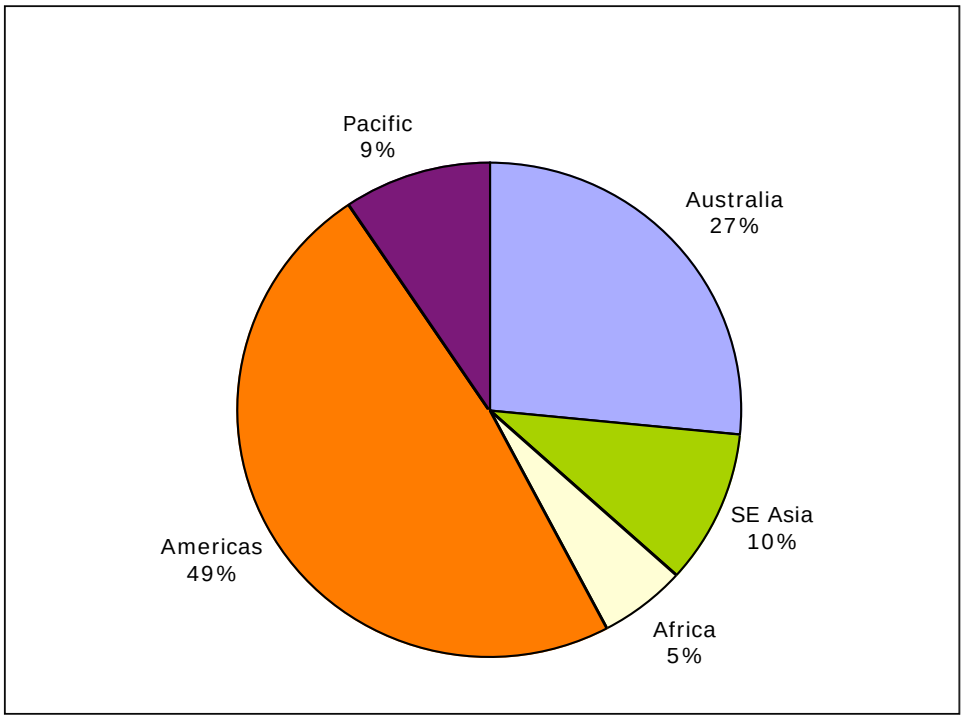



Figure 3. Percentage research undertaken on sediment impact on corals in different areas (from 128 papers on coral reef ecology)

Reef destruction results in direct economic impact and indirect costs when the protective function of reefs is removed. These losses will far exceed any short-term economic benefits (e.g. Wilkinson, 1996; Cesar *et al.*, 1997; Berg *et al.*, 1998; Wilkinson, 1999; White *et al.*, 2000) and the first step to mitigation involves assessing the extent of reef destruction. This study was undertaken in a remote developing country with limited facilities for sophisticated research methods. Thus, this review will concentrate on the utility of most commonly used monitoring methods for developing countries and if these methods can potentially be adapted by local communities.

## 2.2. DIFFERENT METHODOLOGIES TO MEASURE CORAL AND REEF STRESS RESPONSE TO SEDIMENT IMPACT:

2.2.1 Individual versus community stress response. Impacts can be studied at organism, community and ecosystem levels. Studies at community and ecosystem levels have the disadvantage that change has usually occurred before it becomes evident (for example, measuring live coral cover or using mortality indeces, Edinger *et al.*, 1998). Studies at the organism level may detect change earlier than studies at higher levels (for example, heat shock proteins which react to a stressor in real time, Wiens *et al.*, 2000). Thus, excursions of physiological and biochemical variables outside of normal limits may indicate that an organism is stressed well before that organism shows visible changes such as tissue lesions or death. Community responses, on the other hand, can provide more insight into large-scale patterns of survival and recovery (Underwood and Peterson, 1988).

Peters and Pilson (1985) presented a scheme that summarised the types of measurements used to assess sediment stress in corals that was also later adopted by Rogers (1990). This scheme has been augmented with the results of more recent research, including that which considers community level responses, and is presented in Table II below.

Table II. General ways to assess coral and reef response to sediment impact.

| | CORAL RESPONSE TO SEDIMENT STRESS | REEF RESPONSE TO SEDIMENT STRESS |
|---|---|---|
| Visual observations | Behaviour:<br>1) Unusual polyp contraction and expansion<br>2) Extrusion of mesenterial filaments<br>3) Unusual mouth opening responses<br>4) Change in feeding behaviour<br>5) Increased mucus production/muco-ciliary activity<br>6) Polyp bail-out<br><br>Appearance:<br>7) Lesions, partial mortality, disease<br>8) Size-frequency composition<br>9) Changes in coral morphology<br>10) Changes in larval dispersal, recruitment and settlement | Appearance:<br>1) Increase in bleaching<br>2) Changes in community composition, usually decrease in species diversity and live coral cover and structural complexity<br>3) Decrease of bioindicator organisms<br>4) Increase in bioerosion and fouling patterns |
| Physiological Measurements | Metabolism:<br>1) Variation in metabolic rate based on respiration<br>2) Change in excretion rate/excretory products<br><br>Biochemistry:<br>3) Differences in biochemical composition<br>4) Genetic effects<br><br>Growth:<br>5) Decrease or increase of calcification rates, linear extension rates or skeletal density<br>6) Patterns in the isotopic composition of the coral skeleton<br>7) Patterns in other inclusions in the coral skeleton<br>8) Changes in the thickness of the living tissue layer<br><br>Photosynthesis:<br>9) Changes in zooxanthellae or photosynthetic pigmentation | Metabolism:<br>1) Reef metabolism: productivity and respiration, calcification and solution of reef rock |
| Histopathological Examinations | 1) Reduced gonad development or change in reproductive cycle and fecundity<br>2) Change in morphology and/or composition of tissues and cells, abnormal accumulation of biogenic deposits<br>3) Presence of microparasites or pathogens | |

Table III lists detailed methodologies used to study both coral and reef stress response to sediment stress under the general headings shown in Table II. The most commonly used methodologies are discussed in more detail below.

Table III. Examples of specific measurements of coral response to sediment impact

| GENERAL METHODS | SPECIFIC MEASURES | REFERENCES |
|---|---|---|
| VISUAL OBSERVATIONS | | |
| BEHAVIOUR | Polyp contraction and expansion, and sediment rejection | (Rotmann, 1998)<br>(Lasker, 1980)<br>(Anthony, 1999a)<br>(Anthony, 2000)<br>(Gleason, 1998)<br>(Logan, 1988)<br>(Riegl, 1995)<br>(Stafford-Smith and Ormond, 1992)<br>(Stafford-Smith, 1993) |
| | Extrusion of mesenterial filaments | (Hodgson, 1990)<br>(Riegl, 1995)<br>(Stafford-Smith, 1992) |
| | Increased mucus production | (Fabricius and Dommisse, 2000)<br>(Kato, 1987)<br>(Coffroth, 1985)<br>(Stafford-Smith, 1992)<br>(Rice and Hunter, 1992) |
| APPEARANCE OF CORALS | Lesions & partial mortality | (Hodgson, 1990)<br>(Rogers, 1983)<br>(Van Katwijk *et al.*, 1993)<br>(Wesseling *et al.*, 1999)<br>(Stafford-Smith, 1992)<br>(Raimondi *et al.*, 1997)<br>(Marszalek, 1981)<br>(Croquer *et al.*, 2002)<br>(Nugues and Roberts, 2003b) |
| | Disease & bleaching | (Ravindran *et al.*, 2001)<br>(Kato, 1987)<br>(Nugues and Roberts, 2003a) |
| | Morphological changes | (Hands *et al.*, 1993)<br>(Riegl *et al.*, 1996)<br>(Irving and Connell, 2002)<br>(Bell, 2002)<br>(Sauer, 1996)<br>(Todd *et al.*, 2004)<br>(Schleyer and Celliers, 2003) |
| | Changes in larval settlement, recruitment | (Babcock and Davies, 1991)<br>(Gilmour, 1999)<br>(Torres and Morelock, 2002)<br>(Crabbe and Smith, 2003)<br>(Tamelander, 2002)<br>(Szmant, 2002) |
| APPEARANCE OF REEFS | Large-scale bleaching | (Done, 1996a)<br>(Rotmann, 2001 b)<br>(Rice and Hunter, 1992)<br>(Burke *et al.*, 2002)<br>(Berkelmans *et al.*, 2002)<br>(Nemeth and Nowlis, 2001) |
| | Bioindicator organisms | (McClanahan and Obura, 1997)<br>(Van Katwijk *et al.*, 1993)<br>(Aerts and Vansoest, 1997)<br>(Umar *et al.*, 1998) |
| | Bioerosion and fouling | (Rotmann, 2001 a)<br>(Macdonald and Perry, 2003)<br>(Edinger *et al.*, 2000) |

| | | |
|---|---|---|
| APPEARANCE OF REEFS (cont'd) | Monitoring community changes | (Done, 1996b)<br>(NSR, 2000)<br>(Neil, 1990)<br>(Chao, 1988)<br>(Guzmán and Guevara, 1998)<br>(McClanahan and Obura, 1997)<br>(Muzik, 1985)<br>(Riegl, 1995)<br>(Van Katwijk *et al.*, 1993)<br>(Yamano *et al.*, 2000)<br>(Yamazato, 1987)<br>(Gleason, 1998)<br>(Rice and Hunter, 1992)<br>(Risk, 1983)<br>(Brown *et al.*, 1990)<br>(Gabrie *et al.*, 1985)<br>(Kelmo *et al.*, 2003)<br>(Brown *et al.*, 2002)<br>(Edinger *et al.*, 1998)<br>(Meesters *et al.*, 1998)<br>(Nugues and Roberts, 2003b)<br>(Chansang *et al.*, 1981)<br>(Torres and Morelock, 2002)<br>(Hunter and Evans, 1995)<br>(Acevedo *et al.*, 1989)<br>(Hands *et al.*, 1993)<br>(Chiappone *et al.*, 2001)<br>(Nemeth and Nowlis, 2001)<br>(Rogers and Garrison, 2001)<br>(Torres *et al.*, 2001)<br>(Edinger *et al.*, 2000)<br>(Crabbe and Smith, 2003) |
| PHYSIOLOGICAL MEASUREMENTS | | |
| METABOLISM | Coral metabolism | (Peters and Pilson, 1985)<br>(Anthony and Fabricius, 2000)<br>(Edmunds and Spencer-Davies, 1989)<br>(Riegl, 1995)<br>(Telesnicki and Goldberg, 1995b) |
| | Reef metabolism | (Charpy *et al.*, 1998)<br>(Boucher *et al.*, 1998)<br>(Clavier and Garrigue, 1999) |
| BIOCHEMISTRY | Heat-shock-proteins | (Wiens *et al.*, 2000) |
| | Lipids | (Guzman and Holst, 1993)<br>(Anthony and Fabricius, 2000) |
| | Lysosomes | (Rees *et al.*, 1999) |
| | DNA | (Meesters *et al.*, 2002) |
| PHOTOSYNTHESIS | PAM | (Philipp and Fabricius, 2003)<br>(Jones *et al.*, 2003) |
| | Other | (Mascarelli and Bunkley-Williams, 1999)<br>(Philipp and Fabricius, 2003)<br>(Muslim and Jones, 2003)<br>(Cruz-Pinon *et al.*, 2003) |

| | | |
|---|---|---|
| GROWTH | X-radiography | (Dodge *et al.*, 1992)<br>(Heiss, 1996)<br>(Lough *et al.*, 1995)<br>(Tomascik and Sander, 1985)<br>(Brown *et al.*, 1990)<br>(Hudson *et al.*, 1989)<br>(Aller and Dodge, 1974)<br>(Budd *et al.*, 1993)<br>(Barnes and Lough, 1999)<br>(Torres and Morelock, 2002)<br>(Readman *et al.*, 1996)<br>(Swart *et al.*, 1996a)<br>(Bastidas and Garcia, 1999)<br>(Edinger *et al.*, 2000)<br>(Crabbe and Smith, 2003) |
| | Gamma-densitometry | (Lough *et al.*, 1995)<br>(Barnes and Lough, 1999)<br>(Bastidas and Garcia, 1999) |
| | Buoyant weighing | (Peters and Pilson, 1985)<br>(Davies, 1989)<br>(Anthony, 1999c)<br>(Rice and Hunter, 1992)<br>(Brown *et al.*, 1990) |
| | Alizarin Red S | (Todd *et al.*, 2004)<br>(Brown *et al.*, 1990)<br>(Chansang *et al.*, 1992) |
| | Isotopes | (Risk *et al.*, 1994)<br>(Heiss, 1996)<br>(Chakraborty and Ramesh, 1997)<br>(True, 2001) |
| | Other inclusions | (Naqvi *et al.*, 1996)<br>(Bastidas and Garcia, 1999)<br>(Guzmán and Jiménez, 1992)<br>(Fallon *et al.*, 2002)<br>(David, 2003)<br>(Mokhtar *et al.*, 2002)<br>(Guzman and Garcia, 2002)<br>(Alibert *et al.*, 2003) |
| | Tissue thickness | (Lough *et al.*, 1995)<br>(Barnes and Lough, 1999)<br>(True, 1995)<br>(True, 2001)<br>(Rotmann, 2001 a)<br>(Rotmann, 2003)<br>(Cruz-Pinon *et al.*, 2003) |
| | Fluorescent banding | (Brown *et al.*, 1990)<br>(Hudson *et al.*, 1994)<br>(Isdale *et al.*, 1998)<br>(Risk *et al.*, 1992) |
| | Other | (Goh and Chou, 1995)<br>(Heiss, 1996)<br>(Vago *et al.*, 1994) |
| HISTOPATHOLOGICAL MEASUREMENTS | | |
| REPRODUCTION | Number of gonads & gonad size | (Van Veghel and Kahmann, 1994)<br>(Dubinsky and Stambler, 1996)<br>(Guzman and Holst, 1993) |
| | Recruitment | (Gilmour, 1999)<br>(Tamelander, 2002)<br>(Richmond, 1993) |
| TISSUE | Microscopic changes in cells | (Peter & Pilson, 1985) |
| DISEASE & PATHOGENS | Presence of microparasites | (Richardson, 1997) |

2.2.2. Methods most commonly used to detect reef stress response to sediment impact

*2.2.2.1. Reef monitoring:* The response of coral reefs to sediments is chiefly followed by monitoring for change in reef communities (see Table III). “Monitoring is the collection of information about the state of a system or resource and its changes over time” (Dahl, 1981, p 545). A good monitoring program should detect changes in a community, provide some idea of the rate of change and the likely stress factors (Risk, 1999). The most commonly used indicator for reef stress response is abundance of key organisms, such as common species of hard corals and live coral cover.

Changes in population structure, size frequencies of key organisms, mortality indices for key organisms (e.g., ratio of dead coral cover to the sum of dead and live coral cover) and the species composition of reef communities (evenness, richness, diversity) may also indicate stress effects on reefs. ‘Normal’ values of these indicators are hard to define, due to their considerable spatial and temporal variability (Hughes and Connell, 1999). Coral cover may not be a reliable index of coral health, since, even in unspoiled communities, not all parts of the reef are available to corals (Gomez *et al.*, 1994). Also, many reefs are growing in - or being initiated in, non-optimal habitat conditions. In such conditions, live coral cover can be high, but species diversity is low, and hardy, more resilient species are favoured. A low coral cover may simply reflect local and regional variation in abundances, or the short-term impact of a recent natural disturbance (Kenchington, 1978). Also, an increase in the number of colonies following an impact, does not necessarily imply that the assemblage has recovered in

its colony size structure, rates of reproduction and growth, species composition and diversity (Connell, 1997). Counting coral colonies per unit area without measuring their size creates problems because a few large colonies can be statistically drowned by many small fragments. Moreover, the number of colonies in a monospecific stand may be impossible to determine (Pichon, 1978; Dahl, 1981). Hedgpeth (1973) also warns of the highly speculative basis for concepts such as diversity, as a limited grouping of species does not necessarily indicate a stressed or unstable situation.

The effect of a particular disturbance can also depend on the impact of antecedent stress factors; thus even a recurrent stressor can have different effects at different times (Hughes, 1999). It is argued that a single survey will provide a snapshot of the reef status (Hughes, 1993), but a longer-term approach is required to understand the processes underlying changes in assemblages, because many ecological processes are slow and many reef organisms are long lived (Hughes, 1993; Wilkinson, 1999). However, long-term monitoring can be expensive and time consuming, and large amounts of data must be collected (Risk, 1999). Often, 30-50 years are required to accumulate enough baseline data to allow useful generalizations to be made. Monitoring based on corals can introduce a large time-lag, between the process and the response (Lough and Barnes, 1997; Risk, 1999). Risk (1999) simply regards most monitoring programs as a ‘waste of money’. The best way to investigate stress effects on reefs, is to measure the abundance of corals before and after the disturbance and at impact and control sites (BACI design, e.g. Connell, 1997; Kaly and Jones,

1997), as undertaken by NSR (1989) on Lihir Island. However, in the majority of studies this was impossible, as most were begun in response to a disturbance (Connell, 1997). The main resources that constrain BACI sampling designs are money, time and the availability of suitable sites in which it is possible to distinguish human impacts from natural variations (Kaly and Jones, 1997).

*2.2.2.2. Coral bleaching:* Reef-building corals often lose their symbiotic algae when subjected to stress. The corals then appear white rather than brown or green because their white skeleton is visible through the transparent animal tissues. This effect is known as bleaching and it is easily identified with the naked eye. Indeed, large-scale bleaching can be detected using remote sensing techniques. However, if the stressor is a large-scale sediment plume, remote sensing techniques may not be able to penetrate the water column to detect bleached reefs. Bleaching increases in severity for weeks after a stress factor has been removed and there can be a substantial delay between the stressor and an observable bleaching response (Berkelmans and Oliver, 1999). Spencer *et al.* (2000) suggest that the lack of a standardized method to quantify the level of bleaching is a major problem, often resulting in overestimation of the scale and severity of bleaching by inexperienced observers. Bleaching has mainly been linked to increases in sea surface temperature and/or UV light (e.g. Lesser, 1996; Hoegh-Guldberg, 1999; Anderson *et al.*, 2001), and it has rarely been linked solely with increases in sediment, although sediment impact is commonly mentioned as a possible cause for coral bleaching (e.g. Glynn, 1996; Meehan and Ostrander, 1997). However, one study found that

bleaching increased by 38% in colonies exposed to sedimentation rates between 10-14 mg $cm^{-2}$ $d^{-1}$ (but see Nemeth and Nowlis, 2001). These authors also found that sedimentation may lead to declining live coral cover through the secondary effects of bleaching. True (in review, Chapter 5, p 12) called bleaching the 'final act of desperation' and thought that this action would be accompanied by a virtual shutdown of metabolism and, if the stressor persisted, death. The rather limited evidence linking bleaching as an unequivocal stress response to sediment impact and that it is regarded as a 'last resort' stress response suggest it to be of limited use as a rapid indicator of reef stress response. The inherent, large, observer-dependent bias describing 'bleaching' also limits its use for local communities assessing their reef's 'health' to mainly anecdotal evidence.

*2.2.2.3. Main methods used to assess visual stress response of corals or reefs:* There can either be a general visual assessment of a reef where aspects of its condition are recorded (e.g. bleaching) or a census obtaining estimates of population changes. They may be used in parallel. The extent of the area, the objective of the survey and the time and resources available should influence the choice of methodology. Different methods to monitor stress response of reef communities are described in Table IV:

Table IV. Main methods of visually assessing reef or coral stress response to sediment, their advantages and disadvantages.

| METHOD | AREA COVERED | DESCRIPTION | COMMENTS | EXAMPLES |
|---|---|---|---|---|
| Quadrats | ~0.5-1$m^2$ | Usually 1$m^2$ quadrats are randomly placed on reef and all species in quadrat are identified, measured and recorded | Variable results due to small spatial scales at which reef dynamics are unpredictable<br>Usually limited to reef flat | (Aronson and Precht, 1995)<br><br>(Loya, 1978) |

| | | | | |
|---|---|---|---|---|
| Line Point Intercept | ~30-50m | A line is laid out along the depth contour and transition points between adjacent life forms are recorded to the nearest cm | Regarded as most efficient method to spend monitoring underwater<br>Do not take structural diversity into account<br>Impractical for surveying more than a few sites | (Brown and Howard, 1985)<br>(Green and Smith, 1997)<br>(Aronson and Swanson, 1997) |
| Video and photo transects | ~100m | Photos or video recordings are taken along either side of a transect and examined later | Video: cost-savings in field expenses and in the production of a permanent visual record<br>Standardised, can be replicated over large spatial scales, non technical doesn't need specialist knowledge<br>Reduced taxonomic resolution, expense of equipment<br>Photos: higher number of samples and detailed examination of data<br>But missed taxa and underestimated cover, camera and parallax error<br>Difficult to distinguish outline of species of similar morphologies | (Carleton and Done, 1995)<br>(Done and Turak, 1994)<br>(Vogt *et al.*, 1997)<br>Chávez (1997)<br>Dethier *et al* (1993)<br>(Dodge *et al.*, 1982) |
| Weighted Bar Swimming Transect | ~1000m | Uses a 1m length of small diameter PVC pipe filled with gravel, marked at 25cm intervals. Observer swims along compass bearing, places bar on bottom every 3 kicks and records coral condition | Less time consuming and less quantitative hazardous counts of coral condition than linear methods but not good for benthic coverage data | (McField, 1999) |
| Free swimming observer | ~2000m | An observer swims over a study area recording reef status | Large extent and continuity of linear coverage per unit time can investigate community morphology and substrata composition in detail | McManus & Wenno (1981)<br>Porter & Meier (1992) |
| Manta Tow | ~5000m | Observers gets towed behind a boat on manta board and stops every 2 minutes to record main reef features | Ability to survey large areas in short period of time<br>Chief disadvantage is loss of info with speed<br>Difficult to determine dead coral cover and rubble/sand estimates | Erdmann et al, 1997<br>(Kenchington, 1978)<br>(Miller and De'ath, 1996; Miller and Müller, 1999) |
| Spot checks | ~8000m –12000m | The boat stops every few hundred metres and the main features are recorded by placing head with mask underwater | Ability to cover very large area is advantage<br>Disadvantage is that it's a subsample technique covering small proportion | (Kenchington, 1978) |
| Aerial photograph -ic surveys | ~10-100km | Stereophotography or visual census from fixed-wing aircraft | Can be used to map bleached & remote reefs.<br>Large area can be assessed in short time, but generally underestimates bleaching and can not see partially bleached corals<br>Radiometric and geometric corrections necessary are difficult | (Berkelmans, 2001)<br>(Mumby *et al.*, 1997) |

| | | | | |
|---|---|---|---|---|
| Remote sensing | ~100-1000km | Can be used from several platforms e.g. satellites, aircraft, ships and from underwater platforms | Rapid, current, non-intrusive and comprehensive assessments of habitat destruction<br>Reconnaissance of different habitat types is limited to few metres depth, habitat definition is course and few environmental descriptors can be related to it<br>Ground truthing necessary<br>It incurs majority of costs | (Raines *et al.*, 1992)<br>(Andréfouët *et al.*, 1999)<br>(Dustan, 2000)<br>(Green *et al.*, 1997b) |

These methods are often expensive and require significant investments in personnel and computing resources, which makes them generally impractical for developing nations and local communities. Even in developed countries the data they yield may be inappropriate in a managerial sense (Risk and Risk, 1997). There is no single set of measurements that is always ideal for all population and community attributes (Ohlhorst and Liddell, 1992) and Hughes (1993) and Erdmann *et al.* (1997) found that among-observer error remains substantial. Monitoring community changes and reef responses to stressors, is an important way of identifying the large-scale impacts of human activities and the potential of recovery for a given reef. However, besides being time and energy-expensive and financially costly, large-scale monitoring programs do not provide early warnings but instead record progressive, previous decline. Thus, they are not the best methods to assess if a new stress factor is active. With regards to detecting sediment impact, bioindicator organisms and life-history processes sensitive to environmental change will indicate stressors faster, cheaper and in a less time-consuming manner than large-scale community measures.

*2.2.2.4. Bioindicators:* The selection criteria for optimal bioindicators are discussed in Chapter 1, Section 1.1, using tissue thickness in corals as an example. Fauna other than corals may also have a profound effect on the reef community as a whole and may be used as reef stress response bioindicators (Endean, 1976). Bioindicators can be grouped as *in situ* pollution indicators, transplanted or naturally occurring bioaccumulation indicators, indicators used for laboratory toxicity testing and biodiversity indicators (Erdmann and Caldwell, 1997). They are so useful as they assess only pollutants that are bioavailable and thus stressful and they can help assess synergistic relationships between pollutants (Erdmann and Caldwell, 1997).

To choose appropriate species as indicators or detectors of anthropogenic impacts it first needs to be determined how representative they are of other species that are likely to be affected (Underwood and Peterson, 1988). According to Underwood and Peterson (1988), species that are likely to suffer stresses under natural conditions and are most likely to succumb quickly to new stresses imposed by pollutants (*stenoecious species*), may be useful as bioindicators. Erdmann and Caldwell (1997), on the other hand, state that bioindicators should be capable of continuous stress assessment over a wide range of stress factors (*euryoecious species*). Each approach has its advantages depending if rapid reef response to a new, acute stressor is assessed (favouring stenoecious species) or if long-term reef response to chronic stress factors is the objective (needing species which can survive the stressor over longer time frames, e.g. sediment-tolerant *Porites* corals, as used in this study).

Animals used as bioindicators of sediment stress on coral reefs include: fish (Grigg, 1994), sponges (Aerts and Vansoest, 1997), coelobites (Dong, 1982), stomatopods (Erdmann and Caldwell, 1997), hydroids (Mergner, 1977) and bacteria due to increased mucus production (Segel and Ducklow, 1982). Wilkinson (1992) proposes fish as the best indicators of reef health as they are often the first organisms to respond to exploitation. Erdmann and Caldwell (1997) strongly disagree, stating that a reduction in butterflyfish responding to reduced live coral cover serves no early warning function and provides no insight into the nature of the stressor (see also Reese, 1981). They also criticise the use of certain fish species due to their heavy exploitation for aquarium and food trades, and thus the likelyhood that their populations may be directly diminished rather than symptomatic of reef health. Most bioindicators proposed so far would be impractible in developing countries as they are often subject to human exploitation and/or require the use of SCUBA or expensive chemical analytical techniques (Erdmann and Caldwell, 1997). The proposed bioindicator used by Erdmann and Caldwell (1997), namely stomatopod abundance, did also fail to simply relate to coral cover. In light of these controversies, it seems the most appropriate bioindicators to study reef stress response are the corals themselves, as used in this study.

*2.2.2.5. Bioerosion and Fouling:* Bioerosion is the term used for “erosion of substrata by biological processes”, including organisms from at least 12 phyla (Hallock, 1988, p 275). As bioerosion is a key process of carbonate destruction in coral reef carbonate budgets, it can provide an integrated perspective of whole reef health (Holmes *et al.*, 2000). Bioerosion can be

assessed using slabs of massive coral skeletons and X-raying or photographing them, then examining the prints for incidence of bioeroders (Pari *et al.*, 1998). Another method analyses rubble of branching corals for incidences of bioerosion (Holmes *et al.*, 2000). The latter technique is cheaper, simpler and does not require the expertise and expense of X-radiographic analysis. It is also non-destructive. However, bioeroders in live corals can be different from those of dead corals (Le Campion-Alsumard *et al.*, 1995) and they also differ between colony morphologies (Moretzsohn and Tsuchiya, 1992; Musso, 1992), thus care must be taken in comparing results from different methods. Bioerosion is put into the category of reef response, as, even though one method monitors single colonies, the actual feature measured are reef organisms other than corals. Bioeroding organisms typically increase in abundance with increasing nutrient availability (Hallock, 1988; Hunter and Evans, 1992; Holmes *et al.*, 2000) and pollution (Pari *et al.*, 1998). Sedimentation was suggested to increase bioerosion (Kiene and Hutchings, 1994; Sammarco, 1996) but Edinger and Risk (1992) found that bioerosion actually decreased with increased sedimentation as carbonate sediment particles were made inaccessable to boring organisms. Bioerosion is affected by grazers and predators (Sammarco, 1996) and can thus not be directly related to anthropogenic changes easily. Although evidence shows that declines in coral abundance often coincide with phase shifts to macroalgae, it does not necessarily mean that one was the cause of the other, rather than the consequence (McField, 1999). Overall, bioerosion, just like most other indicators of coral and reef stress response, will only be detected once the impact has already occurred and severely stressed the corals.

2.2.3. The most commonly used methods to determine coral response to sediment stress. The single most commonly used indicator of *coral stress response* is changes in coral growth. Changes in coral growth can be measured using several methodologies (for examples see Table III), not all of which are useful for assessing sediment stress response (discussion below). Studies on the metabolism and biochemistry of corals and their symbionts are increasingly common with cheaper and better technology (for examples see Table III). Simple, straightforward measurements like the thickness of the tissue layer and visual observations of lesions and partial mortality have received more interest in the past decade, especially for their potential use in developing countries. Behavioural observations, such as visually assessing polyp retractions etc, suffer from many problems associated with laboratory experiments, and are difficult to make in the field. It is also very difficult to reduce behaviours to measurable parameters (Ellis, 1984). Measurements on the reproductive output of corals are amongst the most useful indicators, as the 'health' of an animal can usually be linked to its availability of energy reserves for reproduction and fecundity (but see Rinkevich, 1996). However, reproductive measurements are not easily made and often capture only short periods in a coral's seasonal reproductive cycle. The most important methods used to examine coral response to sediment stress are discussed in detail below.

*2.2.3.1. Coral growth:* Coral colonies deposit a calcium carbonate (aragonite) exoskeleton immediately beneath the living tissue, which basically is a thin layer on the surface of a very large structure consisting mainly of dead matter (Kinzie and Buddemeier, 1996), which has no

metabolic requirements, once deposited (Buddemeier, 1978). Changes in skeletal growth are thought to be good indicators to gain an understanding of interactions between corals and the environment (Kinzie and Buddemeier, 1996). These growth measures are related to both each other and the rate of new organic tissue formation, but they are not synonymous (Barnes and Devereux, 1988). The misconception that they are, has lead to misuses and confusion in the literature where the term 'growth' has been used to describe all skeletal growth measures and also living tissue mass increase as well as the rate of reef structural accumulation in some instances (Kinzie and Buddemeier, 1996). External factors can control tissue and skeletal growth within a colony to some extent but will influence both growth variables in different ways (Darke, 1991). Different environmental stressors acting in synergy have also been found to have profound effect on coral growth rates (Edinger *et al.*, 2000). Average *P. lobata* linear extension rates were, for example, not significantly different between two unpolluted offshore sites (16 and 16.3 mm $yr^{-1}$), a highly sewage-polluted site (13.5 mm $yr^{-1}$) and a site with high sedimentation (13.8 mm $yr^{-1}$, Edinger *et al.*, 2000). However, the polluted sites showed low live coral cover, high bioerosion and high mortality indices. Edinger *et al.* (2000) suggested that the combined effects of eutrophication and sedimentation explained the lack of extension rate response. One of the biggest problems using growth as environmental indicator is the fact that to this day, too little is known of the physiological process of coral growth. It has often been oversimplified to conveniently fit whatever argument needed to be made. Skeletal growth in massive *Porites*, the most common genus of corals used for growth studies has been described in detail in

Chapter 1, Section 1.2. The methods most commonly used to determine coral growth response to sediment impact is discussed below.

X-Radiography as a tool to examine annual bands*:* Even though often interpretated as direct photographic illustrations of skeletal density, X-radiographs are images beyond normal experience and require very careful interpretations (Barnes and Lough, 1989). Barnes and Lough (1989) reviewed problems related to density banding from over 70 papers. More recent reviews can also be found (Barnes and Lough, 1993; Le Tissier *et al.*, 1994; Lough *et al.*, 1997). A suitable growth bioassay should provide accurate measurements over a short period of time and be sufficiently simple for semi-skilled operators to apply (Davies, 1992). X-radiography is expensive, time-consuming, needs experts dating the slices, access to a large circular saw and an X-radiograph machine. Also, coral colonies have to be killed or cored and the method is highly destructive. Using X-radiography to link sediment impact to coral stress response by a decrease in linear growth, has been largely unsuccessful in recent studies. Torres and Morelock (2002) found decreasing linear extension with increases in turbidity, but only in one out of three species and without statistical significance. No changes in skeletal growth rates were found with increases in sedimentation from mining operations (Barnes and Lough, 1999). Anthony *et al.* (2002) also found skeletal growth to be much more weakly correlated to sediment impact than tissue growth. On the other hand, studies from 20-30 years ago have often found negative correlations between linear extension rates and sedimentation and/or turbidity (Aller and Dodge, 1974; Dodge *et al.*, 1974; Dodge and Vaisnys, 1977; Hudson,

1981; Hubbard and Scaturo, 1985; Hudson *et al.*, 1989). Possible reasons for these contrasting results in density banding studies over the years are given in Chapter 1, Section 1.2. and in the discussion on skeletal inclusions, below. Even though density banding can be useful for timing in sclerochronological studies, it is not sensitive enough to rapidly determine sediment impact in corals.

Alizarin Red S dye is easy to obtain, simple to use, cheap with a long shelf-life and it makes a discrete mark in the skeleton, from which linear extension rates can be measured (Lamberts, 1978). Living corals subjected to Alizarin Red S dissolved in seawater incorporate this magenta dye into their newly forming skeleton. It is however, mildly toxic, enough for corals to prematurely release their planulae (Lamberts, 1978). It also decreases calcification for a short duration after staining (Dodge *et al.*, 1984). Dodge *et al.* (1984) believe that the methods applying the stain may have worse effects on calcification than its toxicity. As with the buoyant weighing method (see below), pre-stress measurements are needed in order to compare any changes in linear extension after a stressor has been introduced. Chansang *et al.* (1992) and Brown *et al.* (1990) found no significant differences in coral growth using this method between highly turbid and control areas. Although the simplicity of this method is beneficial for remote locations, it has not been proven to be a reliable coral stress response indicator to sediment impact.

Buoyant weighing is simple, non-destructive and quicker than conventional methods to determine coral growth changes, according to

Davies (1992). It involves weighing the coral in seawater, and from knowledge of the density of the water and the density of the skeleton, making a prediction of the weight of the skeleton. However, errors must be accounted for tissue weight, changes in density due to mucus and bioeroders and the assumption that all corals consist entirely of aragonite of a known density, which they do not (Davies, 1989). Also, the assumption that the voids in the porous skeleton are filled with liquid of the same density as the surrounding medium, can introduce errors if air bubbles form on the underside of corals (Jokiel *et al.*, 1978). There are additional problems in using this method in the field, where it is hard to find a sensitive balance for underwater measurements. If corals are kept in tanks to measure changes in buoyant weight the stress factors introduced do not always mirror real-life concentrations in the field (e.g. Anthony, 1999c). Furthermore, frequent handling can promote lower calcification rates (Dodge *et al.*, 1984). Some studies have found a significant decrease in buoyant weight with decreasing light (Hidaka, 1992) and increasing turbidity (Davies, 1989). Although this method has proven promising in detecting coral stress responses to increased turbidity, the need for laboratory settings reduces its usefulness in remote locations.

Isotopes and other skeletal inclusions: Skeletal density bands provide a good method for dating chemical and isotopic records included in the skeleton during skeletal deposition (Barnes and Devereux, 1988). An important feature is the fact that skeletal make-up in terms of isotopic and minor and trace element chemical composition is closely related to, and maybe in equilibrium with, the composition of the ambient seawater or the

tissue fluids (Kinzie and Buddemeier, 1996). The main isotopes measured in coral skeletons using mass spectrometry are $\partial^{18}O$ and $\partial^{13}C$. $\partial^{18}O$ is mainly used as a proxy for temperature (Suzuki *et al.*, 1999) and salinity (Halley *et al.*, 1994). $\partial^{13}C$ is an indicator of a coral's metabolic status (Swart *et al.*, 1996b; Guzmán and Tudhope, 1998). Several studies have found correlations between $\partial^{13}C$ and depth/light attenuation, as well as turbidity/sedimentation increases associated with the monsoon (Chakraborty and Ramesh, 1997; Heikoop *et al.*, 2000). Insoluble residues incorporated in the coral skeleton are also potentially good indicators of increased sediment stress in corals. However, they differ among species and display little correlation with width of density bands within species at different localities (Budd *et al.*, 1993). Knowledge needs to be gained on the methods of incorporation of insolubles into the skeleton by tissue damage and polyp behaviour. Corals usually reject sediment falling onto their tissues, therefore, tissues must be damaged in order to allow uptake of sediment into their skeleton (Davies, 1992). Only species which were efficient suspension feeders showed weak correlations between insoluble residue concentrations and growth band width (Budd *et al.*, 1993). However, McCulloch *et al.* (2003) have found that Ba/Ca ratios in corals provide a long-term record of changes in suspended sediment loads.

The incorporation of metals into an organism's metabolic reactions is thought to have a definite, mainly negative influence on coral populations (Krasnov, 1981). Studying metal concentrations in the coral skeleton can be problematic when the metal levels are below detection limit (e.g. Shotyk and Immenhauserpotthast, 1995). Also, the distribution of metals within

skeletons and tissues and the mechanisms that rule them, are poorly understood (Bastidas and Garcia, 1997). The use of different methods such as studying metal concentrations based on dry and wet weight, skeleton alone or with tissues, total metal content or lattice bound content (Bastidas and Garcia, 1997), makes comparisons between studies very difficult (Shen *et al.*, 1987; Guzmán and Jiménez, 1992). Terrigenous sediment from monsoonal run-off was found to be present in form of rare earth metals in skeletons of *Porites* corals from India and the Arabian Sea (Naqvi *et al.*, 1996; Naqvi and Nagendernath, 1998). Cadmium traces in coral skeletons were thought to be related to zinc smelting outfalls from long-range transport (Shen *et al.*, 1987). Copper peaks in density bands were related to mine tailings in the Philippines by David (2003). Other studies, however, could detect no differences between impact and pristine reefs by studying coral heavy metal loads (Guzmán and Jiménez, 1992). More importantly, several studies found no conclusive evidence for a link between metal concentrations in coral skeletons and sedimentation rates (Bastidas and Garcia, 1997; Bastidas and Garcia, 1999) .

Two requisites are needed to perform a chronology: the dating and the incorporation of a signal in the coral skeleton (Bastidas and Garcia, 1999). Taylor *et al.* (1995) describe a feature of coral growth – the thickness of the tissue layer - that could have immense influence on the incorporation and interpretation of inclusive materials in the coral skeleton. They assume that approximately 50% of skeletal deposition is added to the outer surface (from which all studies date the formation of density bands) and the rest is spread through the tissue layer. Skeletal thickening deposits containing

inclusions would therefore be smudged throughout the tissue layer, more so, if the tissue thickness layer was large (also Barnes *et al.*, 1995). Several papers have tested this hypothesis and included tissue thickness measurements in studies of isotopic ratios (Gagan *et al.*, 1994; Alibert and McCulloch, 1997; Cohen and Hart, 1997; Guzmán and Tudhope, 1998; Linsley *et al.*, 1999; Al-Rousan *et al.*, 2003; Mitsuguchi *et al.*, 2003). None of them, however, could detect an extensive smoothing effect as proposed by Taylor *et al.* (1995). Wellington *et al.* (1996) reported that 80-90% of skeletal mass formed within 1 mm of the outer margin of the skeleton, a result that concurred with Linsley *et al.* (1999). In addition, Alibert and McCullough (1997) found no obvious thickening of the top margin of skeletal walls after examination of SEM images. To record environmental data in a continuous fashion should be the most essential requisite for any high resolution proxy indicator (Carriquiry *et al.*, 1994). However, changes in coral growth rate like those thought to occur during stress response, and our limited understanding of them, will reduce the usefulness of inclusive records in corals. Small sample sizes (often only one coral is used) in addition to the large natural variability are also considered as a weakness of corals as proxy tools (Bastidas and Garcia, 1999). Analysing inclusive records in coral skeletons is time-consuming and extremely expensive, as highly sophisticated instrumentation and technical expertise is needed. For all these reasons they are of limited use for rapid assessment of sediment impact in developing countries.

The thickness of the tissue layer as an indicator of coral stress response to sedimentation and shading has been described in Chapter 1. Its

usefulness as a bioindicator for coral response to turbidity impact is assessed in this study. Although tissue thickness is a sensitive indicator of the 'health' of colonies, it can not simply be adapted into a reactive monitoring tool. This is mainly due to the large natural variability of tissue thickness with localities, within-colonies, with seasons and within a lunar month. Possible correction factors for predictable natural variability in tissue thickness are examined here. However, not all tissue thickness variability can be explained and accounted for. True (*in review*) found that colonies with vastly different tissue thicknesses inhabited similar localities without apparent differences in environmental conditions. He also suggests previous history to have a large influence on the energy use of any individual coral. These unknown factors restrict the use of tissue thickness as a generic monitoring tool. Nonetheless, tissue thickness offers great potential as a simple and real-time measure to estimate the *relative* impact of environmental stressors on corals. It is also potentially useful for local communities to monitor the status of their surrounding reefs, as it is simple and inexpensive and can be done snorkelling (in shallow water).

*2.2.3.2. Histopathological examinations:* The use of histopathological response to sediment impact is rather rare in the coral stress literature (see Table III), probably due to the large amount of time, effort and specialist knowledge required for its use. This is unfortunate, as histopathological examinations are an important tool, not only to investigate sublethal responses and diseases in organisms, but also in correlating physiochemical and physiological changes in population and community level studies (Peters *et al.*, 1981). Also, they can determine

very early stress responses related to tissue damage, especially compared with visual observations (Peters *et al.*, 1981). The most commonly used histopathological method, namely reproduction, is discussed in more detail below.

"The complexities of cnidarian reproductive biology, together with our rudimentary knowledge of reproductive patterns, make forecasting based on current knowledge uncertain at best" (Kinzie, 1999, p.80). It is difficult to predict future consequences of anthropogenic impacts as the reproductive rates of corals are decoupled from the eventual recruitment to adult populations (Underwood and Peterson, 1988). Community structure and function are maintained due to the reproductive behaviour of corals and the recruitment of new colonies, and may be observed directly as indicators of an organism's 'health'. Reproduction is thought to be very poorly tolerant of environmental changes, being one of the first life history traits to show response to stress factors, with regards to their gametogenesis, spawning behaviour and timing, fecundity, fertilization rates, larval development and settlement success (e.g. Larkum and Steven, 1994). Not all these traits can be measured with histopathological examinations, but features like gonad size and potential reproductive output (Lewis, 1997), embryonic development in brooding corals (Koop *et al.*, 2001) and counts of eggs and testes (Fadlallah, 1985) are thought to be good indicators of stress effects measurable on this small scale. However, as reproduction is limited to short breeding seasons, in addition to the lack of prior fecundity measurements for comparisons, long-term reactions such as decreases in fecundity are of small value as indicators of

stress effects (True, 1995). It is also difficult to employ single-parameter models predicting reproductive patterns in different species, as other parameters such as polyp size, colony morphology, skeletal architecture and habitat requirements may be involved as well (Fadlallah, 1985). Injuries or bleaching can also significantly reduce coral fecundity (Guzman and Holst, 1993). The reproductive analysis of coral reponse to a stress factor is difficult, time consuming and expensive as several colonies within a reef and several reefs must be sampled to understand natural variability and the timing of the reproductive season has to be known (Guzman and Holst, 1993). Despite their potential usefulness, measurements relating to the reproductive output of corals, are too fraught with difficulty and expenses to be optimal techniques for developing nations.

## 2.3. CONCLUSIONS:

2.3.1. What is the best method to determine coral stress response to sediment in developing nations? The previous sections have discussed at length the advantages and disadvantages of frequently used monitoring methods. The following table includes all major methods used to determine coral and reef stress response discussed above. This table provides an overview of each method's problems and benefits related to particular issues of importance for assessing anthropogenic impact on corals in developing countries. The eleven columns below were regarded to be the main features of monitoring methods, which may be useful for reef managers in remote and poor areas. They stand for the following.

Is the method:

*1) Simple*: Can the method be used by non-experts (+) or does it need specially trained scientists (-)?
*2) Cheap*: Is this method financially feasible for developing nations with little funding (+) or does it require large expenses (-)?
*3) Non-Destructive*: Does it have little impact on corals (+) or does it kill whole colonies (-)?
*4) Objective*: Is it objective (+) or observer-dependent and thus potentially biased (-)?
*5) Stressors*: Can it assess more than one anthropogenic stress factor (+), or is it specific to certain impacts or mainly used to assess natural/seasonal variations (-)?
*6) Real-time*: Can the effect be seen on time-scales before the corals are seriously damaged (+) or are corals already dead or dying before this method is relevant (-)?
*7) Field-based*: Can it be used in the field in remote locations (+) or is it solely dependent on lab observations (-)?
*8) Lab-based*: Can it be easily supplemented with lab observations to increase understanding on the means of imposing stress on corals (+) or are manipulative studies not applicable (-)?
*9) Variable*: Are small numbers of replicates sufficient (+) or are large numbers needed to reduce natural variability and noise (-)?
*10) Common*: Is it widely used by managers and accepted in the scientific community (+) or fairly obscure and little heard-of and thus hard to compare between studies (-)?
*11) Species*: Can it be used on many reef corals (+) or is it only applicable to certain species of corals, which may not be found in all areas (-)?

Each method was given a ‘ + ’ if the features are affirmative relating to the questions, or a ‘ – ‘ for negative aspects of the methods, as described above. ‘N/A‘ stands for non-applicable and ‘ ~ ‘ is an indicator of intermediate, ie neither strongly positive or negative traits of the particular method (see Table V, below).

Table V. Methodologies and their usefulness in terms of assessing coral and reef stress response in developing countries.

| METHO-DOLOGY | 1) | 2) | 3) | 4) | 5) | 6) | 7) | 8) | 9) | 10) | 11) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| CORAL RESPONSE: | | | | | | | | | | | |
| Behavioural observations | ~ | ~ | + | - | + | + | - | + | - | - | + |
| Lesions, partial mortality | + | ~ | + | ~ | ~ | - | + | + | ~ | ~ | + |
| Size-frequency | ~ | - | + | + | + | - | + | - | - | - | + |
| Morphology | - | - | + | ~ | ~ | - | + | ~ | - | - | + |
| Larval observations | - | - | ~ | ~ | + | ~ | + | + | - | - | + |
| Metabolic rates | - | - | ~ | + | + | + | + | + | ~ | ~ | + |
| Biochemistry | - | - | - | + | + | + | - | + | ~ | ~ | + |
| GROWTH: | | | | | | | | | | | |
| X-radiography | - | - | - | - | ~ | - | - | - | - | + | ~ |
| Boyant weight | ~ | - | ~ | + | + | - | ~ | + | - | + | + |
| Alizarin Red S | ~ | ~ | ~ | ~ | + | - | + | + | ~ | + | + |
| Isotopes and inclusions | - | - | - | + | ~ | - | - | - | - | + | ~ |
| Tissue thickness | + | + | + | + | + | + | + | + | - | ~ | - |
| Photosynthe-tic measures | - | - | + | + | + | + | + | + | ~ | ~ | + |
| Reproductive indeces | - | - | - | + | + | - | - | + | ~ | ~ | + |
| Histopatholo-gical changes | - | - | - | - | + | ~ | - | + | - | - | + |
| REEF RESPONSE: | | | | | | | | | | | |
| Bleaching | - | + | + | - | + | ~ | + | + | - | + | + |
| Monitoring | - | - | + | - | + | - | + | - | - | + | + |
| Bioerosion | - | + | - | ~ | ~ | - | ~ | ~ | + | ~ | + |
| Bioindicators | ~ | ~ | + | - | + | ~ | + | - | ~ | - | NA |
| Reef metabolism | - | - | + | + | + | + | + | - | - | - | + |

The most optimal method for assessing coral stress response to anthropogenic impacts in developing nations is measuring changes in the thickness of the tissue layer (Table V). Its main disadvantages are its

natural variability and the limited number of coral species which can be assessed with this method. The only other monitoring method ranking similarly high, is the use of photosynthetic measurements of the coral-algal symbiosis. As this method's main problems are the need for technical expertise and expensive equipment, it may be of less use than tissue thickness in areas where costs and simplicity are the deciding factors for chosing a method. On the other hand, it assesses stress response from a wide range of coral species. This may offset the higher costs of this method in cases where reef community responses are the main objective. The individual objectives and needs of each study and location have to be assessed before the most appropriate monitoring method can be chosen.

2.3.2. General conclusions: One of the first things a reef manager needs to do is to recognize an area at risk and to quantify the risk so he can assess chances for recovery and consequences in terms of ecological succession and bioconstruction (Done, 1995). Even though the understanding of stress effects on corals and reefs has improved in recent years, there remain uncertainties of what causes reef destruction and how to evaluate future impacts and reef recovery (Eakin *et al.*, 1997). Corals have the potential to be sensitive indicators of environmental change and could possibly even provide us with records of similar perturbations in past environments. Until now, however, both of these important uses have been at best imperfectly evaluated (Kinzie and Buddemeier, 1996). To be able to distinguish the differences between natural and anthropogenic change and to test for significant temporal trends, Grigg (1993) calls for long-term monitoring programs on a global scale. He is concerned that reef science is becoming

too applied and calls for “high quality basic research, quantifying natural variability on annual, decadal, centennial and even millenial time scales” (Grigg, 1993, p 55). Although such large-scale, long-term, global monitoring of the state of reefs is necessary and desired, most countries neither have the funds nor the expertise to undertake such monumental efforts. Also, the rapid, real-time identification of anthropogenic, chronic stressors threatening corals and reefs should have urgent priority over cost, time and energy-expensive monitoring programs on the natural variability of reefs. These are, although academically fascinating, most likely not successful in stopping rapid, global reef deterioriation. A complete assessment must include accurate measures of stress response to an impact on a number of different scales. No single measure can satisfy all the requirements of scientists and managers who must make decisions about potential environmental, economic and social impacts of anthropogenic stressors (Underwood and Peterson, 1988). For example, monitoring has to be augmented with physiological studies which address the mechanisms inducing change in abundance (Hughes, 1993). Suitable for well-funded research projects are studies on the photosynthetic system of the coral-algae symbiosis, coral metabolism and biochemical changes such as the induction of heat shock proteins in response to stress. These studies could be supplementing long-term, large-scale monitoring programs to assess the more rapid, sublethal changes as early warning indicators. In developing nations, with fewer expert scientists and little funding, the study of tissue thickness in massive corals could be an extremely valuable addition to rapid spot-checks assessing general reef response.

# 3.0 TISSUE THICKNESS & LUNAR CYCLES

3.1. INTRODUCTION: The moon exerts physical and biological influence upon the Earth and its ecosystems. Lunar cycles have been demonstrated in many marine fauna (an overview of literature published since 1985 is given in Table I, Appendix B, p 221). The reproductive cycles of many marine animals are linked to lunar cycles, with the release of spawn and larvae apparently cued by certain phases of the moon (e.g. Harrison *et al.*, 1984; Babcock *et al.*, 1986; Kingsford and Finn, 1997; Kubota and Tomari, 1998; Kubota, 2000). Such releases are not universally associated with one particular lunar phase, although spawning and larval release tend to occur around the full moon (Table I, App. B). The moon's influence on reproduction in scleractinian corals has been well studied since the discovery of large-scale, multi-species broadcast spawning in the mid-1980's (Harrison *et al.*, 1984; Babcock *et al.*, 1986). Other environmental factors undoubtedly influence coral reproductive cycles (for example sea surface temperatures, e.g. Glynn *et al.*, 1996) but the blue spectrum of moonlight seems to be an important reproductive trigger in many corals (Gorbunov and Falkowski, 2002).

It has long been thought that fine density bands found in certain types of corals are formed under lunar control because 12-13 fine bands are found within an annual density band in fast growing species (Buddemeier, 1975; Buddemeier and Kinzie, 1975; Houck, 1977). This is supported by evidence from Alizarin staining that dissepiments are formed monthly in *Porites* corals (Barnes and Lough, 1993). *Porites* have perforate skeletons in which

vertical skeletal elements have many holes, and thus all skeletals cavities above the last dissepiment are interconnected. Thus, the uplift of the lower surface of the tissue (polyp base) and emplacement of new dissepiments must occur at the same time over the entire colony. Otherwise, skeleton occupied by tissue would not be completely isolated from unoccupied skeleton. An environmental cue for this synchronous process has been suggested (Barnes and Lough, 1993), principally because the level of co-ordination between coral polyps seems unlikely to be achieved in other ways. *Porites* colonies grow very large (colonies with growth radii exceeding 7 m are not rare); tissue on one side of a 7 m high, hemispherical *Porites* colony will be more than 20 m distant across the curved surface from tissue on the opposite side. Lunar cycles are a logical environmental cue for this synchronous uplift as they are known to trigger spawning and larval release (see review by Gorbunov and Falkowski, 2002). This explains not only the relationship between fine bands and dissepimental spacing noted by Barnes and Lough (1989) but also why fine banding has only been described from genera of massive corals that have perforate skeletons, such as *Porites*, *Asteopora*, *Hydnophora* and *Pavona* (Barnes and Lough, 1992).

Thickening of skeleton occurs throughout the depth of the tissue layer (Barnes and Lough, 1992). However, the depth of the tissue layer is suddenly and periodically reduced by uplift of its lower margin and deposition of thin horizontal bridges, dissepiments, to isolate skeleton occupied by tissue from skeleton no longer occupied by tissue. Tissue uplift reduces tissue thickness by around 20%. Consequently, regions of skeleton

just below a dissepiment will have been thickened for less time than regions of skeleton just above a dissepiment. If tissue covers skeleton that took 6 months to extend (i.e. tissue invests around half the annual growth increment) and if thickening occurs at an even rate through the depth of the tissue, then thickening on skeletal elements would vary by around 17% (1/6) between the top and bottom of the interdissepimental space.

Despite this recognition of a probable link between lunar cycles and dissepiment emplacement and fine band formation, systematic analysis to determine the timing and way in which this process occurs has not to date been carried out. Most workers have not taken into account the ~20% change in tissue thickness over a lunar month when measuring tissue thickness in massive *Porites* (e.g. Barnes and Lough, 1992; 1999). True (1995) is an exception: he always sampled colonies during the week before the full moon to reduce any possible variations in tissue thickness associated with lunar phases and skeletal growth. Although his results suggested that tissue thickness did not decrease in the week leading up the full moon, he did not assess changes in tissue thickness over a lunar cycle. The research reported in the first part of this chapter (Study 1) aims to determine how tissue thickness changes over a lunar cycle to establish:

1) The time at which the abrupt, ~20% reduction in tissue thickness occurs. This information will make it possible to avoid errors in interpretation of tissue thickness measurements due to sampling just before and just after this change.

2) Rates of change in tissue thickness over the lunar month. It is known that monthly reduction of tissue thickness is rapid, but there is no information to date about the rate of subsequent increase of tissue during the lunar month. This information will make it possible to target periods when the rate of change is low, and thus systematic differences in tissue thickness are minimised and can be accounted for.

There are additional issues that arise. Buddemeier (1975) suggested that some corals have fewer than 12-13 fine density bands per year because fine bands are not formed in winter in slower growing corals. True (1995) thought that monthly dissepiment formation may not occur at certain times of the year because of variations in sea surface temperature (SST), insolation and food availability, and because of reproductive cycles. Such possibilities need to be investigated to develop a fuller understanding of how tissue thickness varies over a year and how this annual cycle might be affected by the location of a colony. The second study reported in this chapter examines how tissue thickness varies between different times of the year and whether consistent annual cycles can be identified in colonies from different locations and water depths around Lihir Island.

Finally, the third study reported in this chapter examines whether tissue uplift (and thus monthly thinning) is constrained when tissue thickness becomes critically thin, as might occur when a coral is stressed by suboptimal growth conditions. True and colleages (True, 1995; True *et al.*, *in preparation*) reported that tissue thickness in *Porites* on the GBR does

not drop below 2.0-2.5 mm in living corals. They argued that, as tissue thickness approaches this value, tissue is resorbed in some areas and the resources so generated are used to maintain tissue thickness in other areas. For example, True *et al.,* (*in prep.*) found that tissue on shaded *Porites* colonies did not fall below a thickness of 2.0-2.5 mm during the 6 month treatment period but the number and size of lesions progressively increased. They interpreted this as demonstrating that a minimum tissue thickness was being maintained in some areas by resorbing tissue from other areas. It seems reasonable to suppose that tissue uplift resulting in an abrupt change in tissue thickness will not be possible once tissue thickness decreases close to its minimum value. Formation of new dissepiments will not occur if tissue uplift is not possible. This issue goes further. There is evidence that extension is somehow linked with tissue reserves (Anthony, 1999b; Barnes and Lough, 1999; Ferrier-Pages *et al.*, 2003) and that corals in significant energy deficit may sustain skeletal growth rates in the short term by catabolising tissue reserves (Anthony, 1999b). If this is the case, then minimal values of tissue thickness and cessation of dissepiment formation might be linked with reductions in extension rate or cessation of extension. These issues are examined in Study 3.

3.1.1. Study sites (displayed in detail in Appendix A):

Several study sites were chosen for these three studies. The sites are described in Table VI and shown in Figure 4.

Table VI. Summary of information on full moon studies, main observed site characteristics and study dates. Detailed site descriptions and photographs are presented in APPENDIX A.

| Study sites | MASAHET ISLAND | | MALI ISLAND | | KAPIT IV | KAPIT III | KAPIT II |
|---|---|---|---|---|---|---|---|
| Impact zone | Control | | Control | | Control | Impact | Impact |
| Depth (m) | Shallow (3 m) | Deep (13 m) | Shallow (7.5 m) | Deep (18 m) | Deep (19 m) | Deep (17 m) | Shallow (2 m) |
| Visibility | Up to 50 m | | Around 25 m | | Up to 15 m | ≤5 m | < 5 m |
| Date sampled | February 2001 & 2003 May 2002 | | May 2002 | | May 2002 | February 2001 & 2003 | May 2002 |
| Study number | (1) & (2) | | (2) | | (2) | (3) | (2) |
| Distance to mine | ~18.5 km | | ~12 km | | ~6.5 km | ~3.3 km | ~2.5 km |
| Communi-ties | ~55% live coral cover, no algae, no sediment on corals | | ~65% live coral cover, *Halimeda,* no sediment on corals | | Few *Porites* some sediment | *Porites* & fungiids, algae Sediment on corals | *Porites & Millepora,* algae Sediment on corals |

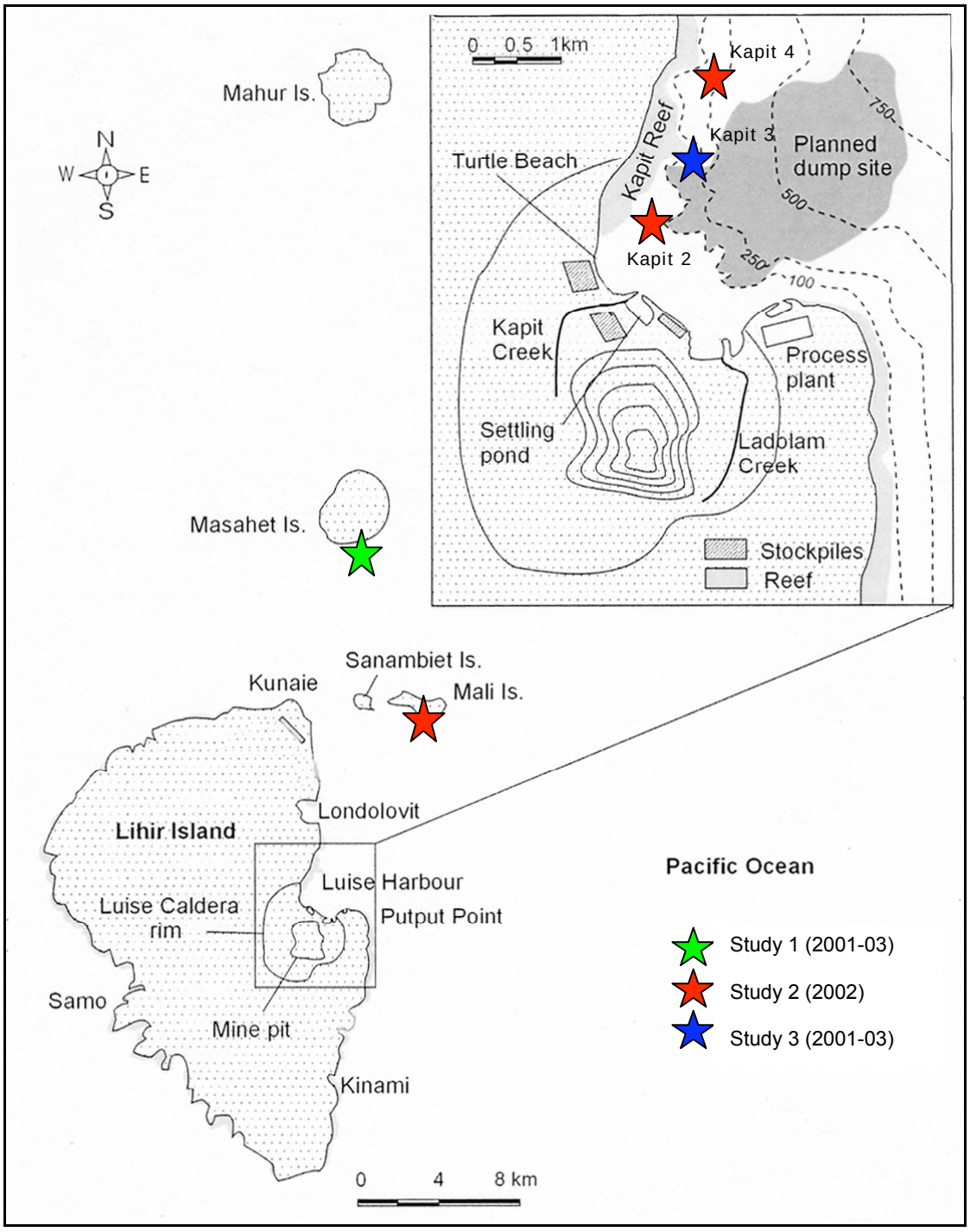
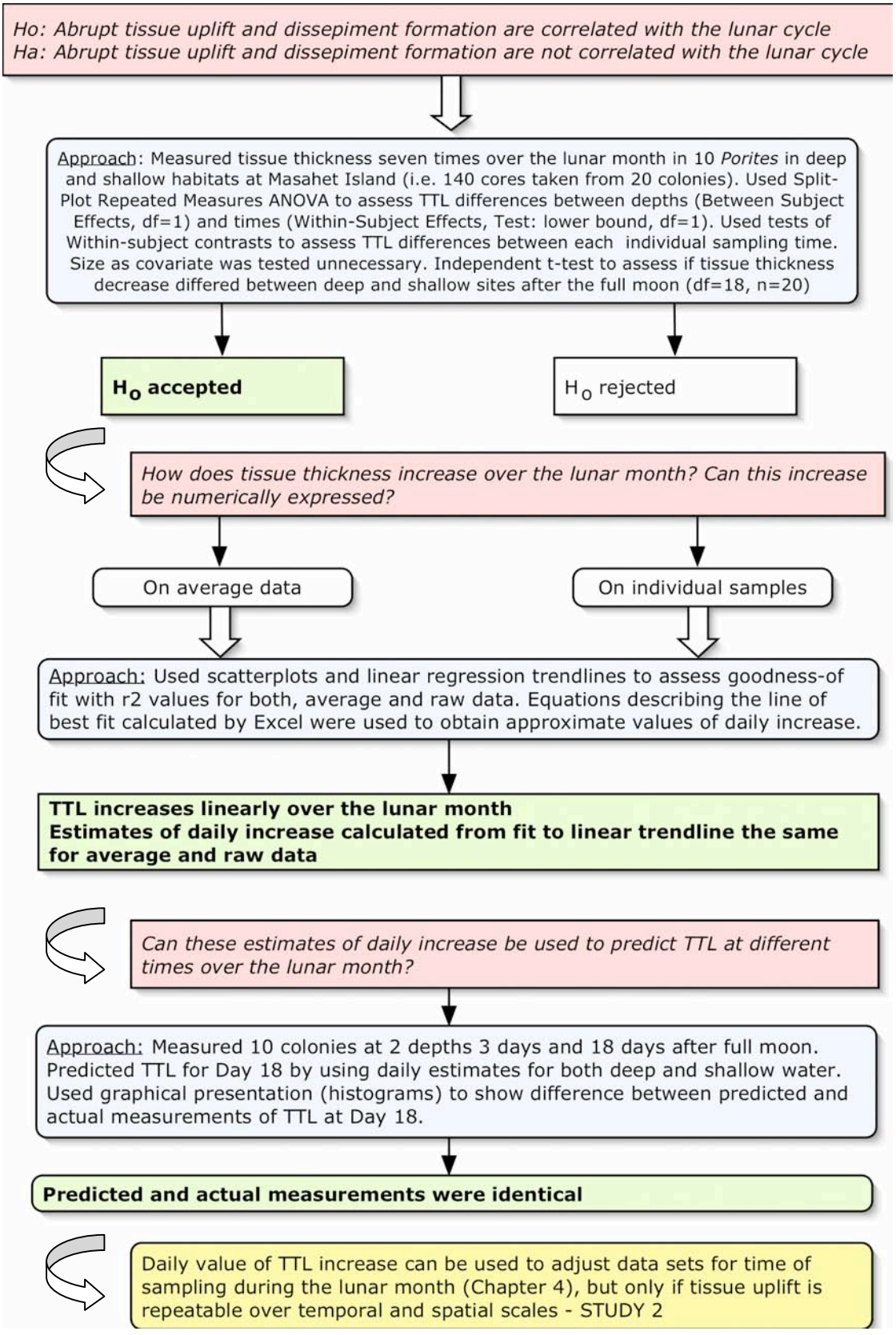


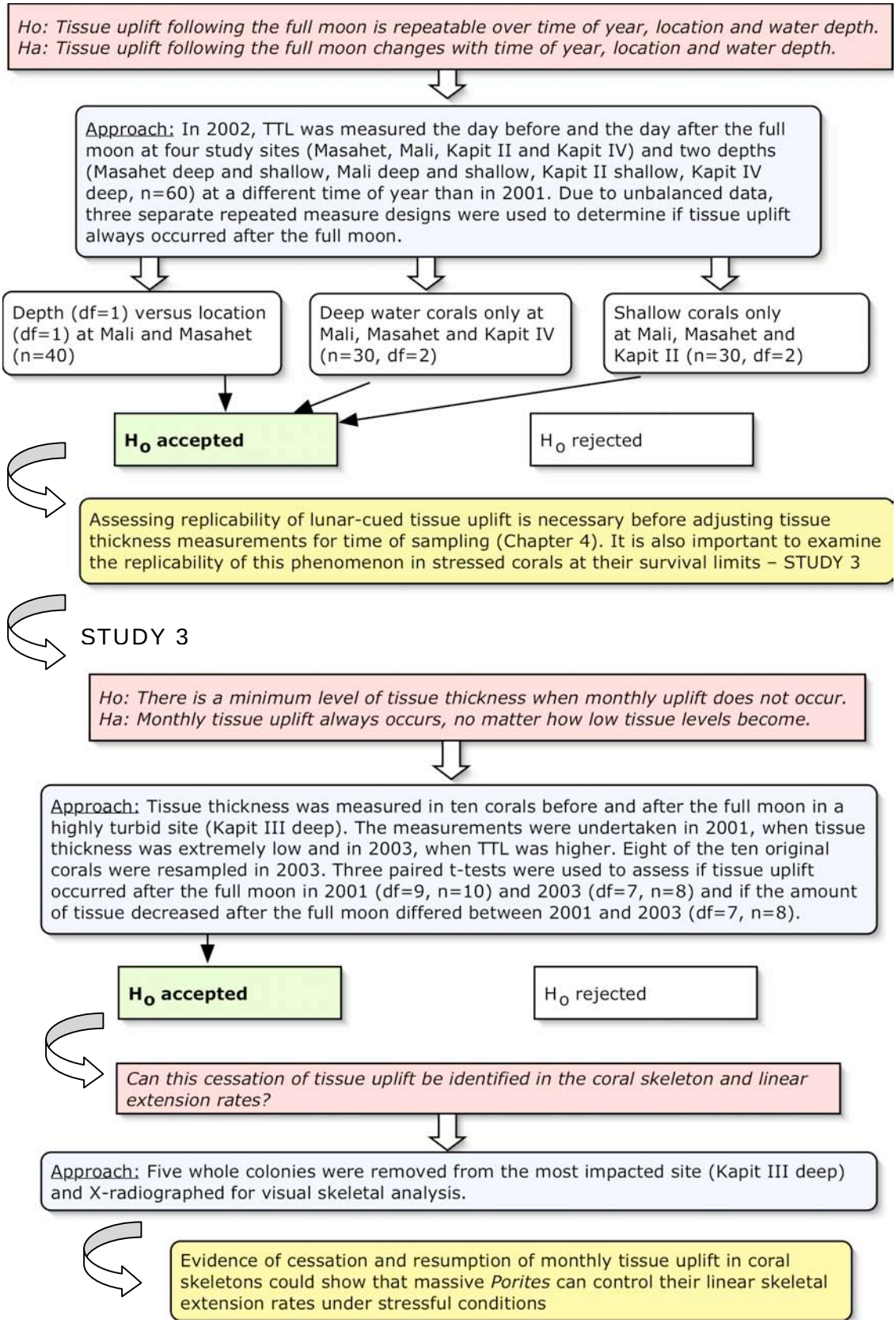

Figure 4. Location map of Lihir Island (PNG) and distribution of study sites for 3 studies between February 2001 and February 2003 (modified from S Thomas, 2003).

3.1.2. Flowchart of studies: NB – on all Figures, TTL=tissue thickness

STUDY 1



STUDY 2




STUDY 3

## 3.2. METHODS AND RESULTS OF INDIVIDUAL STUDIES:

### 3.2.1. STUDY 1 - Tissue thickness changes over the lunar month

*3.2.1.1. Methods:* Masahet Island was selected as the site at which to assess natural changes in tissue thickness over a lunar month, because it is located almost 20 km from the mine and is not significantly affected by mine activities (confirmed in results reported in Chapter 4). Ten massive *Porites* in both deep (>10 m) and shallow (3 m) water were randomly selected in February 2001 (see Chapter 1, Section 1.5 for further details). To identify and quantify changes in tissue thickness over the lunar month, small cores were extracted from the selected colonies and tissue thickness measured weekly for the first three weeks leading up to the full moon on March 8, 2001. In the final week, tissue thickness was measured three days before, one day before, one day after and three days after the full moon. Sampling frequency was the maximum possible allowed given occupational health and safety regulations governing dive bottom time in this remote location. Seven cores were extracted from the summit of each coral colony spaced as widely as possible to minimise effects due to tissue resorption near injured areas (see True, 1995). The effects of repeated coring were not examined in this study because True (1995) determined that repeated coring of *Porites* colonies, similar to that carried out here, did not affect tissue thickness. The statistical design for Study 1) was a Split-Plot Repeated Measures analysis (see Fig. 5; $D_{(x)}$ = depth (1 = shallow; 2 = deep), ID = 10 coral replicates nested within 2 depths, T = 7 times over the lunar month).

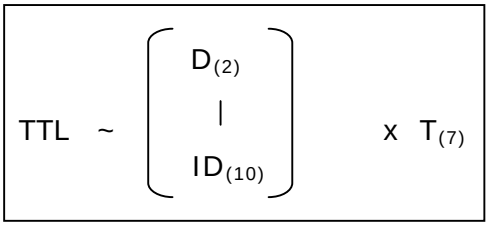



Figure 5. Statistical design for Study 1 - Split-Plot Repeated Measures Analysis

The Repeated Measures Analysis yielded results for both univariate and multivariate tests. Mauchly's test for sphericity determined if the correlation was constant, i.e. if a univariate split-plot design was appropriate or if a multivariate design had to be used. Mauchly's Test of Sphericity was highly significant ($p < 0.000$; $df = 20$), attesting to the need for multivariate analysis. Data transformation was not necessary. Additionally, colony size as potential covariate was examined by plotting residual tissue thickness against size (colony diameter) with markers set by depth to differentiate for potential depth effects. There was no interaction with depth and no significant effect of colony size upon tissue thickness, hence, colony size was not included as a covariate. An independent t-test assessed if the amount of tissue decreased following the full moon was significantly different between deep and shallow sites.

After visually examining graphs of averages and raw data values, it became apparent that tissue thickness increased in a roughly linear fashion over the lunar month. To determine if the monthly increase in tissue thickness could be fitted to a linear trendline, $r^2$ values and the regression equations describing the line of best fit calculated by Microsoft Excel were examined in line graphs of both, average and individual tissue thickness values over the lunar month. The regression equations are $Y = a + bX$, where $X$ is the

independent variable, which is multiplied by a coefficient *b*, the slope factor; *Y* is the dependent variable and *a* is the intercept of the function line with the Y-axis (Sokal and Rohlf, 1996). This linear relationship is an adequate description of the functional dependence of *Y* (the tissue thickness increase) on *X* (every day between two full moons). Therefore, the slope factor *b* here is an estimate of the daily value of tissue increase during one lunar month. To test if predictions made using these daily values could be used to adjust for changes in tissue thickness over a lunar month, ten colonies were sampled three and eighteen days after the full moon at Masahet Island in February 2003. The value of daily increase (*b*) was multiplied by 15 (the number of days between the two measurements) and added to the tissue thickness measured on Day 3 after the full moon. These predicted values were then compared with the actual tissue thickness measurements on Day 18 after the full moon in 2003.

*3.2.1.2. Results:* Two main trends were apparent in measurements of tissue thickness over a lunar month (Fig. 6). First, there was a statistically significant, average decrease of 16% +/- 2.8% in tissue thickness in shallow water corals (range: 8-30%) and a statistically significant, average decrease of 18% +/- 2.5% in tissue thickness in deep water corals (range: 11-30%) following the full moon on March 8, 2001. Secondly, deep-water corals had significantly thinner tissue than shallow water ones (Fig. 6). Shallow and deep water corals decrease each month during uplift of the polyp base by a statistically insignificant amount (independent samples t-test, $F_{(18)}=0.403$, $p=0.736$).

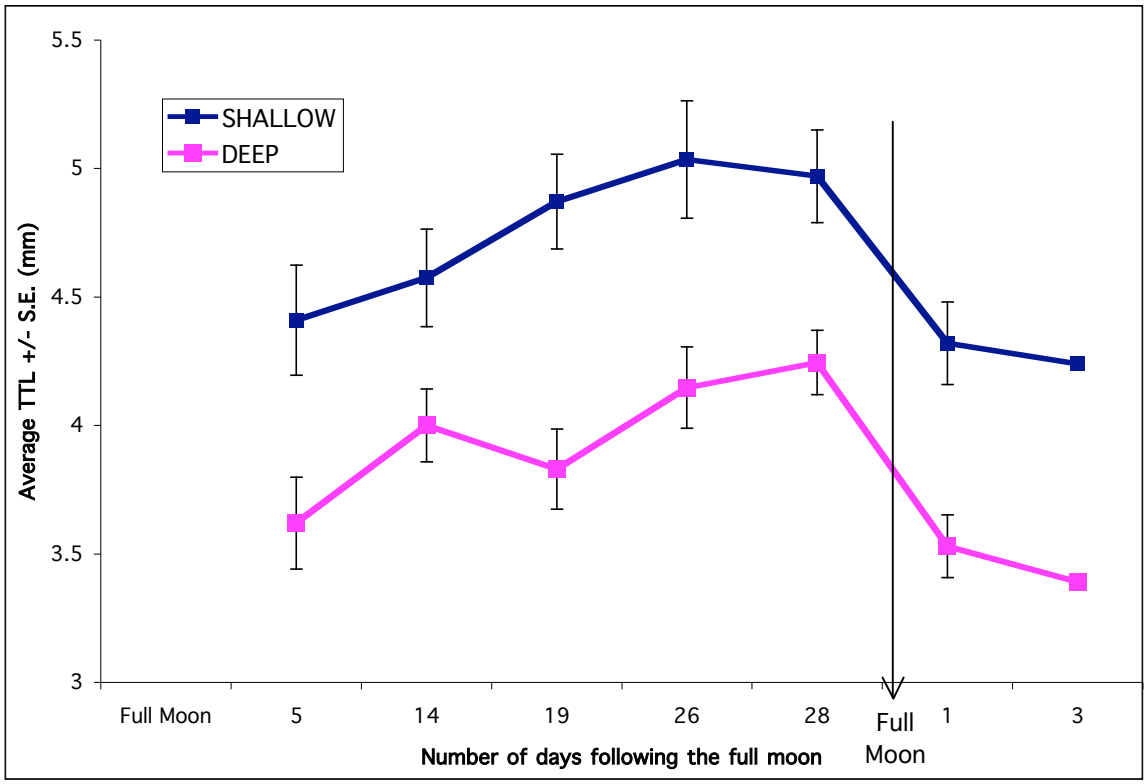



Figure 6. Changes in average tissue thickness over the lunar month (February 2001). NB from now on tissue thickness is called TTL on Figures, S.E. is the standard error of the mean.

There was a significant relationship between average tissue thickness and time over the lunar month (Table VII). The analysis tested if tissue thickness was different at different times during the lunar month, between water depths and for interactions between the two.

Table VII. Repeated Measures ANOVA results.

| Source | Type III Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| TIME | 12.354 | 1 | 12.354 | 13.2 | 0.002 |
| TIME*DEPTH | .621 | 1 | .621 | .663 | .426 |
| Error (TIME) | 16.846 | 18 | .936 | | |
| DEPTH | 3.326 | 1 | 3.326 | 19.584 | 0.000 |
| Error | 3.057 | 18 | .170 | | |

NB: first row – Tests of Within-Subject Effects (Lower-bound), second row – Between-Subject Effects. In all tables, significant p-values are printed in bold.

Significant differences in tissue thickness occurred between several sampling times during the lunar month. The timing and significance of these changes are summarised in Table VIII and can be seen in Fig. 6. The largest change occurred between the day before and the day after the full moon ($F_{(1)}=44.9$, $p<0.000$; Table VIII).

Table VIII. Repeated Measures ANOVA results – Tests of Within-Subjects Contrasts.

| Source | | MS | df | F | p |
|---|---|---|---|---|---|
| TIME | wk 1 vs wk 2 | 1.741 | 1 | 6.184 | .023 |
| | wk 2 vs wk 3 | 7.938E-02 | 1 | .458 | .507 |
| | wk 3 vs 3d bf | 1.157 | 1 | 7.012 | .016 |
| | 3d bf vs 1d bf | 5.445E-03 | 1 | .063 | .805 |
| | 1d bf vs 1d af | 9.385 | 1 | 44.914 | 0.000 |
| | 1d af vs 3d af | .253 | 1 | 4.903 | .040 |
| TIME* DEPTH | wk 1 vs wk 2 | .338 | 1 | 1.201 | .288 |
| | wk 2 vs wk 3 | 1.086 | 1 | 6.265 | .022 |
| | wk 3 vs 3d bf | .117 | 1 | .709 | .411 |
| | 3d bf vs 1d bf | .133 | 1 | 1.534 | .231 |
| | 1d bf vs 1d af | 2.450E-02 | 1 | .117 | .736 |
| | 1d af vs 3d af | 1.512E-02 | 1 | .293 | .595 |

NB: wk = week, d= day, bf=before full moon, af= after full moon

Interactions between different water depths and different times during the lunar month were not statistically significant ($F_{(1)}=0.663$, $p=0.426$; Table VII), except for one outlier between weeks 2 and 3 ($F_{(1)}=6.265$, $p<0.025$; Table VIII). Tissue thickness was significantly thinner in deep water corals compared with shallow water corals ($F_{(1)}=19.584$, $p<0.000$; Table VII). Out of twenty colonies, nineteen decreased their tissue thickness immediately after the full moon. The average increase in tissue thickness following the full moon was best described by a linear regression (using $r^2$ values for goodness-of-fit to a linear trendline, Fig. 7).

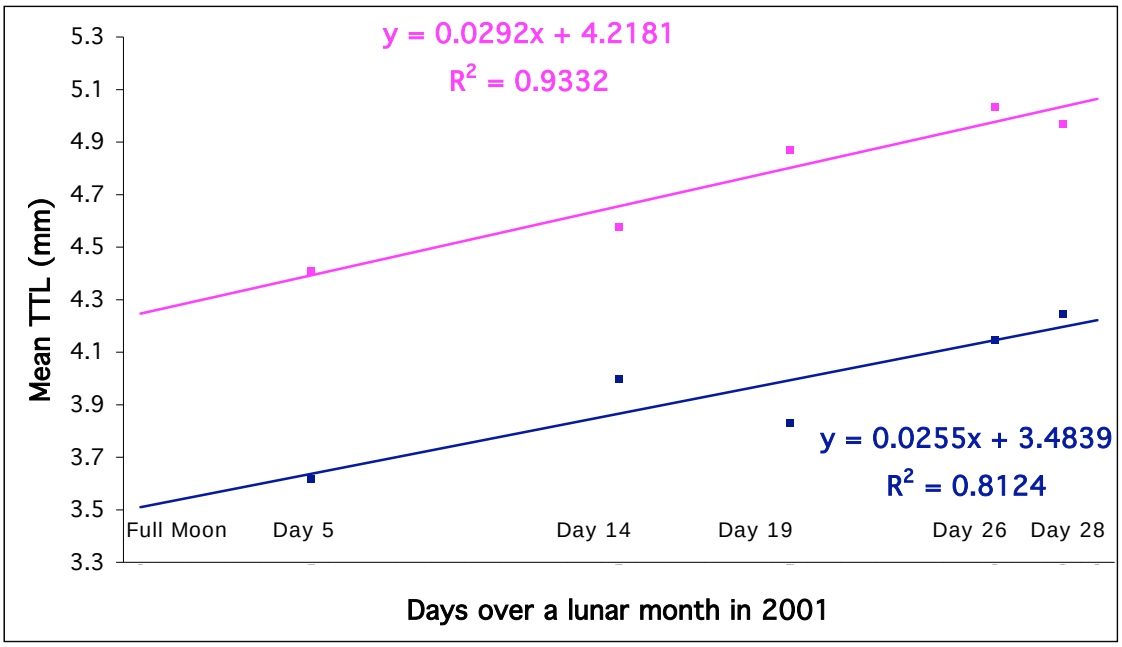



Figure 7. Change in average tissue thickness over a lunar month in deep (blue) and shallow (pink) sites on Masahet Island, 2001. NB: Day 5 = five days after the full moon occurring February 9th, 2001. Day 28 = one day before full moon March 8th, 2001

Extremely high $r^2$ values (93% for shallow, 81% for deep water corals) attested the good fit of average tissue thickness data to a linear trendline. A daily average increase value for tissue thickness of 0.029 and 0.026 mm $day^{-1}$ in shallow and deep water corals, respectively, was extracted from the regression equations calculated by Excel. This regression was undertaken on the average tissue thickness measurements of ten colonies at both shallow and deep sites. When assessing the goodness-of-fit to a linear trendline with the raw data (Fig. 8), the $r^2$ values were much lower, reflecting the greater variability in the raw data set (see also Sokal and Rohlf, 1996). However, the regression equations for the raw data were almost identical to the equations of average data (Fig. 7) and daily increase in tissue thickness was assumed to be 0.028 mm in shallow and 0.025 mm in deep corals (Fig. 8).

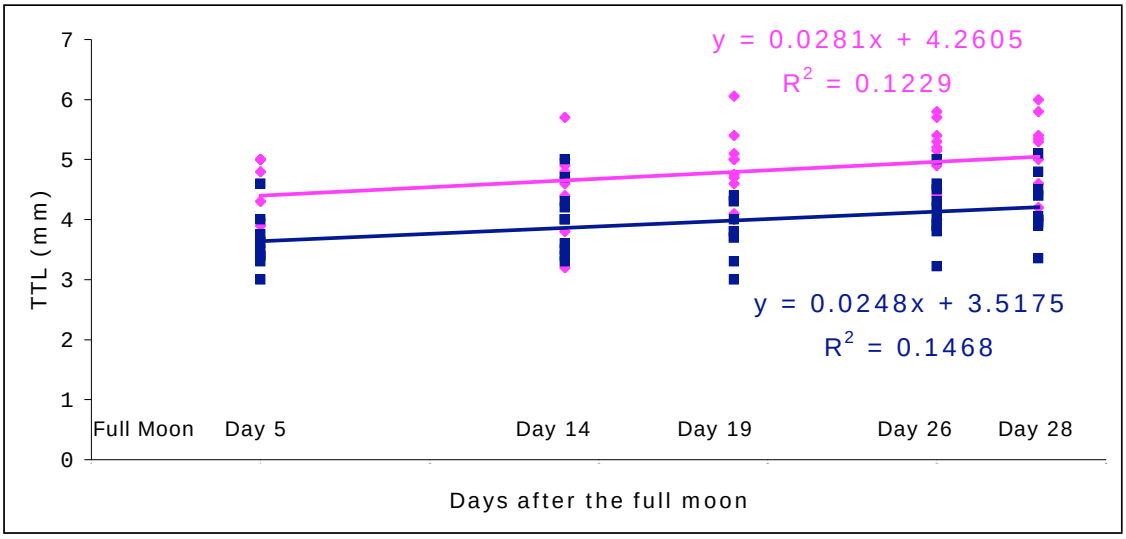



Figure 8. Change in individual tissue thickness over a lunar month in deep (blue) and shallow (pink) sites on Masahet Island, 2001. NB: Day 5 = five days after the full moon occurring February 9th, 2001. Day 28 = one day before full moon March 8th, 2001

The daily values for increase in tissue thickness obtained from coral sampling in 2001 were compared with actual increases in tissue thickness obtained in 2003 (see Fig. 9). The predicted and actual average tissue thickness values from Day 18 (after the previous full moon) were the same (Fig. 9).

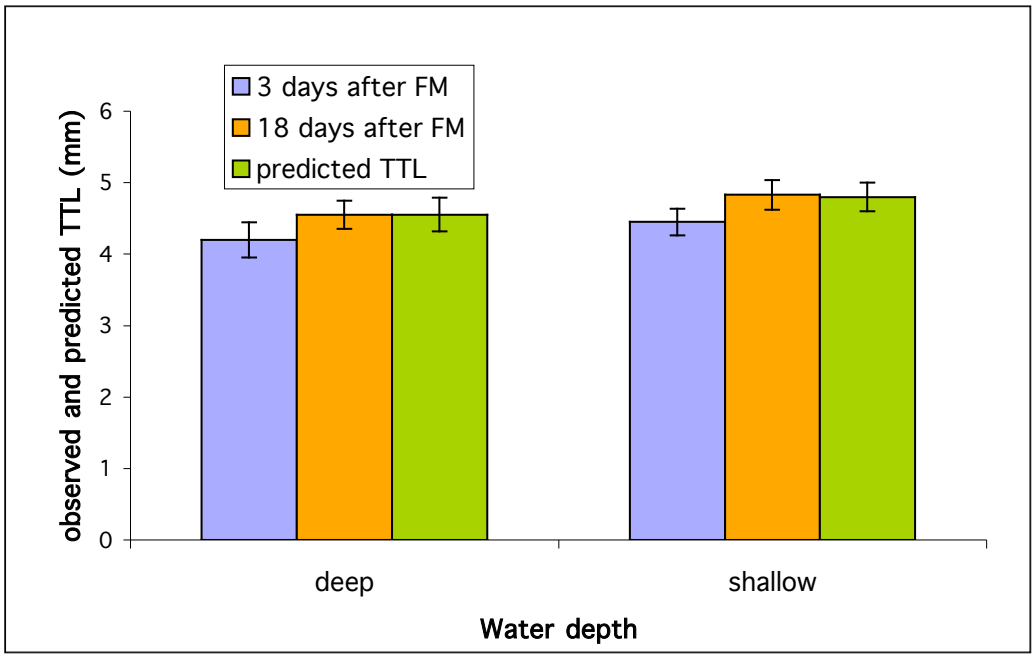



Figure 9. Observed tissue thickness measurements and predicted tissue thickness calculated from daily increase values

3.2.2. STUDY 2 – Tissue uplift variability over space and time:

*3.2.2.1. Methods:* To determine if the full moon always provides the key for tissue uplift and dissepiment formation, as indicated by Study 1, measurements of tissue thickness were made on *Porites* colonies from three additional sites (Fig. 4). Cores were removed from 60 colonies one day before and one day after the full moon on May 26, 2002. Ten corals were sampled at deep and shallow water at both Masahet and Mali Island (40 corals total). These were control sites (Table VI). To assess differences due to turbidity stress, ten corals were sampled at Kapit II shallow and, as this study site does not have deep water habitats, ten corals were measured in deep water at Kapit IV. It was only found after these measurements were taken that corals from both sites at Kapit II and IV were not affected by mine-related turbidity (see Chapter 4). Therefore, differences in tissue thickness response to the full moon due to turbidity could not be assessed in this study. However, turbidity effects on the monthly growth cycle of corals are assessed in Study 3. Because deep and shallow corals collected at Kapit Reef did not come from the same study site, the dataset was treated as unbalanced and three separate statistical analyses were undertaken (Fig. 10):

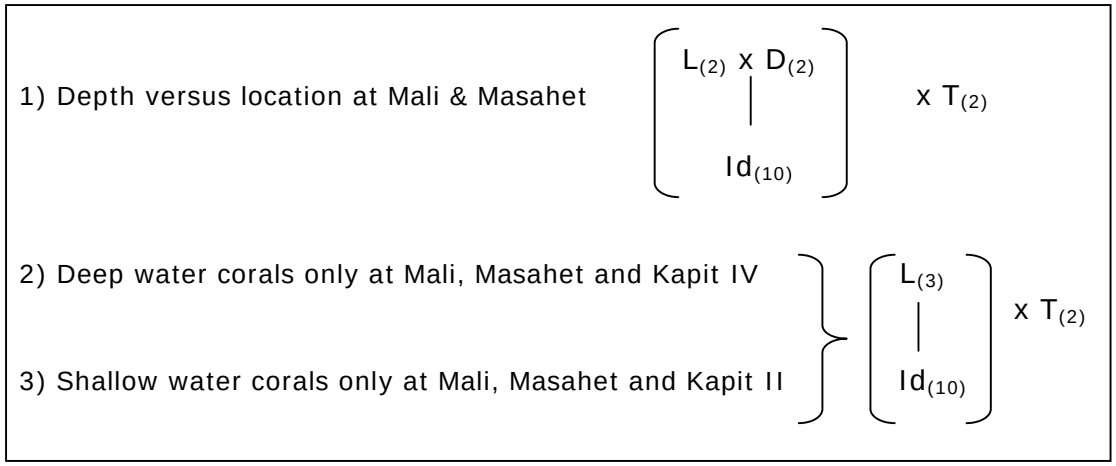



Figure 10. Statistical designs for Study 2. Repeated Measures ANOVAs. NB: L=location (Mali, Masahet, Kapit II or Kapit IV), D=depth (shallow, deep), Id=individual colonies, T=time (before and after full moon)

Each analysis was undertaken as a repeated-measures ANOVA. Sphericity was assumed in all tests, as there were only two time variables. The data was log transformed in Analysis 2) (Fig. 10). As multiple tests were done, a Bonferroni correction was used in order to reduce the potential for committing a Type I error. As there were three analyses, the $\alpha$ value of 0.05 was divided by three and a conservative value of $\alpha$=0.01, was adopted.

*3.2.2.3. Results:* Tissue thickness decreased significantly after the full moon in all depths and locations ($F_{(1)}$=13.284, p<0.000; Table IX).

Table IX. Repeated Measures ANOVA 1). Masahet versus Mali deep versus shallow corals. NB: $\alpha$=0.01

| Source | Type III Sum of Squares | df | Mean Square | F | p |
|---|---|---|---|---|---|
| TTL | 13.284 | 1 | 13.284 | 88.123 | 0.000 |
| TTL*DEPTH | 5E-04 | 1 | 5E-04 | .003 | .954 |
| TTL*LOCATION | 8E-03 | 1 | 8E-03 | .053 | .819 |
| TTL*DEPTH*LOCATION | 5E-02 | 1 | 5E-02 | .332 | .568 |
| Error(TTL) | 5.427 | 36 | .151 | | |
| DEPTH | 4.704 | 1 | 4.704 | 13.379 | 0.001 |
| LOCATION | 1.058 | 1 | 1.058 | 3.009 | 0.91 |
| DEPTH*LOCATION | 8E-03 | 1 | 8E-03 | .023 | 0.881 |
| Error | 12.659 | 36 | .352 | | |

NB: First row within-subject effects (Sphericity assumed), second row between-subjects effects

There were no significant differences in tissue thickness changes between Mali and Masahet corals ($F_{(1)}=3.009$, $p=0.91$; Table IX), however, shallow corals always had greater initial tissue thickness than deep water corals ($F_{(1)}=13.379$, $p<0.001$; Fig. 11). Tissue thickness decreased significantly after the full moon in both shallow (by, on average 21% +/- 2.8%) and deep (by, on average 25% +/- 2.1%) study sites (Table X and XI). The amount of the change did not differ between locations (Fig. 11).

Table X. Repeated Measures ANOVA 2). Shallow corals in Masahet, Mali and Kapit II. NB: $\alpha=0.01$

| Source | Type III Sum of Squares | df | Mean Square | F | p |
|---|---|---|---|---|---|
| TTL | .934 | 1 | .934 | 89.633 | 0.000 |
| TTL*LOCATION | 5.776E-02 | 2 | 5.776E-02 | 2.772 | 0.08 |
| Error (TTL) | .281 | 27 | 1.042E-02 | | |
| LOCATION | 8.093E-02 | 2 | 4.047E-02 | .994 | .383 |
| Error | 1.1 | 27 | 4.073E-02 | | |

Table XI. Repeated Measures ANOVA 2). Deep corals in Masahet, Mali and Kapit IV. NB: $\alpha=0.01$

| Source | Type III Sum of Squares | df | Mean Square | F | p |
|---|---|---|---|---|---|
| TTL | 10.5 | 1 | 10.5 | 57.77 | 0.000 |
| TTL*LOCATION | 5.733E-02 | 2 | 2.867E-02 | .158 | .855 |
| Error (TTL) | 4.907 | 27 | .182 | | |
| LOCATION | 1.817 | 2 | 1.817 | 5.887 | .08 |
| Error | .309 | 27 | .309 | | |

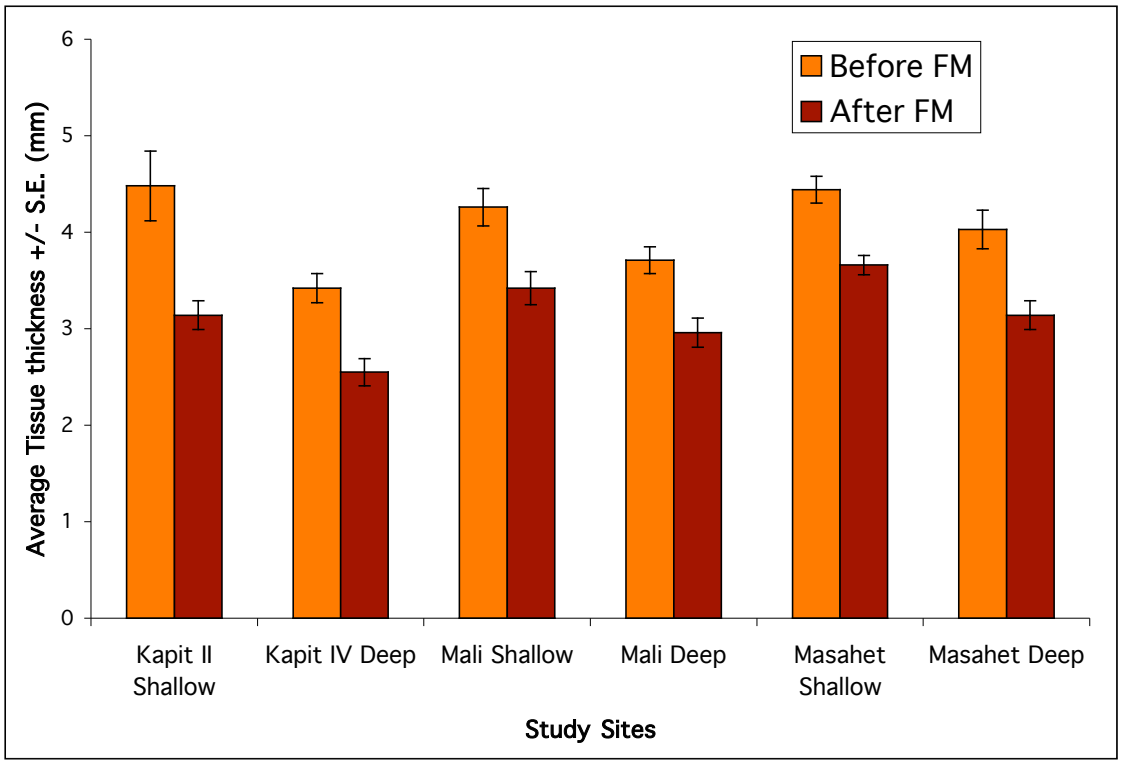



Figure 11. Comparison of average tissue thickness in all study sites the day before and after the full moon. NB: FM = Full Moon

3.2.3. STUDY 3) – Variability in tissue uplift with turbidity stress:

*3.2.3.1. Methods*: The change in tissue thickness before and after a full moon was also examined in colonies growing at Kapit III (Fig. 4), a site that commonly experiences mine-related turbidity (Table VI). Cores were removed from ten colonies of *Porites* one day before and one day after the full moon that occurred on March 8, 2001. Only eight of these colonies could be identified in 2003. Cores were removed from these eight colonies one day before and one day after the full moon that occurred on February 18, 2003. A paired t-test was used to determine if there was a significant difference in the amount of tissue lost after the full moon between the same individuals sampled in 2001 and those sampled in 2003.

In 2003, five colonies were collected from Kapit III and returned to the Australian Institute of Marine Science for sclerochronological analysis (see Chapter 1, Section 1.5. for details). X-radiographs were taken of skeletal slices to determine linear extension rates from the annual density banding pattern and to examine if the different patterns of change in tissue thickness between 2001 and 2003 at Kapit III left different signatures in the coral skeleton.

*3.2.3.2. Results:* In 2001, tissue thickness immediately before the full moon at Kapit III was, on average, 2.1 mm (+/- 0.08 mm, Fig. 12).

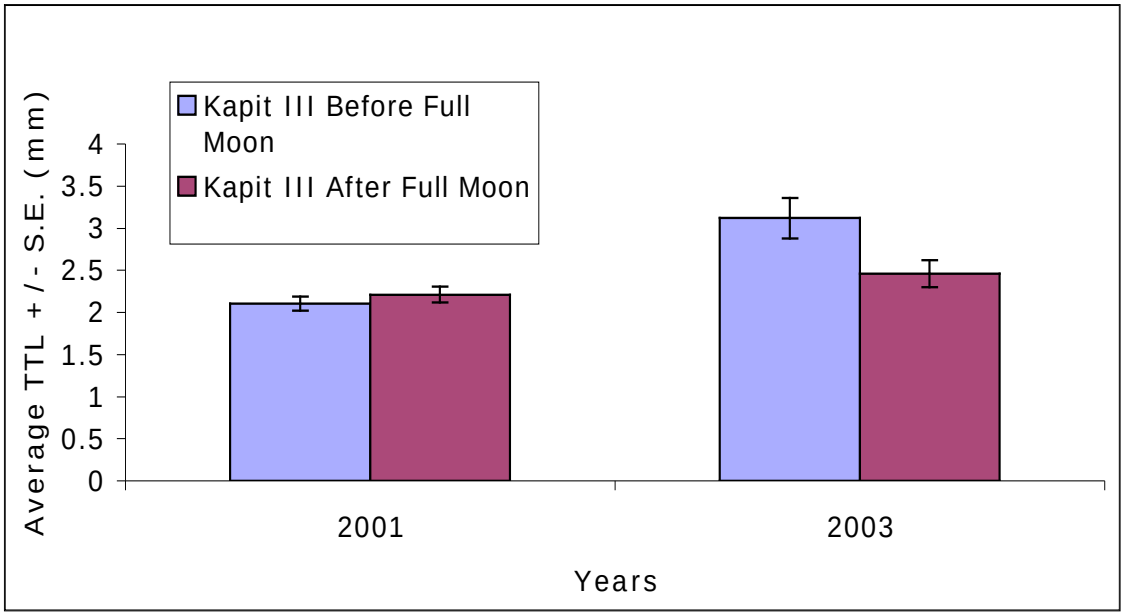



Figure 12. Average tissue thickness changes in response to the full moon in 2001 and 2003 at Kapit III.

None of the corals examined in 2001 decreased their tissue thickness following the full moon (paired t-test, $t_9$=-1.944, p=0.088). By 2003, however, average tissue thickness had increased to 3.1 mm (+/- 0.2 mm), and all eight corals responded with a decrease in tissue thickness after the full moon on February 18, 2003 (paired t-test, $t_7$=6.199, p<0.000; Fig.

12). The change in tissue thickness following the full moon in February 2001 was significantly different from the decrease following the full moon in February 2003 (paired t-test, $t_7=6.47$; $p<0.000$). Examination of the raw data from Kapit III showed that the minimum tissue thickness level at which tissue uplift following the full moon stopped occurring, was 2.2 mm.

The X-rays of skeletal slices cut from five whole skeletons collected in Kapit III were visually examined. As clear density banding was not evident, linear extension rates could not be reconstructed (see X-ray positives, Appendix C). In two colonies (KT III 0 and NKT III, Appendix C) more dense bands than usual could be found just below the outer edge (see red arrows), possibly indicating a decrease or halt in skeletal extension rates in 2001. One colony (KT III 4, App. C) did not display any discernable features in its skeleton but in three colonies the distinctive concrete plugs and a narrow skeletal overgrowth of these plugs in all cases, was apparent (Kapit III 3, 0 and 7, App. C, also Plate 5, Chapter 1).

3.3. DISCUSSION: Study 1) proved that tissue thickness decreased, between 10-30%, the day following the full moon in both, deep and shallow water *Porites* corals. For the first time, evidence was provided that tissue uplift following dissepiment formation was linked to a particular lunar cue. In results obtained here, linear regressions of tissue thickness against time of month showed that tissue thickness in corals from Lihir Island increased by 28 µm per day over the lunar cycle in shallow water corals and by 25 µm per day over the lunar cycle in deep water corals. These values were tested against tissue thickness data from corals growing on Masahet Island

in 2003 and found to be valid to estimate change in average tissue thickness from day 3 to day 18 after the full moon. A quantitative value for adjusting daily increase in tissue thickness over the lunar month could potentially smooth out previous tissue thickness data sets which were not sampled with lunar variability in mind. More importantly, allowing for monthly tissue thickness variability would mean that comparable measurements of tissue thickness can be made at any time during the lunar month. This is especially important when large scale monitoring efforts, such as those described in Chapter 4 or by Barnes and Lough (1992), are undertaken.

In Study 1, an average 4% decrease in tissue thickness was suggested to occur between Day 14 and Day 19 after the full moon in deep water in the middle of the lunar month (see Fig. 7). This outlier (also identified by statistical analysis, see Table VIII) is most likely explained by sampling error as some of the deep water corals decreased in the middle of the lunar month, which is not possible without dissepiment formation following tissue uplift. In addition, the decrease was not large enough for dissepiment formation to have occurred. It is also unlikely to occur without the lunar cue, on account of the evidence regarding tissue thickness decrease following the full moon presented here. Sampling error at this particular time was likely as I could not dive on this particular day and field assistants were later found to have cored from areas away from the colony summit, thereby affecting results (for explanation see Chapter 5, Section 5.1.1.).

Tissue uplift immediately following the full moon was seen in corals sampled at different times of the year (February and May), in different years (2001, 2002 and 2003), at different study sites (Masahet and Mali Island as well as Kapit II, III and IV) and at both, shallow and deep water habitats. Thus, Study 2) gave additional evidence that the full moon provided the cue for tissue uplift. Since their first appearance in the literature, fine density bands have been equated with the lunar cycle (Buddemeier, 1974). Fewer than 12-13 fine density bands per year could therefore indicate fewer than 12-13 tissue uplift periods per year. This would complicate the use of adjusting for time of sampling during the lunar month unless it was known exactly when tissue uplift stopped occurring. From models, it was predicted that linear extension rates were likely to be three times faster in summer than in winter (Barnes and Lough, 1996). Buddemeier (1975) and Houck (1978) found smaller amounts of fine density bands in Hawaiian corals where seasonal banding indicated slower growth. True (*in review*) also found large seasonal variability in tissue thickness on the Great Barrier Reef (GBR), most likely related to reductions in sea surface temperature (SST) in the winter months. As opposed to Hawaii and the GBR, Lihir Island has no major seasonal fluctuations in SST and insolation, only in wind direction (NSR, 1989). As tissue thickness decreased by similar amounts in both February and May after the full moon, seasonal variability in tissue thickness or dissepiment formation – as suggested from Hawaii or the GBR - may not occur on Lihir Island.

Other factors may also impair monthly tissue uplift following each full moon. True (1995) suggested gametogenesis to have a potential influence

on tissue thickness, as large energy reserves are needed for reproduction (see also Chapter 2). True (*in review*) found that reproductive periods coincide with the period of maximum tissue thickness. Increased tissue reserves may be needed for the energy-extensive process of gametogenesis. This was supported by the finding that the endodermal layer surrounding the female gonads became progressively thinner with subsequent maturation of the oocytes in *Porites* (Tomascik and Sander, 1987b). Tomascik and Sander (1987b) suggested resorption of ephithelial cells as an important source of nutrients for developing oocytes. Massive *Porites lobata* - the main species found on Lihir Island - are a broadcasting species, usually exhibiting reproductive activity only during two months of the year with clear lunar periodicity (Glynn *et al.*, 1994). It is possible that dissepiment formation and tissue uplift do not occur during this period, however, during the sampling times in this study, there was no evidence of broadcast spawning.

Previous studies suggested that tissue thickness could not fall below 2-2.5 mm (e.g. True, 1995). In 2001, corals in Kapit III were found to have an average tissue thickness of 2.1 mm. An additional monthly decrease of 20% would have reduced tissue levels to as low as 1.6 mm. This decrease could lead to whole-colony death or at least to greatly increased amounts of partial mortality due to tissue resorption. More and/or larger tissue lesions would result in greater competition by fouling organisms, which would decrease the chances of lesion regeneration in affected corals (e.g. Bak and Steward-Van Es, 1980). It was also found that regeneration of lesions depended on the amount of tissue bordering a lesion, as well as

lesion size (Van Woesik, 1998). In this study, however, no increases in lesions or bioerosion was observed on corals with low tissue levels. True (1995) also suggested physiological restraints of continuing tissue decrease after reaching 2-2.5 mm. Calyx depth (around 2 mm, True, 1995) as well as the depth of existential features such as mesenteries are likely to impose a limit for further tissue reduction.

In Kapit III, no monthly tissue uplift could be found at tissue thicknesses below 2.2 mm. When tissue thickness increased above this level, monthly tissue uplift resumed. Since Kapit III was highly impacted by mine-related turbidity, massive *Porites* corals seem to have developed adaptive mechanisms to survive turbidity stress. Decreasing their energy expenditure for growth in order to preserve minimum tissue reserves is one possible adaptive mechanism for massive *Porites*. This possibility has yet to be mentioned in the literature, although Edmunds and Spencer Davies (1989) found lower energy investment into tissue growth in light-stressed corals. Other studies also found decreased coral tissues in low-light habitats in *Montastrea monasteriata* (Anthony and Hoegh-Guldberg, 2003) and *Fungia spp* (Masuda *et al.*, 1993). The key mechanism for maintaining positive rates of photosynthesis in decreased light levels was thought to be lower tissue mass resulting in reduced dark respiration rates (Anthony and Hoegh-Guldberg, 2003). This could suggest that the minimum tissue levels found at Kapit III were part of photoadaptation by reducing respiration and thereby maintaining photosynthesis in this turbid environment. Other studies also found *Porites* adapted to turbidity stress by reducing respiration rates by a third (Edmunds and Spencer-Davies, 1989). These

authors found a net daily energy surplus of 67% in *Porites* under sediment stress compared with 45% in unstressed colonies. Meesters *et al.* (2002) examined RNA/DNA ratios in massive *Porites* in different light/turbidity regimes. They found that RNA/DNA ratio was significantly negatively correlated with decreases in light, possibly indicating a genetic adaptation in the metabolic functioning of corals in the turbid environment – i.e. photoadaptation (see also Kuffner, 2001). Several studies have found corals to have great capacities for adapting to stress events and to have good potential for recovery after the stressor is removed (e.g. Grigg, 1995; Riegl, 1995). The fact that all eight colonies measured at Kapit III increased in tissue thickness by a third between 2001 and 2003 (from 2 mm to 3 mm) also suggests either photoadaptation, or a reduction in turbidity. The latter is unlikely as the mining operations and procedures creating the turbidity stressor remained unchanged between the years studied.

No monthly decrease in tissue thickness indicates that tissue uplift and associated dissepiment formation had ceased. Vertical skeletal extension is needed for the tissue layer to increase as tissue can not grow below the last dissepiment layer. Skeletal extension will stop, or at least decrease if dissepiment formation ceases, as this is an intrinsic part of linear growth in massive *Porites* (e.g. Barnes and Lough, 1993, also Chapter 1, Section 1.2). However, skeletal extension rates were found to be less responsive to environmental stress factors than tissue mass in other studies on massive *Porites* (e.g. Barnes and Lough, 1999; Anthony *et al.*, 2002). Anthony *et al.* (2002) did not examine corals at their absolute energy limits and the corals

examined by Barnes and Lough (1999) on Misima Island, PNG, died from sudden sediment burial, rather than continuous skeletal extension after energy reserves were exhausted (tissue levels of the dead corals were still higher than 2.2 mm). Significant decreases in skeletal extension may only occur when tissue thickness reaches this minimum level and can no longer sustain skeletal growth rates (e.g. Anthony, 1999b). True (*in review*) found that shading caused both, a reduction in tissue thickness and a slowing-down of linear extension, but he did not specify at what tissue levels skeletal extension rates slowed. In 2003, the corals had resumed tissue uplift following the full moon. This suggests a return to monthly dissepiment formation, and therefore, greater vertical skeletal growth than in 2001. Evidence for this assumption was sought in skeletal density banding patterns of colonies collected at Kapit III. Unfortunately, density bands from X-radiographs of skeletal slices could not be dated due to the confused density banding patterns in the colonies collected (X-radiographs in App. C). This could result from growing inshore, in a more variable environment with regards to turbidity, light, temperature or freshwater fluctuations than offshore corals which usually display much clearer density banding patterns (Lough and Barnes, 1992). Two of the colonies that were X-radiographed showed a band of greater density just below their growth surface, which could indicate a cessation/reduction in linear extension found in 2001 (see red arrows on X-radiographs in App. C). More importantly, the fact that all visible concrete plugs were overgrown by skeleton at Kapit III was a definite testament that skeletal extension had occurred since 2001.

This was the first study showing evidence for cessation and subsequent resumption of growth processes in massive *Porites* under turbidity stress. Increases in lipid levels following tissue uplift have been found by True (*in review*), which suggests that some tissue is converted into lipid storage products. *Porites*' ability to repeatedly mobilize energy reserves during monthly tissue uplift episodes may be an important mechanism to survive stress episodes. However, if continually more energy reserves are being used than can be mobilised during tissue uplift or by auto- or heterotrophy, tissue levels will drop to a minimum limit (found here to be 2.2 mm), where a further, sudden 20% tissue decrease can not be sustained. At this limit, the corals seem to arrest energy-expensive processes until photoadaptive mechanisms create an energy surplus (see diagram below).

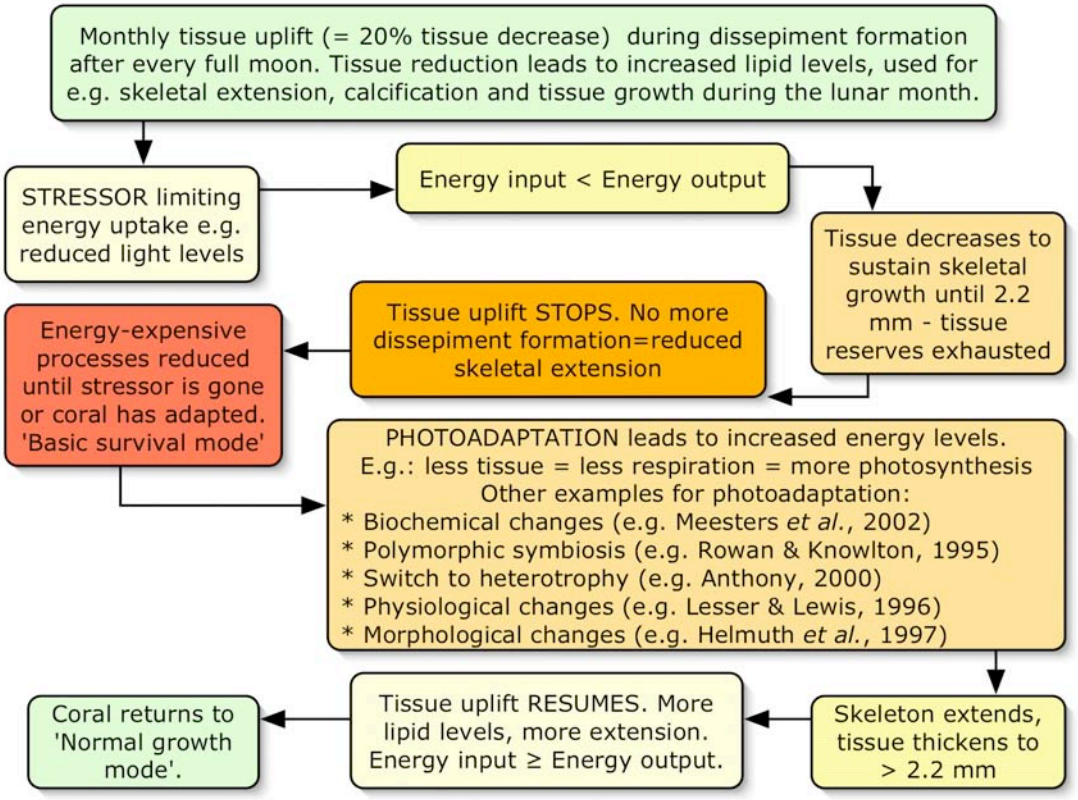



Diagram showing a possible mechanism of *Porites'* response to increased turbidity. This scenario relates only to a stressor which will not kill the corals outright. NB: colour gradients denote levels of severity of coral stress response.

Photoadaptation (for different examples see Edmunds and Spencer-Davies, 1989; Rowan and Knowlton, 1995; Lesser and Lewis, 1996; Helmuth *et al.*, 1997) may lead to a sufficient energy surplus to sustain a resumption or increase of vertical skeletal growth. Skeletal extension creates space for more tissue growth, and monthly tissue uplift resumes once the threshold limit of 2.2 mm is surpassed. Photoadaptation via changes in the coral's behaviour, such as increasing heterotrophy and digesting sediment particles, is one of the most commonly quoted examples (e.g. Wilkinson, 1999; Anthony, 2000). Even though they are regarded as being amongst the most sediment-tolerant coral genera (Stafford-Smith and Ormond, 1992; McClanahan and Obura, 1997; Nystrom *et al.*, 1997; Torres and Morelock, 2002), *Porites* are known to be poor heterotrophs (Moberg *et al.*, 1997; Anthony, 1999a). The cessation and resumption of monthly tissue uplift as a response to limits in tissue reserves is likely to play an important role in this genus' ability to survive turbidity loads that are fatal to most other coral genera.

## 3.4. SUMMARY:

- Tissue thickness decreased between 10-30% following the full moon;
- Tissue thickness increased, on average, linearly during the lunar month until reaching maximum thickness the day before the full moon. A value of daily increase of around 28 µm in shallow and 25 µm in deep corals could be used to adjust for time of sampling on corals at Lihir Island;
- The tissue uplift response to the full moon could be replicated through time, space and water depth at Lihir Island;

- There was no evidence of seasonal variability in tissue response to the lunar cue;
- Tissue uplift and dissepiment formation did not occur in corals in which tissue thickness was 2.2 mm or less;
- Tissue uplift and dissepiment formation resumed when tissue levels increased above 2.2 mm.

Summary of aims of studies, importance of studies, methods, predicted and actual outcomes and final comments.

| AIM | IMPOR-TANCE | METHOD USED | PREDICTED OUTCOME | ACTUAL OUTCOME | COMMENTS, FUTURE WORK |
|---|---|---|---|---|---|
| To find lunar cue for tissue uplift STUDY 1 | Time of sampling during lunar month can bias ttl measurements | Sampled ttl 7 times over the lunar month | ttl decreases by ~ 20% following a lunar cue (from Barnes & Lough, 1992) | ttl decreased by, on average 20% after the full moon | First study that proved lunar control over tissue uplift and determined lunar phase involved |
| To determine pattern of ttl increase during lunar month STUDY 1 | Need to know how ttl varies during the month to find calibration | Linear regressions and regression equations | ttl shows varying patterns of increase during the lunar month (D Barnes, pers comm) | ttl increased linearly during the lunar month. Daily increase of ~0.3µm | First study that developed procedure to correct for monthly ttl variability. Needs to be done for other areas to smooth out datasets |
| To assess if this procedure predicts ttl changes STUDY 1 | Adjusting for monthly ttl variability in large datasets reduces noise | Measured 10 colonies at 2 times during the lunar month | Daily values of ttl increase can predict ttl changes during the month | Predicted and actual average ttl measured were the same | First study that adjusted for natural, monthly ttl variabillity. Should be used to smooth out large ttl datasets |
| To assess if monthly tissue uplift is stable over time and space STUDY 2 | If seasonal or physiological factors stop tissue uplift, adjustment can't be used | Measured 10 colonies at 2 depths, 4 sites, 2 months and 2 years | Tissue uplift is affected by seasonal and reproductive changes in ttl (from True, 1995) | Tissue ALWAYS decreased the day after the full moon during the times sampled here | ttl can be adjusted on Lihir as seasonal variability is less pronounced than GBR. Need to check during reproductive season |
| To assess if monthly tissue uplift occurs in highly stressed corals STUDY 3 | Another possible factor that needs to be checked before using adjustment | Measured same colonies in high turbidity site in 2001 & 2003 | Tissue uplift continues until colony dies (from Barnes & Lough, 1999) | Tissue uplift stopped in 2001, all corals < 2.2 mm. Resumed in 2003 when ttl > 2.2 mm | *Porites* may stop energy expensive processes when tissue reserves reach limit. May be a reason why they are so sediment-tolerant |

NB: ttl= tissue thickness; references relate to speculations in the literature which these studies addressed. Arrows denote links between studies.

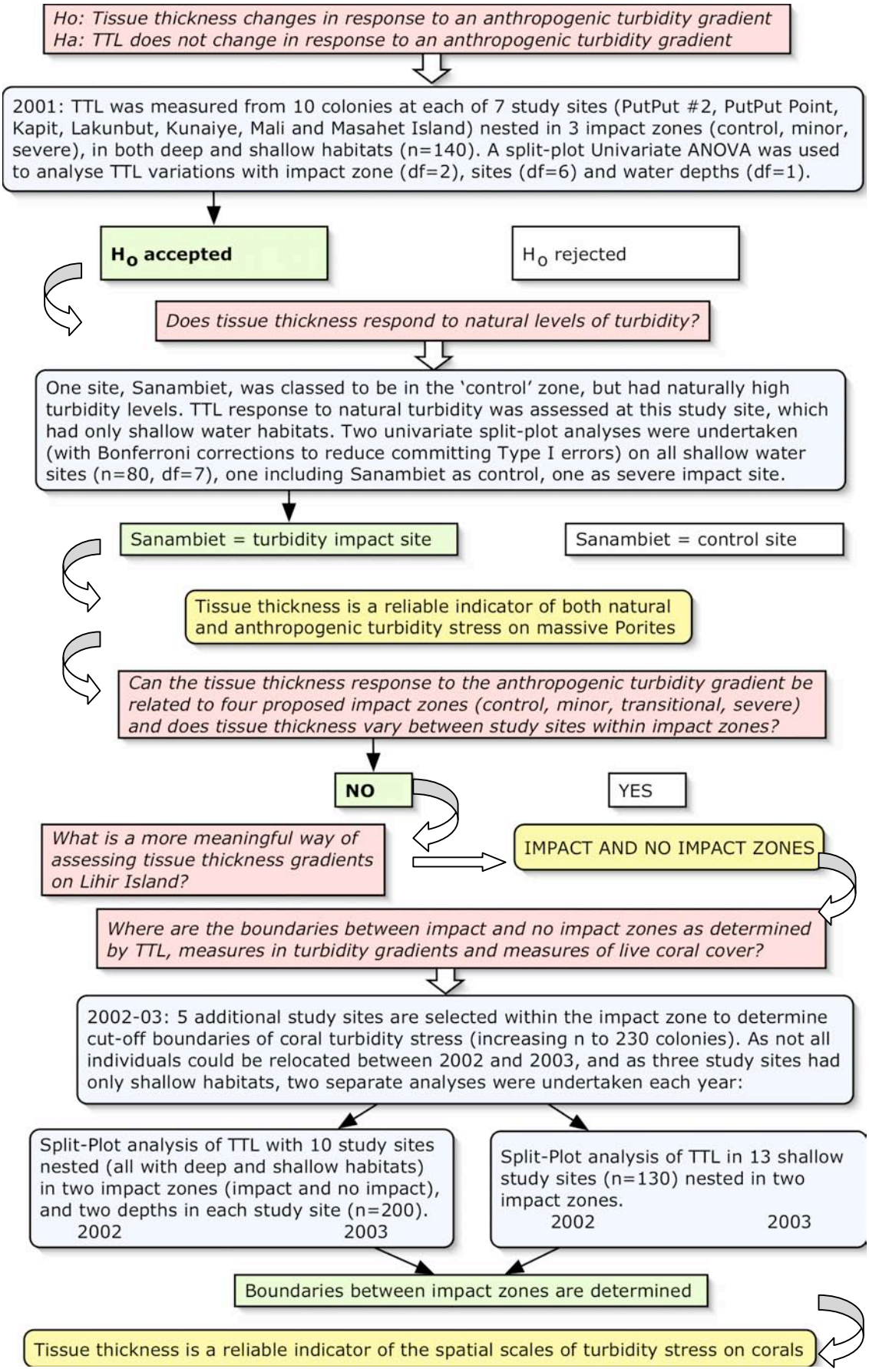
# 4.0 TISSUE THICKNESS AND TURBIDITY

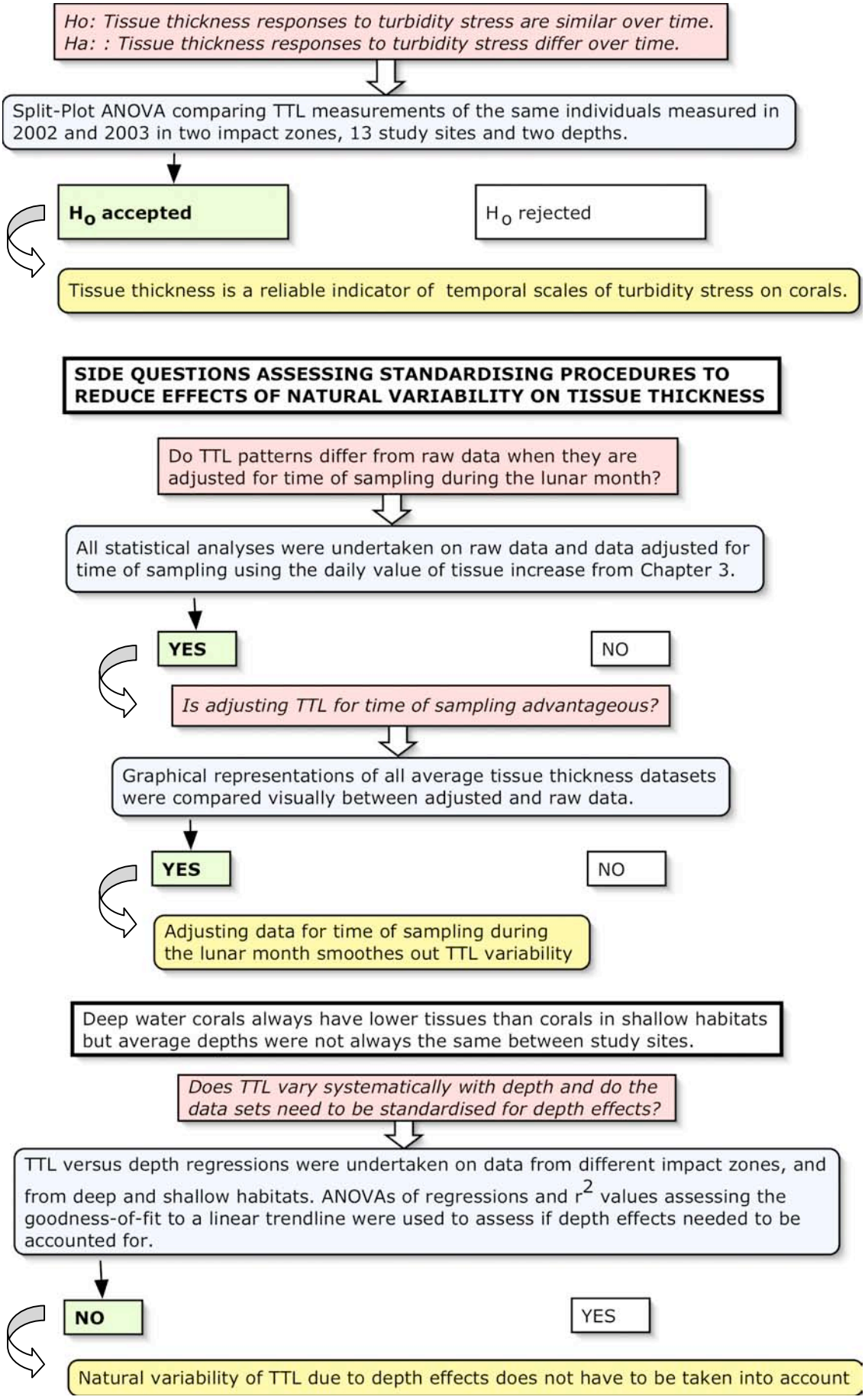
4.1 INTRODUCTION: Sediment has long been known to be a major stress factor for reef corals (see Literature Review, Chapter 2). Anthropogenic sediment impacts are mostly chronic, and usually stem from a point-source, either from terrestrial run-off or ocean dumping. Tissue thickness was determined to be the most useful monitoring method of coral stress response in developing countries (Table V, Chapter 2). Two previous studies have assessed tissue thickness in relation to decreases in water quality due to sediment, one mimicking turbidity impact, the other dealing with high sedimentation: True (1995; *in review*) artificially shaded massive *Porites*. He found an immediate, significant decrease of tissue thickness in shaded versus control colonies. Shading decreased photosynthetically active radiation (PAR) by 75-85% (True, *in review*), which is known to result in reduced primary production (see Te, 1997). However, True's reductions in PAR are more than twice as high than would be expected from suspended solid concentrations of ~ 20 mg $l^{-1}$, as found in the most impacted reef areas on Lihir (see Table 1, Te, 1997). True's shading experiment also removed any potentially positive effects from increased suspended sediment on the corals, such as higher rates of sediment feeding which would offset the negative effects of reduced photosynthesis (e.g. Anthony, 1999a).

Barnes and Lough (1999) examined the impact on massive *Porites* of an up to 100-fold increase in sedimentation resulting from the construction and operation of a gold mine on Misima Island, Papua New Guinea. Tissue

thickness decreased significantly with increasing proximity to the mine site, but corals in the most affected areas were buried and died (Barnes and Lough, 1999). Sediment accumulation did not occur on reefs affected by mining sediments on Lihir Island because of strong currents and water motion. Hence, corals at the depths sampled on Lihir Island were mostly affected by turbidity, which is expected to be a less extreme stressor than sediment accumulation on living coral surfaces (e.g. Woolfe and Larcombe, 1999). Tissue thickness has never been used to assess coral response to turbidity levels, neither has it been examined if tissue thickness would differentiate between natural and anthropogenic turbidity gradients. Work described here was designed to test how different levels of turbidity encountered at Lihir Island affected tissue thickness. Additionally, it was assessed if tissue thickness could be used to delineate distinct turbidity impact boundaries, and how these impact boundaries concurred with other monitoring methods. Finally, a standardising methodology developed in Chapter 3 was adopted to see if it minimised some of the large, natural variability in tissue thickness measurements.

4.2. FLOWCHART OF STUDIES: The following flowchart shows detailed study questions, methods used to answer those study questions and the progressional relationship between study questions.


Ho: Tissue thickness changes in response to an anthropogenic turbidity gradient
Ha: TTL does not change in response to an anthropogenic turbidity gradient
2001: TTL was measured from 10 colonies at each of 7 study sites (PutPut #2, PutPut Point, Kapit, Lakunbut, Kunaiye, Mali and Masahet Island) nested in 3 impact zones (control, minor, severe), in both deep and shallow habitats (n=140). A split-plot Univariate ANOVA was used to analyse TTL variations with impact zone (df=2), sites (df=6) and water depths (df=1).
Ho accepted
Ho rejected
Does tissue thickness respond to natural levels of turbidity?
One site, Sanambiet, was classed to be in the 'control' zone, but had naturally high turbidity levels. TTL response to natural turbidity was assessed at this study site, which had only shallow water habitats. Two univariate split-plot analyses were undertaken (with Bonferroni corrections to reduce committing Type I errors) on all shallow water sites (n=80, df=7), one including Sanambiet as control, one as severe impact site.
Sanambiet = turbidity impact site
Sanambiet = control site
Tissue thickness is a reliable indicator of both natural and anthropogenic turbidity stress on massive Porites
Can the tissue thickness response to the anthropogenic turbidity gradient be related to four proposed impact zones (control, minor, transitional, severe) and does tissue thickness vary between study sites within impact zones?
NO
YES
What is a more meaningful way of assessing tissue thickness gradients on Lihir Island?
IMPACT AND NO IMPACT ZONES
Where are the boundaries between impact and no impact zones as determined by TTL, measures in turbidity gradients and measures of live coral cover?
2002-03: 5 additional study sites are selected within the impact zone to determine cut-off boundaries of coral turbidity stress (increasing n to 230 colonies). As not all individuals could be relocated between 2002 and 2003, and as three study sites had only shallow habitats, two separate analyses were undertaken each year:
Split-Plot analysis of TTL with 10 study sites nested (all with deep and shallow habitats) in two impact zones (impact and no impact), and two depths in each study site (n=200).
2002
2003
Split-Plot analysis of TTL in 13 shallow study sites (n=130) nested in two impact zones.
2002
2003
Boundaries between impact zones are determined
Tissue thickness is a reliable indicator of the spatial scales of turbidity stress on corals


Ho: Tissue thickness responses to turbidity stress are similar over time.
Ha: : Tissue thickness responses to turbidity stress differ over time.
Split-Plot ANOVA comparing TTL measurements of the same individuals measured in 2002 and 2003 in two impact zones, 13 study sites and two depths.
H0 accepted
H0 rejected
Tissue thickness is a reliable indicator of temporal scales of turbidity stress on corals.
SIDE QUESTIONS ASSESSING STANDARDISING PROCEDURES TO REDUCE EFFECTS OF NATURAL VARIABILITY ON TISSUE THICKNESS
Do TTL patterns differ from raw data when they are adjusted for time of sampling during the lunar month?
All statistical analyses were undertaken on raw data and data adjusted for time of sampling using the daily value of tissue increase from Chapter 3.
YES
NO
Is adjusting TTL for time of sampling advantageous?
Graphical representations of all average tissue thickness datasets were compared visually between adjusted and raw data.
YES
NO
Adjusting data for time of sampling during the lunar month smoothes out TTL variability
Deep water corals always have lower tissues than corals in shallow habitats but average depths were not always the same between study sites.
Does TTL vary systematically with depth and do the data sets need to be standardised for depth effects?
TTL versus depth regressions were undertaken on data from different impact zones, and from deep and shallow habitats. ANOVAs of regressions and r2 values assessing the goodness-of-fit to a linear trendline were used to assess if depth effects needed to be accounted for.
NO
YES
Natural variability of TTL due to depth effects does not have to be taken into account

4.3. 2001 STUDY: Massive *Porites* corals from eight study sites were chosen for tissue thickness measurements in 2001 (Fig. 13). Methodology for selecting them is described in Chapter 1, Section 1.5. and study sites are described in detail in Appendix A. Natural System Resources (NSR) predicted in a Draft Environmental Plan (1989) that mining activities would affect corals and reefs in a way that could be described in terms of four impact zones (see Chapter 1, Section 1.4., Fig. 13). The study sites chosen here were situated near NSR coral reef monitoring stations and within three of NSR's impact zone predictions, namely 'severe', 'minor' and 'control' (see Fig. 13). Several study sites had fewer than ten massive *Porites* colonies in sampling areas which were restricted by dive times. Hence, no measurements from the narrow 'transitional' impact zone and control zones on the northern and southeastern part of Lihir Island could be taken. Sampling sites within the 'severe' impact zone were PutPut Point and Kapit, within the 'minor' impact zone were PutPut #2, Lakunbut and Kunaiye and Mali and Masahet Island served as 'control' sites (Fig. 13). Sanambiet Island was chosen as a naturally turbid site to determine if tissue thickness responded similarly to naturally high levels of turbidity as it did to anthropogenically elevated levels. A difference in tissue thickness response to anthropogenic sources of turbidity may indicate additional, mine-derived stressors affecting the corals. Sanambiet Island was excluded from the major analysis, as it only had a shallow study site.

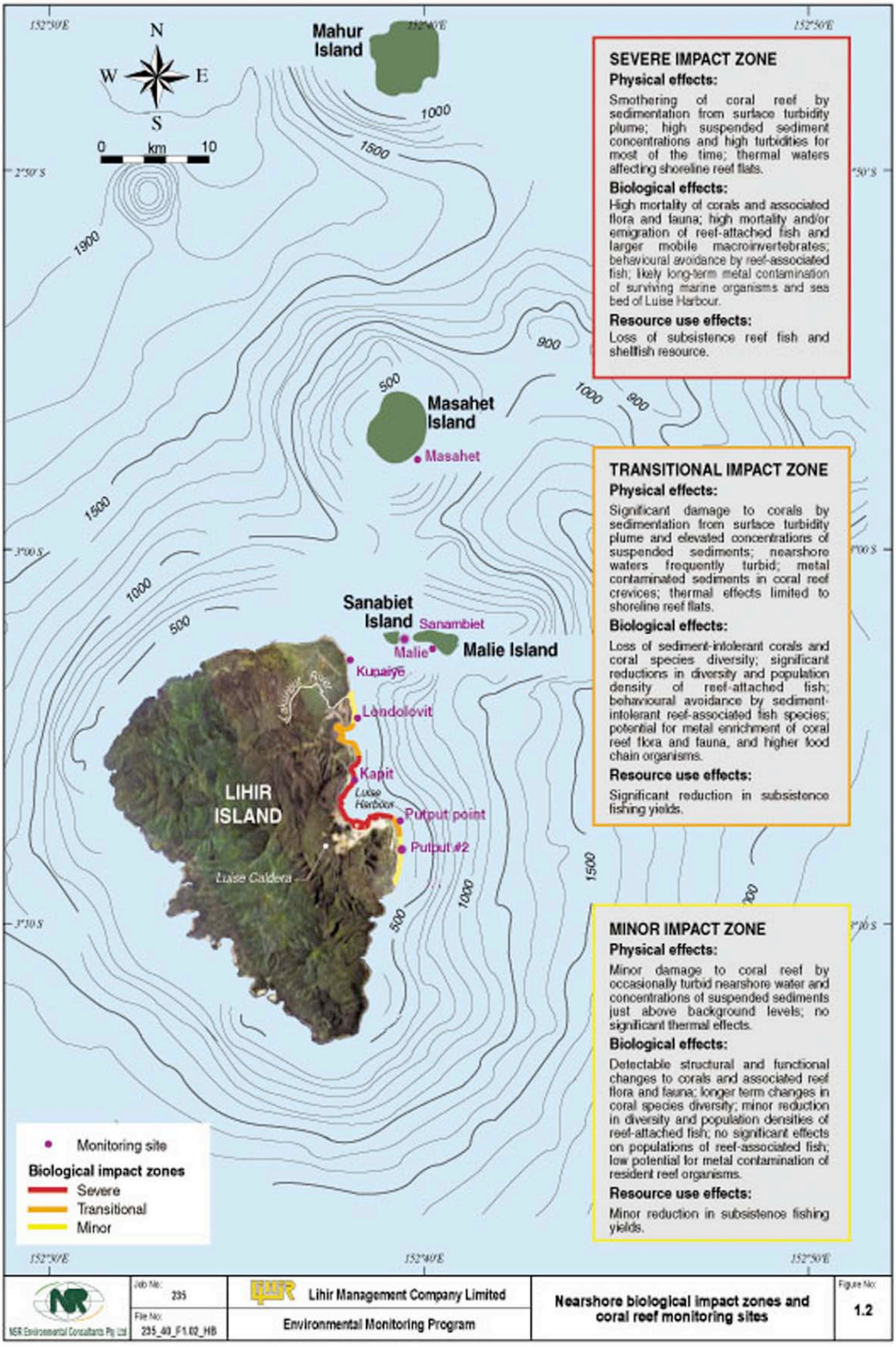



Figure 13. Study sites 2001 and NSR impact zones (modified from NSR).

4.3.1. Study design and analysis: A Uni-Variate Split-Plot ANOVA was used to analyse the tissue thickness measurements of seven study sites within three turbidity impact zones at two depths (Fig. 14), shallow (2-10 m Lowest Astronomical Tide) and deep (14-24 m LAT). The data was log transformed to comply with assumptions of normality and heterogeneity of variances necessary for the application of these statistical tests.

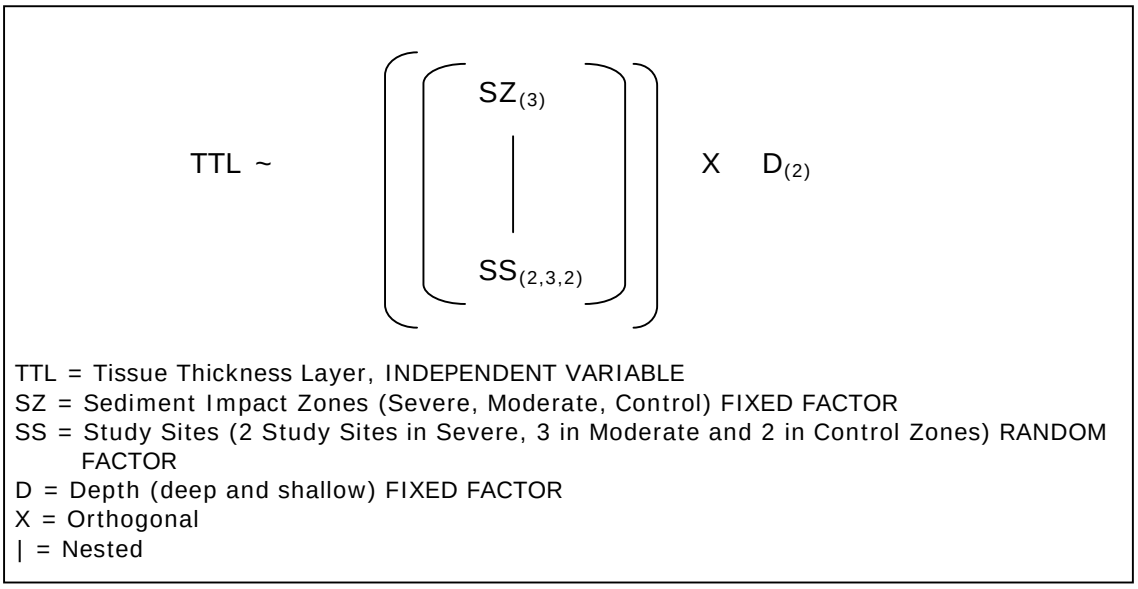



Figure 14. Univariate Split-Plot ANOVA design without Sanambiet

Two separate analyses of only shallow water corals, which included Sanambiet Island, were also undertaken (Fig. 15). One analysis included Sanambiet Island in the severe impact zone, the other included Sanambiet Island in the control zone (Bonferroni corrections changed $\alpha$=0.05 to $\alpha$=0.025 as two separate tests were undertaken for each year). No data transformation was necessary.

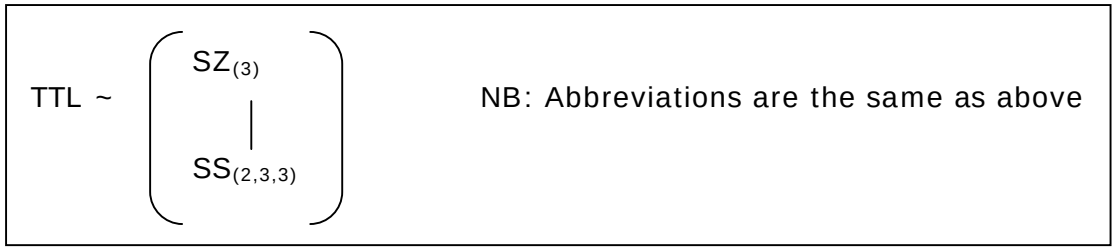



Figure 15. Univariate Split-Plot design of shallow corals, including Sanambiet.

All analyses were made upon unadjusted tissue thickness data and data that had been corrected for changing tissue thickness over the lunar month (see Chapter 3). It was assumed that tissue thickness increased by 28 µm per day after the full moon in shallow water corals and 25 µm per day after the full moon in deep water corals (see Chapter 3, Section 3.2.1.2.). Results for unadjusted tissue thickness data are given only where they are significantly different from adjusted tissue thickness data.

4.3.2. Results of Statistical Analyses*:* In the first analysis excluding Sanambiet Island, tissue thickness changed significantly with sediment impact zones and water depth (see Table XII).

Table XII. Univariate Split-Plot ANOVA results examining tissue thickness changes at all sites (except Sanambiet), between shallow and deep water nested in three impact zones. NB: $\alpha$=0.025

| **Source** | Type I Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| SEDIMENT | 1.498 | 2 | .749 | 12.829 | .019 |
| SITES(SEDIMENT) | .231 | 4 | 5.839E-02 | 2.111 | .249 |
| DEPTH | 1.537 | 1 | 1.537 | 56.221 | .002 |
| SEDIMENT*DEPTH | .118 | 2 | 5.913E-02 | 2.167 | .237 |
| DEPTH*SITES(SEDIMENT) | .110 | 4 | 2.740E-02 | .878 | .479 |

NB: In all tables, statistically significant values is printed bold.

A Tukey's HSD Post-hoc test revealed that corals from the severe impact zone had significantly thinner tissue than corals in all other zones

($p<0.000$, $\alpha=0.025$), which were not significantly different from one another ($p=0.936$; see also Fig. 16). Deep water corals had thinner tissue than shallow ones ($F_{(1)}=56.221$, $p<0.002$; see Fig. 16), in all different sediment zones ($F_{(2)}= 2.167$, $p=0.237$, Table XII). When analysed with the data set which was unadjusted for the lunar cycle, the overall results were the same, except for a significant depth*site interaction ($F_{(4)}=3.065$, $P<0.02$; see also Fig. 16 and 17). In the second analysis of shallow water corals neither sediment nor study sites had a significant effect on tissue thickness when Sanambiet Island was included in the control zone (Table XIII). A Tukey's HSD post-hoc analysis revealed Sanambiet to have thinner tissue (on average 2.74 mm +/- 0.2 mm) than all other sites (average 3.5 mm +/- 0.22 mm) except severe impact sites (average 2.61 mm +/- 0.1 mm).

Table XIII. Univariate Split-Plot ANOVA examining tissue thickness changes between shallow sites (including Sanambiet as control site) and three impact zones. NB: $\alpha=0.025$

| **Source** | Type I Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| SEDIMENT | 8.918 | 2 | 4.459 | 4.3 | .082 |
| SITES(SEDIMENT) | 5.185 | 5 | 1.037 | 2.569 | .032 |

When tissue thickness data from Sanambiet was included in the severe impact zone, sediment zones became significantly different from one another ($F_{(2)}=33.339$, $p<0.001$; Table XIV).

Table XIV. Univariate Split-Plot ANOVA examining tissue thickness changes between shallow sites (including Sanambiet as severe impact site) and three impact zones. NB: $\alpha=0.025$

| **Source** | Type I Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| SEDIMENT | 13.119 | 2 | 6.559 | 33.339 | .001 |
| SITES(SEDIMENT) | .984 | 5 | .197 | .493 | .781 |

A Tukey's HSD Post-hoc test revealed that corals from the severe study sites, including Sanambiet Island, had significantly thinner tissue thickness

(average 2.65 mm +/- 0.17 mm, $p<0.000$) than corals from both minor and control sites, which were the same ($p=0.889$; see also Figure 16).

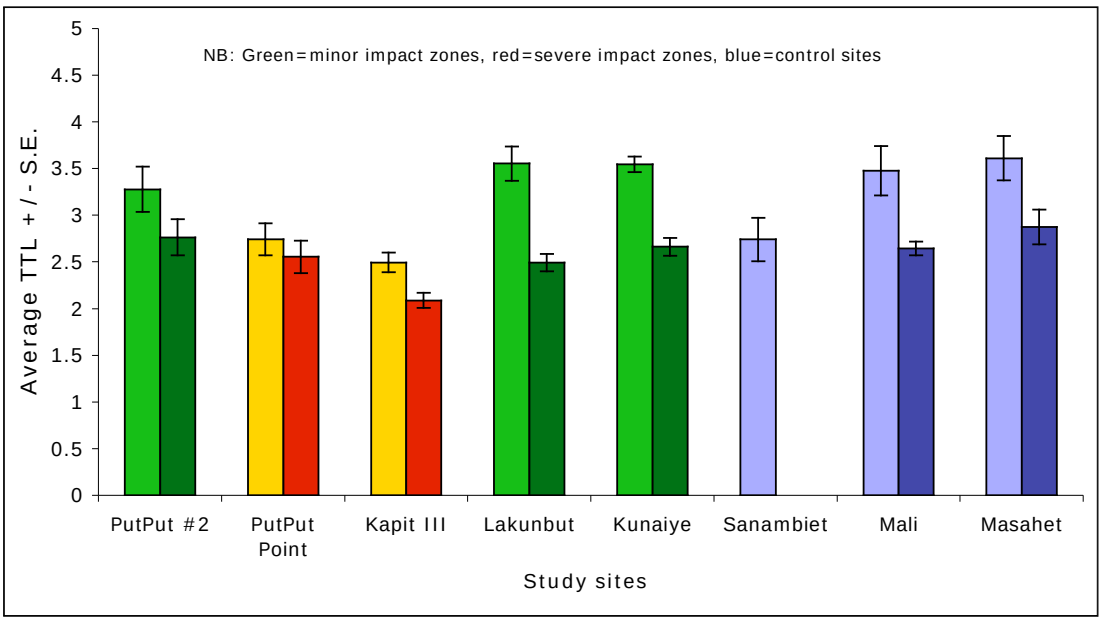



Figure 16. Average tissue thickness adjusted for lunar effects in shallow (light bars) and deep (dark bars) water in 3 impact zones.

NB: TTL=tissue thickness

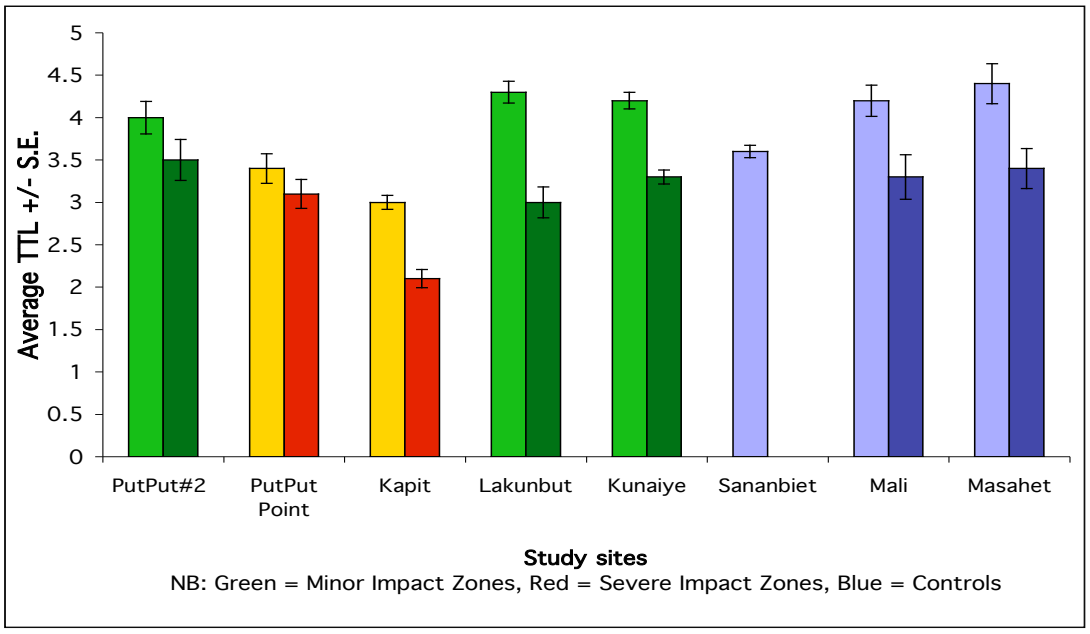



Figure 17. Average tissue thickness unadjusted for lunar effects in shallow (light bars) and deep (dark bars) water in 3 impact zones.

When the first analysis (without Sanambiet Island) was re-done with only two impact zones, the outcome of results was the same (see Table XV,

compare with Table XII): tissue thickness was lower in the impact than control sites ($F_{(1)}=31.41$, $p<0.003$; Table XV) and thinner in deep compared with shallow water ($F_{(2)}=67.717$, $p<0.001$; Table XV).

Table XV. Univariate Split-Plot ANOVA examining tissue thickness changes at all sites (except Sanambiet) between shallow and deep water and only 2 impact zones. NB: p=0.025

| **Source** | Type I Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| SEDIMENT | 1.494 | 1 | 1.494 | 31.41 | .003 |
| SITES(SEDIMENT) | .235 | 5 | 4.691E-02 | 2.069 | .228 |
| DEPTH | 1.537 | 1 | 1.537 | 67.717 | .001 |
| SEDIMENT*DEPTH | .114 | 1 | .114 | 5.073 | .081 |
| DEPTH*SITES(SEDIMENT) | .114 | 5 | 2.281E-02 | .731 | .602 |

4.3.3. Discussion of the results of the 2001 Study*:* Severe impact sites had, on average, 20% lower tissue thickness than all other study sites. Thus, tissue thickness was a reliable indicator of anthropogenic turbidity stress on massive *Porites*. Tissue thickness measurements on corals from Sanambiet Island were the same as from corals in the 'severe impact' zone at PutPut Point (on average 2.74 mm). Sanambiet Island was not one of NSR's coral reef monitoring sites, although NSR did place a sediment tube at this site. However, sediment tube data does not correspond to turbidity levels (Woolfe and Larcombe, 1999; additional problems with results obtained from sediment tubes are discussed in Chapter 2, Section 2.1.4.). Sanambiet Island was visually assessed as having lower light levels than other control sites (underwater visibilities of < 10 m compared to visibilities of 25-40 m in control sites; see Study Site descriptions App. A). When Sanambiet Island was analysed as a 'control' site, impact zones became statistically insignificant (Table XIII). When included as an 'impact' site, the analysis showed the obvious differences that exist between impact zones (Table XIV, see also Fig. 16). If Sanambiet Island were not included as an

'impact' but as a 'control' site (as it was by NSR's impact zone scenarios), it would significantly bias results by removing the statistical significance of turbidity impact shown in the analysis excluding Sanambiet Island (Table XII). Thus, Sanambiet Island was regarded as an 'impact' site even though it was not related to the impact zone associated with mine-derived turbidity along the eastern shore of Lihir Island. Tissue thickness had similar responses to both, natural and anthropogenic levels of increased turbidity on Lihir Island. Therefore, it seems that corals on Lihir Island do not suffer from potential additional stressors from mine-derived sediment in the water column. Although some studies identified increases in metal concentrations in coral skeletons near mining operations (e.g. Fallon *et al.*, 2002; David, 2003), the unreliability of comparing metal inclusions with increases in sedimentation rates was discussed in Chapter 2, Section 2.2.3.1 (also Davies, 1992).

There was no difference in tissue thickness between 'minor impact' and 'control' sites on Lihir Island. Therefore, it was suggested here to only use 'Impact' and 'No Impact' zones in terms of biological relevance. This was also supported by obtaining the same significant results in analyses with both scenarios (three and two impact zones, see Tables XII and XV). Another PhD project, which assessed turbidity regimes at different locations along the eastern shore of Lihir, also suggested a re-evaluation of NSR's predicted impact zones (see below). The 'impact' zone described here included PutPut Point and Kapit. However, there was a distance of several kilometres between these two sites and non-impacted sites at either side. Done (1996b) also criticised NSR for undersampling the sections of coast

between Lakunbut and PutPut #2. Hence, five additional sites were chosen within this region for the main study in 2002 and 2003 (see below).

There were no major differences in results between adjusted compared with unadjusted tissue thickness measurements (see Fig. 16 and 17). As tissue thickness was adjusted for minimum monthly thickness, just after a full moon, it was obviously lower at some study sites than when left untreated for monthly effects (compare Fig. 16 and 17). The adjustment smoothed out the significant depth*site interaction found in the raw dataset (Table XII). Adjusting tissue thickness for up to 20% variability due to time of sampling during the lunar month was, therefore, shown to result in a less variable data set. It was also used for analyses in the 2002-03 Study (below).

4.4. 2002-03 STUDY:

4.4.1. Background: In the 2001 Study, only two sampling sites were situated in the severely impacted area, namely PutPut Point and Kapit. The severe impact zone extended over approximately 8km within Luise Harbour (see Fig. 13). In order to identify cut-off boundaries between impact and no impact zones, five additional study sites were chosen in the impact zone in 2002 and 2003. These were Kapit I, II, IV and V along Kapit reef and PutPut between PutPut Point and PutPut #2 (see Fig. 18). Sediment accumulation sensors (SAS) were deployed at Kapit I, III, V and PutPut Point as part of a companion study (Thomas *et al.*, 2003). Nephelometers measuring turbidity were deployed at Kapit I, III, IV and V and PutPut Point, PutPut and PutPut #2, as well as Kunaiye. Light loggers were

deployed at Kapit I, III and V (Thomas, 2003). Unfortunately, various records from several study sites had to be rejected, either due to calibration failure or battery failure (Thomas, 2003). Findings in tissue thickness measurements are compared with actual turbidity and light levels measured by Thomas (2003). This will assess if there is a correspondence with coral tissue thickness and changes in light and turbidity regimes and how sensitive tissue thickness is to these changes.

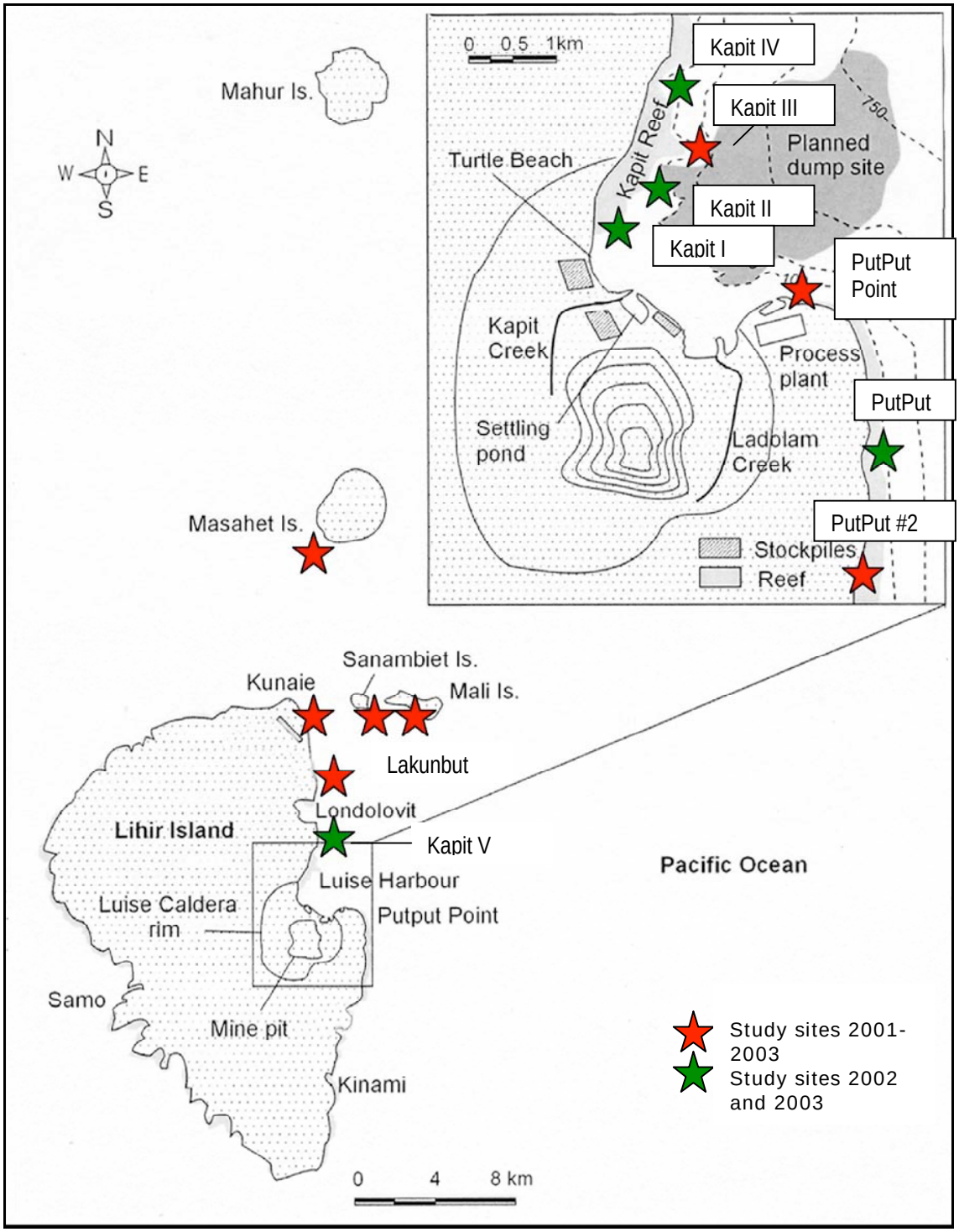



Figure 18. Study sites on Lihir Island 2001-2003 and additional sites selected for Study 2002 and 2003.

4.4.2. Study design and analysis: *4.4.2.1. Tissue thickness along a turbidity gradient:* This study incorporates tissue thickness measurements made in 2002 and 2003 at thirteen sites nested in two impact zones

('impact' and 'no impact') around Lihir Island. The colonies tagged in 2001 were also sampled in this study. However, only 123 out of 143 colonies tagged in 2001 could be relocated in 2002. The greatest losses were at PutPut Point and Kunaiye shallow and Lakunbut deep, where four of the original ten colonies could not be found (precision analysis, however, still attests this to be a sufficient number of replicates for an $\alpha$ value of 0.05; see graphs Appendix D). Missing colonies were replaced with new ones that were also tagged, measured and photographed (as described in Chapter 1, Section 1.5.). An additional ten colonies per site and depth were chosen at Kapit I, II, IV and V and Put Put, increasing the data set to a total of 230 colonies. In 2003, 15 out of these 230 colonies could not be relocated and new substitutes were chosen. Kapit I, II and Sanambiet Island only had shallow water sites. Two separate analyses were, therefore, undertaken in each year (see Fig. 19 for ANOVA I and ANOVA II designs; Flowchart at Section 4.2). ANOVA I assessed tissue thickness variations in all study sites which had deep and shallow habitats (n=200). ANOVA II assessed tissue thickness variability between all shallow study sites (n=130). A third analysis assessed temporal differences in tissue thickness from the same individuals sampled in 2002 and 2003 (ANOVA III, see Fig. 19).

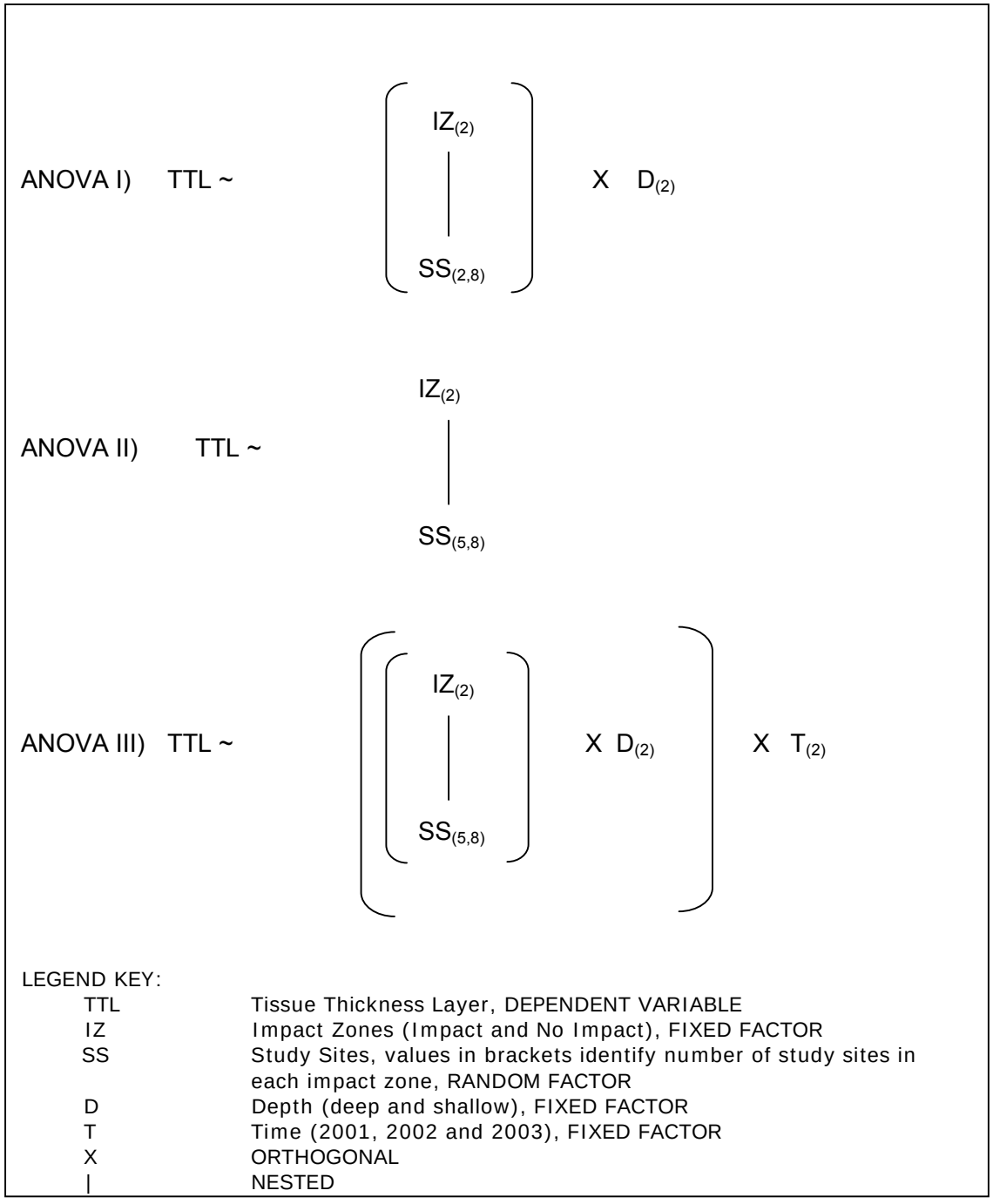



Figure 19. ANOVA designs used in 2002-03 Study.

*4.4.2.2. Depth effects on tissue thickness*: The 2001 study showed differences in tissue thickness between deep and shallow collection sites. Water depths allocated to deep and shallow habitats sometimes varied between study sites (averge range from 2-10 m in shallow, 14-24 m in deep sites). This allowed tissue thickness to be examined with linear

regressions against water depths to identify if depth effects between study sites significantly influenced tissue thickness measurements and needed to be standardised for.

## 4.5. RESULTS 2002-2003:

### 4.5.1. Results assessing tissue thickness changes with turbidity, study sites and water depth in 2002 and 2003:

*4.5.1.1. ANOVA I – $H_o$: Tissue thickness changes with turbidity zones, study sites and water depth:* In 2002, the calibrated data was log transformed as variances were not homogenous. Tissue thickness was found to differ significantly between study sites ($F_{(8)}=5.449$, $p<0.02$) and water depth ($F_{(1)}=45.511$, $p<0.000$) at $\alpha=0.025$ ( both Table XVI). These results differed from unadjusted data where tissue thickness was found to be significantly different between sediment zones ($F_{(1)}=10.658$, $p<0.02$) and water depth ($F_{(1)}= 40.132$, $p<0.000$; see also Fig. 20 and 21).

Table XVI. ANOVA I: Did tissue thickness change with turbidity zones, study sites and water depth in 2002? NB: $\alpha=0.025$

| **Source** | Type I Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| SEDIMENT | 2.359 | 1 | 2.359 | 5.52 | 0.47 |
| SITES(SEDIMENT) | 3.419 | 8 | .427 | 5.449 | 0.014 |
| DEPTH | 3.369 | 1 | 3.569 | 45.511 | 0.000 |
| SEDIMENT*DEPTH | 2.451E-03 | 1 | 2.451E-03 | .031 | 0.864 |
| DEPTH*SITES (SEDIMENT) | .627 | 8 | 7.843E-02 | 1.669 | 0.109 |

Although general patterns in average tissue thickness remained similar between adjusted and raw data, the following differences were apparent (compare Fig. 20 and 21): tissue thickness at PutPut Point deep (average 2.8 mm +/- 0.2 mm) became more similar to tissue thickness from deep control sites at PutPut #2, Kapit IV, V and Mali (average 2.9 mm +/- 0.16

mm; see Fig. 20). Overall, tissue thickness decreased with increasing proximity to the mine site and increased with distance from the mine (Fig. 20), with the exception Kapit II and Sanambiet (discussed below).

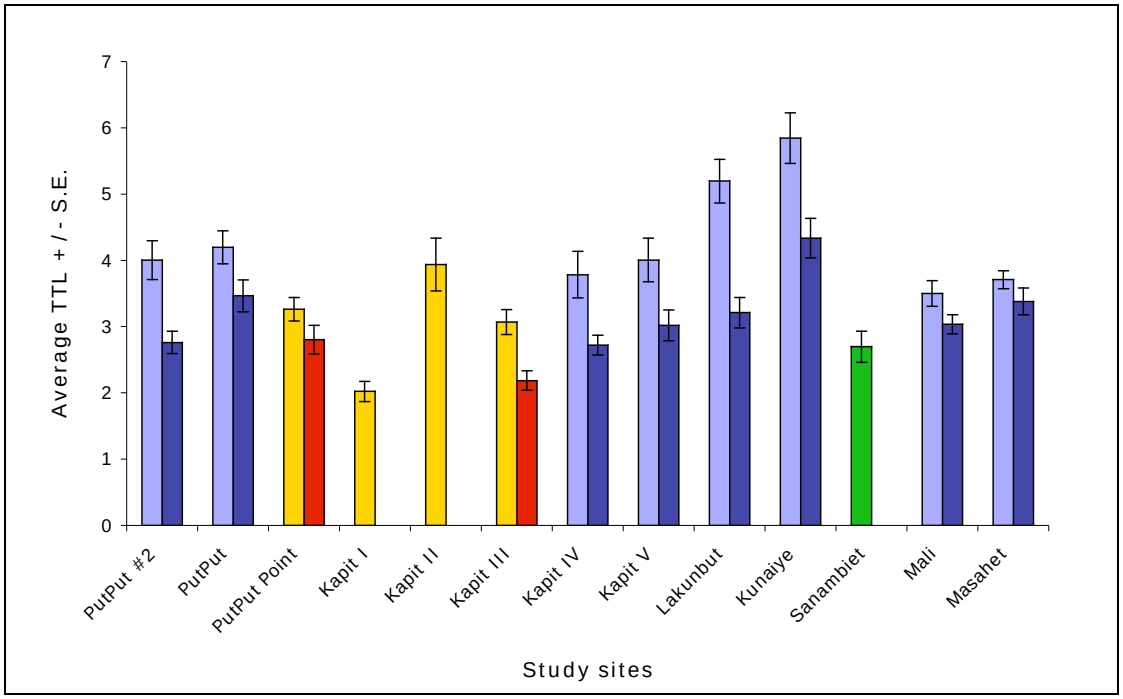



Figure 20. Average tissue thickness adjusted for sampling time in 2002

NB for Fig. 20 and 21: Blue = no impact, red = impact, green= natural impact, dark bars = deep, light bars = shallow sites in both Figures

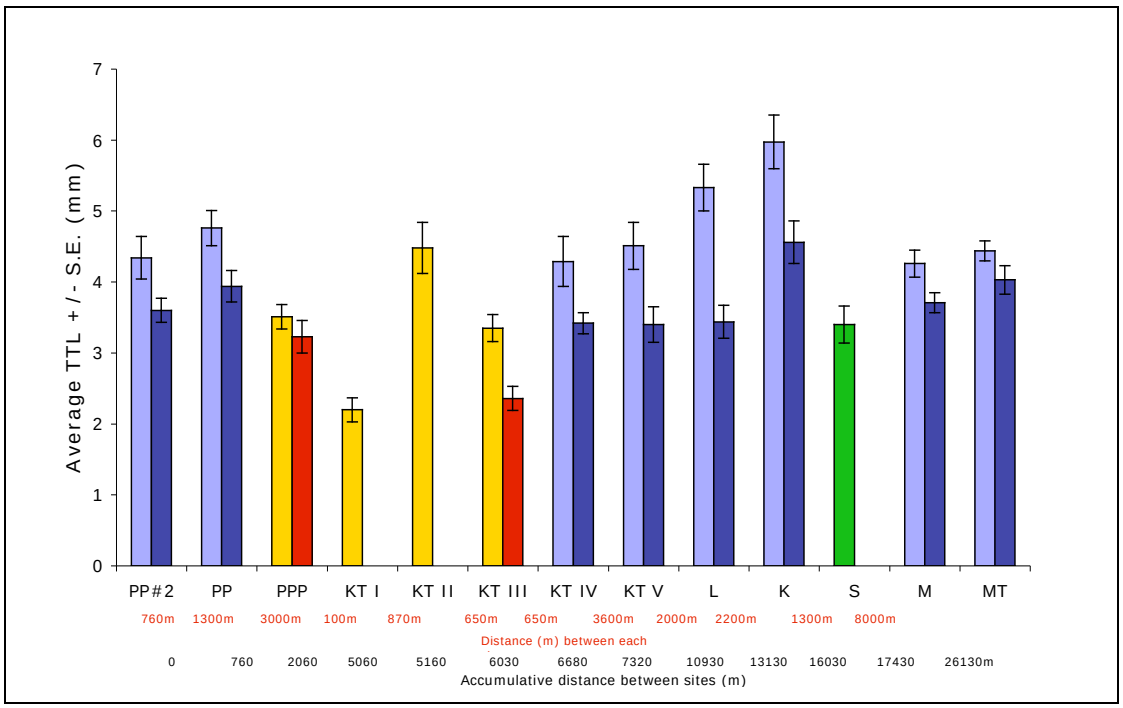



Figure 21. Average unadjusted tissue thickness in 2002 with distance from mine site

In 2003, some small differences were found in results compared with 2002: tissue thickness differed significantly in different impact zones ($F_{(1)}=8.592$, $p<0.02$) and water depths ($F_{(1)}=7.123$, $p<0.001$), as well as between depths at different study sites ($F_{(8)}=6.439$, $p<0.000$; all Table XVIII). As opposed to 2002, adjusted tissue thickness was not different between study sites. The results were similar to results from unadjusted tissue thickness data, except that tissue thickness did not significantly differ between impact zones ($F_{(1)}=1.202$, $p>0.025$).

Table XVII. ANOVA I: Did tissue thickness change with turbidity zones, study sites and water depth in 2003? NB: $\alpha=0.025$

| **Source** | Type I Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| SEDIMENT | 3.238 | 1 | 3.238 | 8.592 | 0.019 |
| SITES(SEDIMENT) | 3.015 | 8 | .377 | 1.337 | 0.345 |
| DEPTH | 7.123 | 1 | 7.123 | 25.278 | 0.001 |
| SEDIMENT*DEPTH | 1.127E-02 | 1 | 1.127E-02 | .04 | 0.846 |
| DEPTH*SITES (SEDIMENT | 2.254 | 8 | .282 | 6.439 | 0.000 |

Differences between deep and shallow study sites were shown to be less pronounced in adjusted, compared with unadjusted data (see Fig. 22 and 23). This was particularly true for PutPut Point, Kapit III and Kapit V (see Fig. 22). Also, adjusting tissue thickness for time of sampling at Day 1 after the full moon decreased average tissue thickness, particularly in severe impact zones by, on average, 9% in shallow and 17% in deep water. Exceptionally large differences between deep and shallow sites could be found in PutPut Point, Kapit IV, V and Lakunbut with tissue thickness being, on average, 40% thinner in deep water (see Fig. 22 & 23). Tissue thickness responded to the expected turbidity gradient, with the exception of the following sites: PutPut Point shallow, Kapit II, Kapit IV and Kapit V deep.

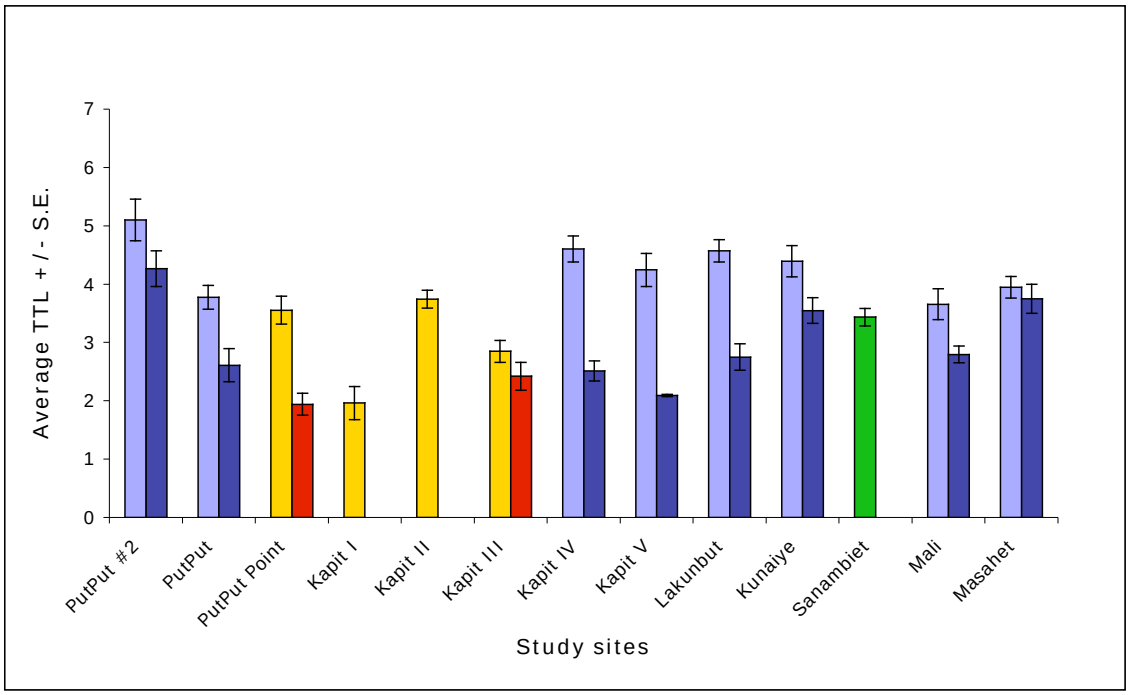



Figure 22. Average tissue thickness adjusted for sampling time in 2003

NB for Fig. 22 and 23: Blue = no impact, red = impact, green= natural impact, dark bars = deep, light bars = shallow sites

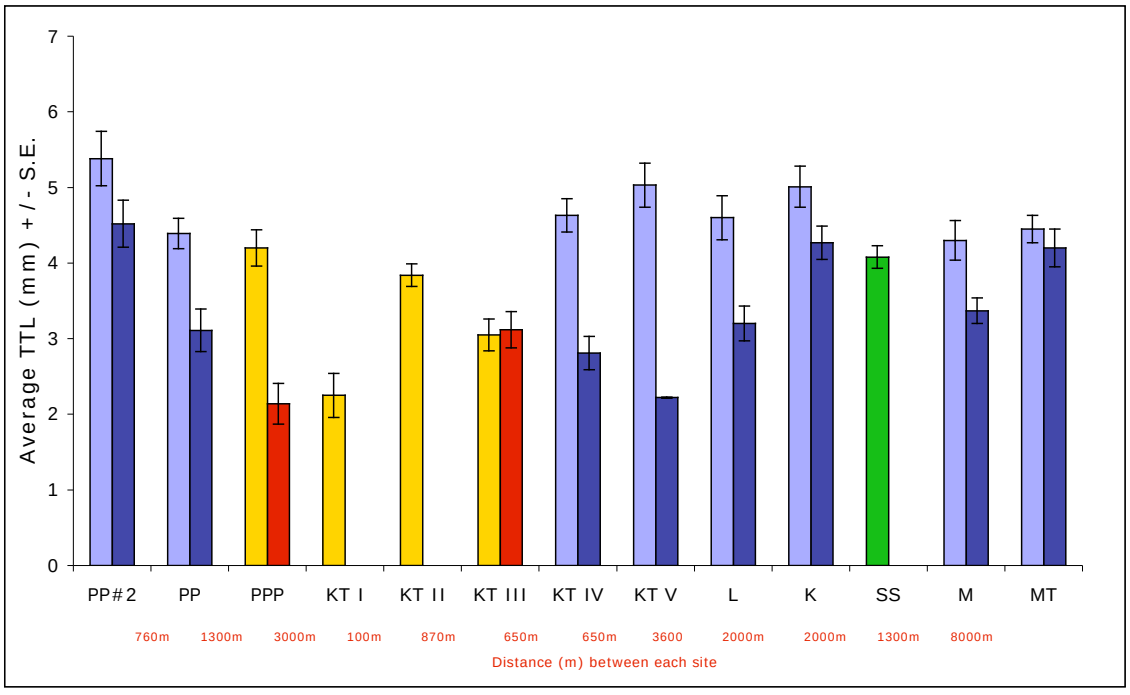



Figure 23. Average unadjusted tissue thickness in 2003.

*4.5.1.2. ANOVA II – $H_o$: Tissue thickness changes with turbidity zones and study sites in shallow water corals:* The natural log transformed data of

only shallow colonies yielded the following results for 2002: tissue thickness differed between sediment zones ($F_{(1)}=11.568$, $p<0.001$; Table XIX) and study sites ($F_{(1)}=7.189$, $p<0.000$; see Table XIX). The same results were obtained from tissue thickness data which was not adjusted for time of sampling. Tissue thickness decreased towards the mine site, with the exception of Kapit II (see Fig. 20).

Table XVIII. ANOVA II: Does tissue thickness change with turbidity zones and study sites in shallow water corals in 2002? NB: $\alpha=0.025$

| **Source** | Type I Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| SEDIMENT | 4.467 | 1 | 4.467 | 11.568 | 0.006 |
| SITE(SEDIMENT) | 4.248 | 11 | .386 | 7.189 | 0.000 |

In 2003, the same results as in 2002 were found for shallow water colonies in both adjusted and unadjusted datasets: tissue thickness differed significantly between sediment zones ($F_{(1)}=12.614$, $p<0.001$, Table XXI) and study sites ($F_{(1)}=6.02$, $p<0.000$; see Table XXI). In 2003, tissue thickness was similar in shallow colonies at the impact sites PutPut Point, Kapit II and Sanambiet (average 3.65 mm +/- 0.18 mm) compared with shallow colonies from not impacted sites at PutPut and Mali Island (average 3.7 mm +/- 0.23 mm; Fig. 22).

Table XIX. ANOVA II: Does tissue thickness change with turbidity zones and study sites in shallow water corals in 2003? NB: $\alpha=0.025$

| **Source** | Type I Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| SEDIMENT | 3.031 | 1 | 3.031 | 12.614 | 0.005 |
| SITE(SEDIMENT) | 2.643 | 11 | 2.643 | 6.02 | 0.000 |

4.5.2. Results assessing if tissue thickness response shown by particular corals could be replicated during similar stress events through time

*4.5.2.1. ANOVA III – $H_o$: Tissue thickness patterns were the same between February 2002 and February 2003*: This analysis examined the differences in tissue thickness measurements between the same individuals sampled in 2002 and 2003. Tissue thickness differed significantly between sediment zones ($F_{(1)}=10.7$, $p<0.001$, Table XXIII) and water depths ($F_{(1)}=43.652$, $p<0.000$; see Table XXIII). It was also significantly different between depths and study sites ($F_{(8)}=3.722$, $p<0.000$, Table XXIII) and depths between study sites in 2002 and 2003 ($F_{(11)}=5.374$, $p<0.000$; Table XXIII). Both adjusted and unadjusted data yielded the same results.

Table XX. ANOVA III – Does tissue thickness change between the same individuals in 2002 and 2003, at different study sites, impact zones and water depths? $\alpha=0.01$

| **Source** | Type I Sum of Squares | df | Mean Square | F | Significance p |
|---|---|---|---|---|---|
| SEDIMENT | 7.093 | 1 | 7.093 | 10.7 | 0.007 |
| SITES(SEDIMENT) | 7.816 | 11 | .711 | 1.548 | 0.212 |
| DEPTH | 9.245 | 1 | 9.245 | 43.652 | 0.000 |
| SEDIMENT*DEPTH | 1.661E-02 | 1 | 1.661E-02 | .085 | 0.778 |
| DEPTH*SITES(SEDIMENT) | 1.698 | 8 | .212 | 3.722 | 0.000 |
| YEAR | .111 | 1 | .111 | .341 | 0.571 |
| SEDIMENT*YEAR | 6.355E-03 | 1 | 6.355E-03 | .022 | 0.884 |
| SITES(SEDIMENT)*YEAR | 3.367 | 11 | .306 | 5.374 | 0.000 |
| DEPTH*YEAR | .260 | 1 | .260 | 4.573 | 0.033 |
| SEDIMENT*DEPTH*YEAR | 2.873E-03 | 1 | 2.873E-03 | .05 | 0.822 |

PutPut #2 had greater tissue thickness in 2003 than 2002 in both water depths (see Fig. 24 and 25). PutPut, PutPut Point and Kapit V, however, had thinner tissue in 2003 than 2002, but in deep water colonies only (see Fig. 25). In shallow water, Kunaiye showed decreases in tissue thickness. Sanambiet Island, however, increased between 2002 and 2003 (Fig. 24).

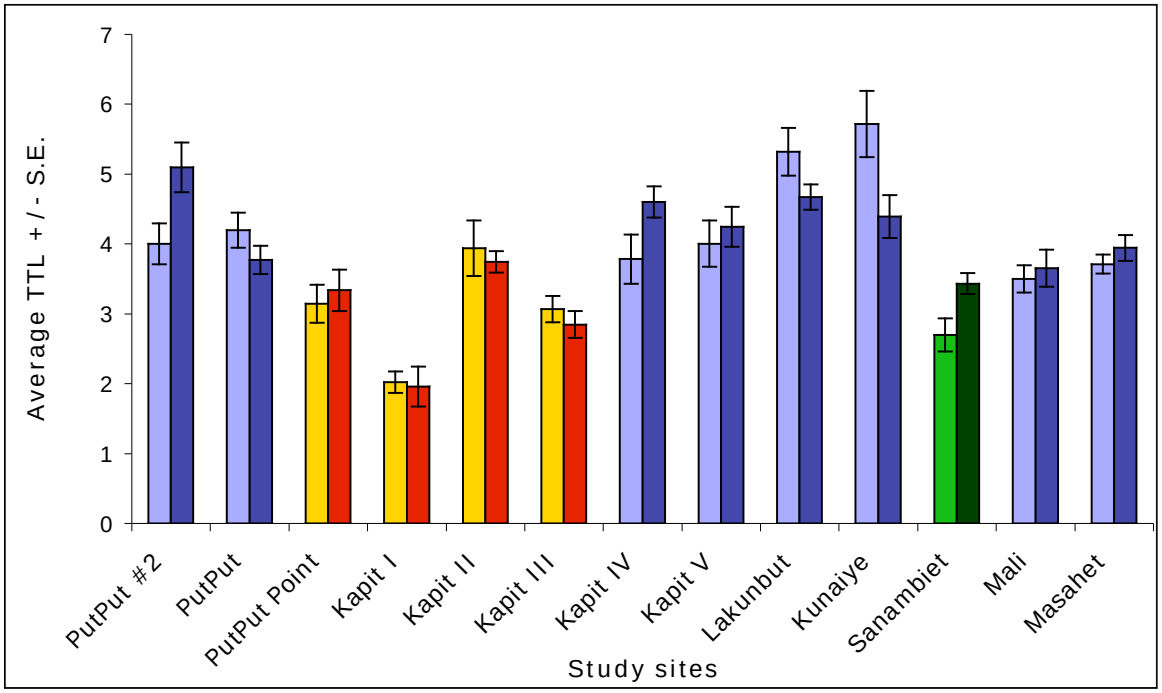



Figure 24. Average tissue thickness values adjusted for sampling time from the same shallow water individuals measured in 2002 (light bars) and 2003 (dark bars).

NB for Fig. 24 and 25: Blue=no impact, green=natural turbidity impact, red=anthropogenic turbidity impact

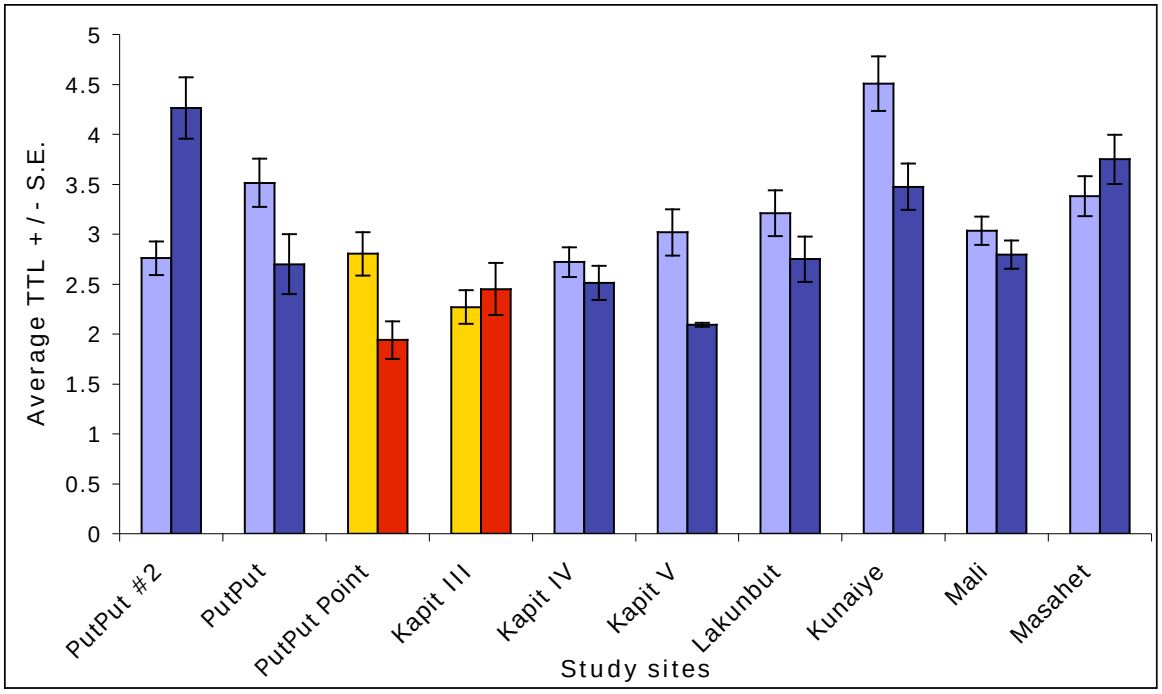



Figure 25. Average tissue thickness values adjusted for sampling time from the same deep water individuals measured in 2002 (light bars) and 2003 (dark bars).

In all years, tissue thickness was always thinner in impact compared with no-impact zones, in shallow (by, on average, 28% +/- 8%; see Fig. 26) and deep (by, on average 24% +/- 13%; see Fig. 27) habitats.

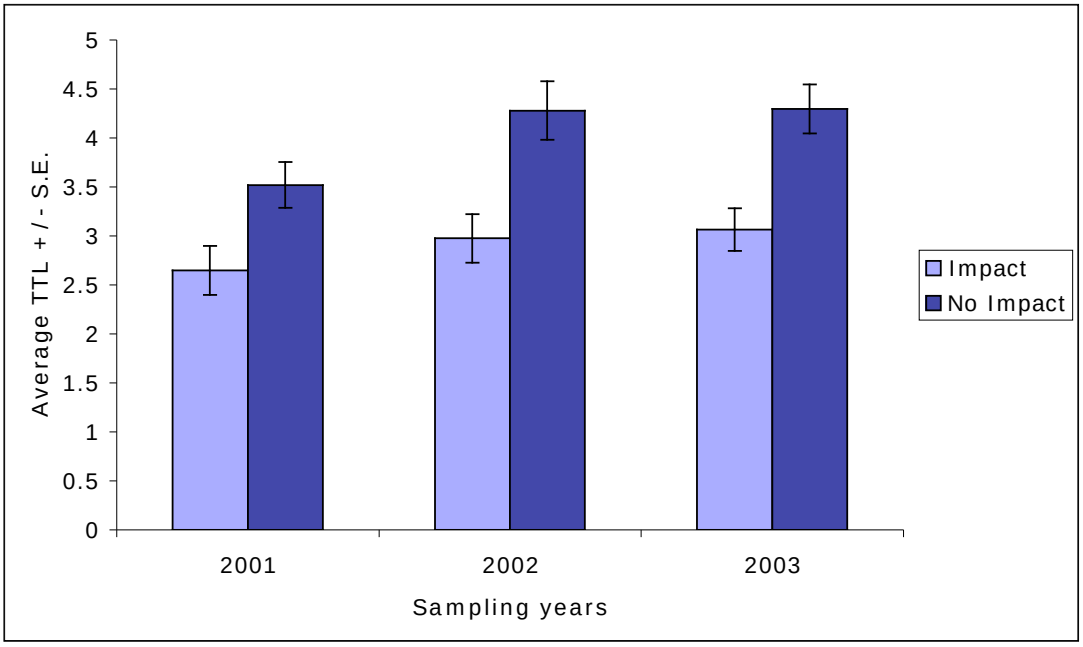



Figure 26. Average tissue thickness of shallow water corals from all study sites within impact and no impact zones in 2001, 2002 and 2003.

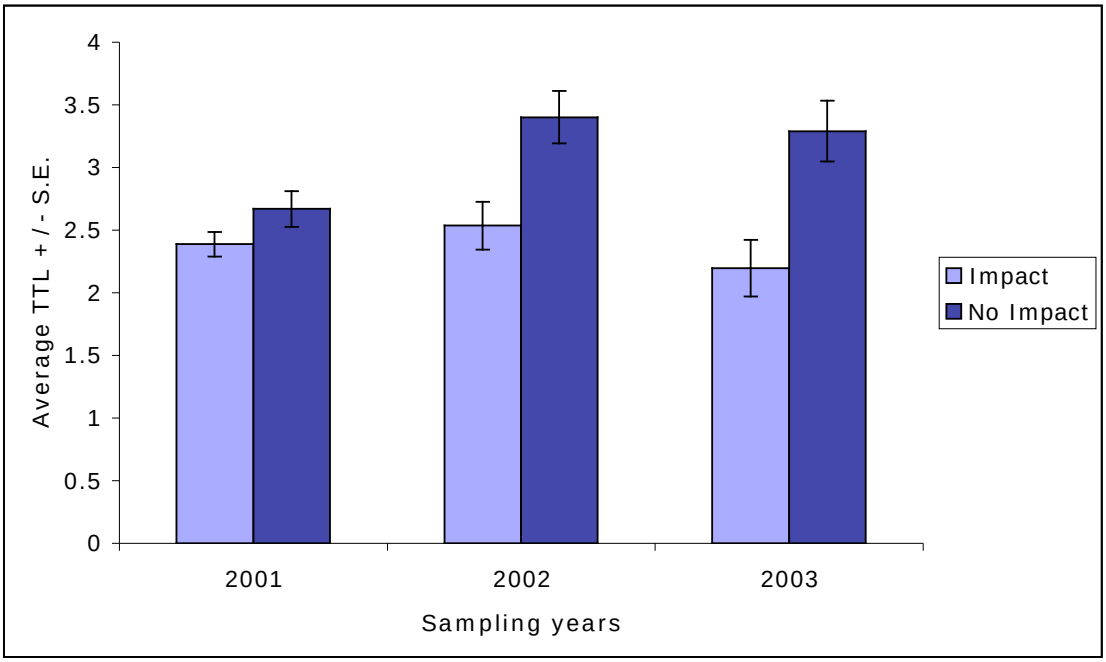



Figure 27. Average tissue thickness of deep water corals from all study sites within impact and no impact zones in 2001, 2002 and 2003.

4.5.3. Does tissue thickness vary systematically with increasing depth?

Average tissue thickness was not significantly different with shallow (ANOVA of regression $F_{(1,129)}=0.835$, $p=0.362$) or deep (ANOVA of regression $F_{(1,98)}=0.167$, $p=0.684$) water depths (see also Fig. 28). Tissue thickness data (in mm) was plotted against depth (in metres) for different impact zones and deep and shallow habitats, but the $r^2$ values were never significant (highest $r^2 < 0.25$). Scatterplots were also undertaken with 2003 tissue thickness data for impact zones, depths and combinations of the two. $R^2$ values in these graphs were also not significant (highest $r^2 < 0.3$).

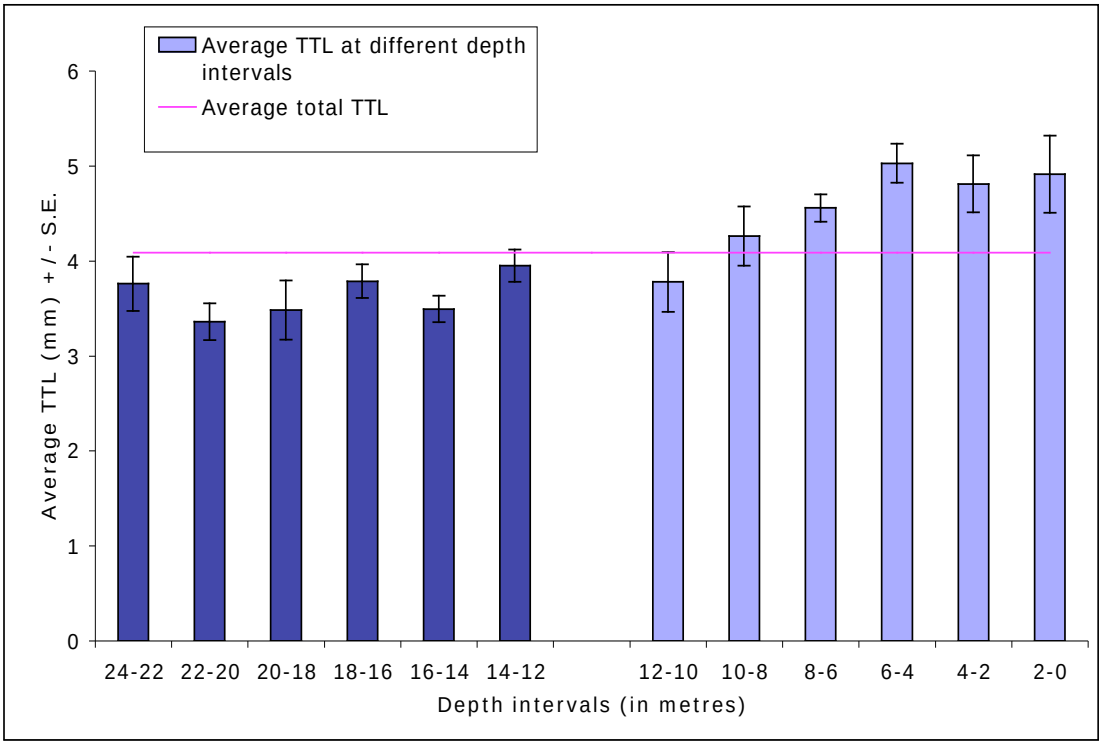



Figure 28. Average tissue thickness measurements at different depth intervals in non-impacted zones in 2002. (NB: dark bars= deep water, light bars= shallow water)

## 4.6. DISCUSSION:

4.6.1. Tissue thickness response to different turbidity gradients on Lihir Island. Tissue thickness decreased with increasing proximity to the mine site at Lihir Island, similar to Barnes and Lough's (1999) findings for Misima Island. There seems to be a relationship between turbidity and tissue thickness that can be recognised along both anthropogenically induced gradients and natural turbidity gradients, as seen on Sanambiet Island. In contrast to Misima Island, where corals in the severe impact zone were buried by sediment accumulation (Barnes and Lough, 1999), turbidity was the main factor most likely to impact corals as a result of mining activities on Lihir Island (Thomas, 2003). Dead *Porites* colonies were not observed on any reefs in this study and there was no visual evidence for sediment burial of colonies. High currents and wave action kept sediments in suspension at Lihir Island. Consequently, mining activities had less impact on Lihir Island than at Misima Island. Tissue thickness, however, was still sensitive enough to respond by a ~ 30% decrease to intermediate levels of turbidity (=15-30mg $l^{-1}$, measured by Thomas, 2003 and corresponding to 'transitional impact' zones predicted by NSR).

4.6.2. What is the biologically relevant impact zone of turbidity on tissue thickness and where are its cut-off boundaries on Lihir Island? The biologically relevant turbidity impact on massive *Porites* corals on Lihir Island (as assessed by their tissue thickness) reached from Kapit III to the North to PutPut Point to the South over a distance of approximately 4 km (half the distance of severe sediment impact proposed by NSR; Fig. 29). Lower tissue thickness levels at Kapit I and Kapit III, as well as PutPut

Point coincide well with increased turbidity levels, as those found by Thomas (2003). Kapit II is an outlier as its corals had relatively high tissue thickness, and is discussed in detail below. Tissue thickness at all other sites did not respond to minor turbidity levels of <10mg $l^{-1}$. Either, tissue thickness was not sensitive enough to respond to these low levels of turbidity, or corals may not be negatively affected by minor turbidity levels. The latter is more likely, as no significant decreases in live coral cover were found in the same study sites (NSR, 2002). Other studies even found increases in live coral cover from reefs with intermediate sediment impact (levels not specified by McClanahan and Obura, 1997) and no evidence for decreased diversity or ecological health of sediment-influenced reefs (McClanahan and Obura, 1997; Torres and Morelock, 2002). Massive *Porites* at Kunaiye have been found to have higher levels of tissue thickness than other 'no impact' sites, particularly after recovering from being the site most affected by a major bleaching event in 2001 (Rotmann, 2001b). Additionally, Kunaiye falls within Thomas' (2003) 'background' zone of <5mg $l^{-1}$, however, tissue thickness is not significantly higher than that from other 'no-impact' sites (Tukey's HSD Post-Hoc analysis between minor and control sites $p=0.953$). Therefore, differentiation into more than two biologically relevant impact zones is unnecessary (see Fig. 29).

NSR (1989) predicted large-scale coral mortality over several km of reef in Luise Harbour and significant reductions in species diversity up to Londolovit in the North, and PutPut in the South (see Fig. 29). However, the only significant decreases in live coral cover were found at Kapit (decreased by 43% between 1994 and 1999, NSR Coral Reef Monitoring

Report, 2000) and, to a lesser extent (by 36%) – at PutPut Point (also NSR, 2002). Massive *Porites* were amongst the least affected species. Thomas (2003) identified three zones of turbidity along Lihir Island (see Fig. 29). The 'severe impact' zone is very narrow, surrounding the sediment settling pond, and is identified by median suspended solid concentrations (SSC) above 30mg $l^{-1}$. There is no coral reef within this region, although Kapit I, the beginning of coral reefs on the northern part of Luise Harbour, is located on the boundary between 'severe' and 'transitional' SSC zones. However, Thomas (2003) found a sharp cut-off point in the turbidity levels before reaching Kapit I. The 'transitional' regime is determined by median SSC between 15-30mg $l^{-1}$. This area includes Kapit I, II and III reef sites (see Fig. 29). PutPut Point is right at the border of cut-off between 'transitional' and 'minor' impact zone determined by Thomas (2003). Corals at PutPut Point deep in particular have shown thicker tissue thicknesses than other 'impact' sites, resulting in sediment zones being not statistically significant in 2002 (see Table XVI, Fig. 20). This could be related to the fact that this site is at the boundary to 'minor' turbidity levels, as assessed by Thomas (2003), and therefore, less affected than corals at sites in the 'transitional' turbidity zone. However, in 2003, the deep corals at PutPut Point showed a dramatic decrease in tissue thickness levels. Unfortunately, LMC stopped measuring turbidity levels in 2002 and the decrease in tissue thickness can not be compared with a corresponding increase in turbidity. The 'minor' impact zone is identified by SSC levels < 10mg $l^{-1}$ and includes all other study sites along Lihir Island, except Kunaiye (Fig. 29).

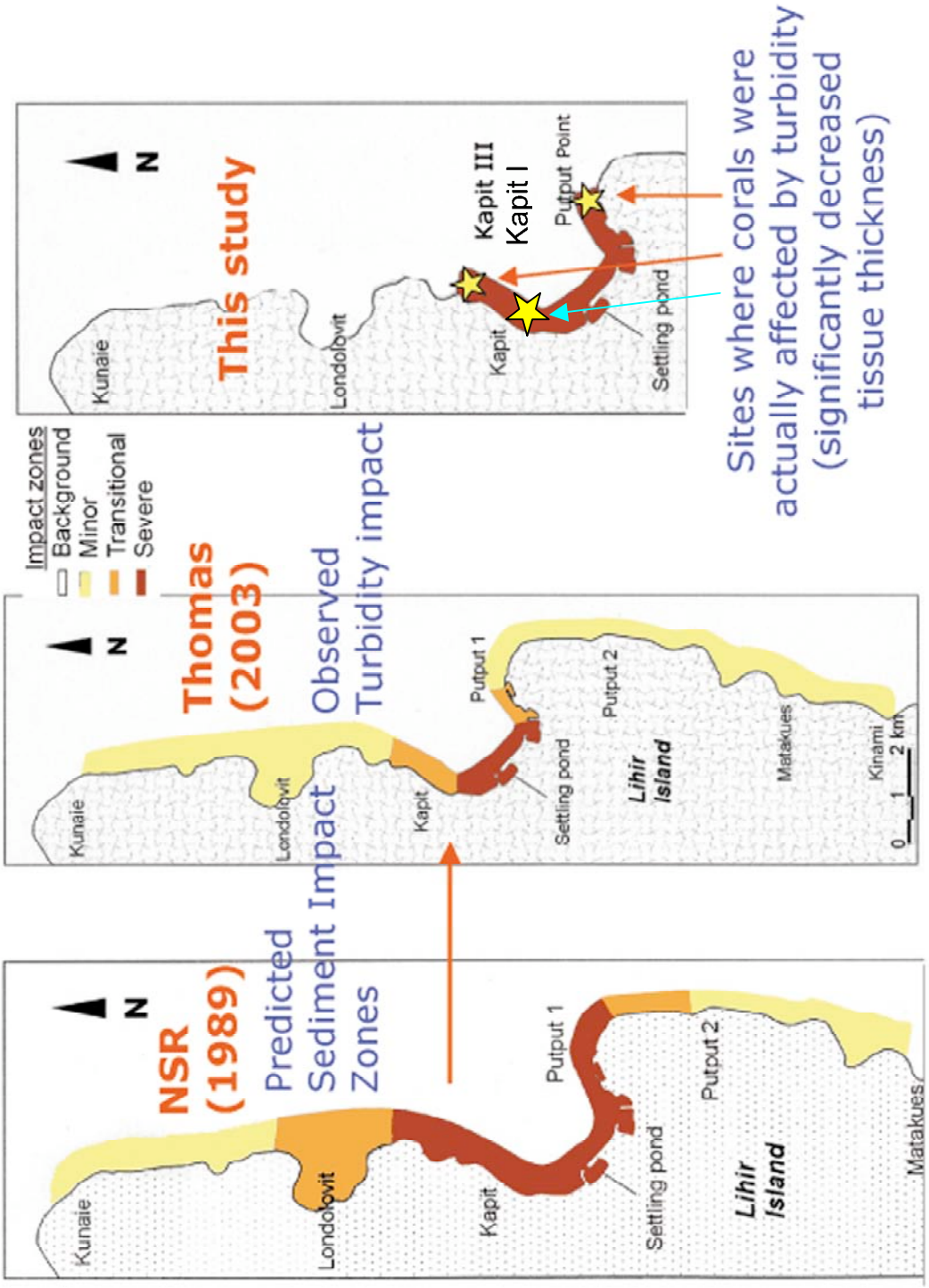



Figure 29. Turbidity impact zones as predicted by NSR (1989), measured by Thomas (2003) and sites of tissue thickness response to turbidity as assessed in this project

4.6.3. Tissue thickness variability between study sites within impact zones.

Higher tissue thickness was measured in massive *Porites* at Kapit II than at

the two sites either side of it (~4 mm, versus 2 mm at Kapit I and 3 mm at Kapit III; see Fig. 24). Adjusting for minimum monthly average tissue thickness smoothed out differences at Kapit II between 2002 and 2003 (Fig. 24). Nevertheless, average tissue thickness at Kapit II was comparable to that measured at controls sites at Mali and Masahet Island and PutPut. The most likely explanations are a combination of more light reaching the corals due to their shallower distribution and the positive effects of increased essential nutrients from a creek outfall near the study site. In detail:

1) *Water depth* – the average water depth in Kapit II was shallower (average 1.89 +/- 0.27 m) than in the other three impacted sites (Kapit I, III and PutPut Point: average 4.86 +/- 0.27 m, average depth of non-impacted shallow sites: 5.67 +/- 0.3 m). As tissue thickness decreases with depth, turbidity effects may be confounded by depth effects. This is particularly true in a study site with high turbidity, where light levels decrease more rapidly than in clear water. The difference in the ratio of light at the average depth at Kapit II versus other depths at other impact sites by light at the surface can be calculated by using Equation 16 from Thomas (2003):

$$I_{z,t} = I_{s,t} e^{-z\psi SSC}$$

Where:
$I_{z,t}$ = irradiance at depth z and time t in $\mu mol.m^{-2}.s^{-1}$;
$I_{s,t}$ = surface irradiance at time t in $\mu mol.m^{-2}.s^{-1}$;
$\psi$ = coefficient relating the extinction coefficient $K_d$ and the SSC (Te, 1997 gives $\psi = 0.035 m^{-1} l.mg^{-1}$).

Using this equation, 25% of surface light would reach 2 m depth, with SSC of 20 mg $l^{-1}$. However, only 3% of surface light would reach 5 m depth,

with the same SSC concentration, which was found to be this site's average light level (Thomas, 2003). Five percent is the level of surface illumination expected in clear water at 20 m depth (Thomas, 2003). Illumination in clear water at 12-13 m depth was reported to be 25-30% in coastal waters in the Carribean (Thomas, 2003). Hence, in terms of the availability of light, Kapit I and Kapit III are effectively twice as deep as Kapit II. As depth was a fixed factor in the statistical analysis it could not be manipulated to remove such potential impacts (but see below).

2) The *drainage/water quality* of the area – Kapit I is located only 100 m further south from Kapit II and has a similar topography and aspect (App A, Fig. 18), but the tissue thickness of corals at Kapit II is almost twice that of corals at Kapit I. The difference between Kapit I and II is possibly related to the creeks draining into the immediate area surrounding the study sites (Pikira Creek near Kapit II and Oanolam Creek near Kapit I, see photographs on Study site descriptions, Appendix A). Visually, Pikira Creek is clearer than Oanolam Creek and the discoloration around its mixing area is less pronounced. Oanolam Creek's outfall results in a continual surface turbidity plume covering the Kapit I study site, which could be part of the reason for reduced tissue thickness in this area.

Water quality tests taken by the LMC Environment Department show differences in water temperature and dissolved oxygen (both higher at Oanolam Creek) and pH (an average of 7.8 at Pikira compared with a highly acidic pH of 3.5 at Oanolam Creek). The very acidic Oanolam Creek is most likely due to the creek being diverted from the low-grade ore

stockpile in 2001. The reduced pH, even though it is dispersed and mixed with seawater, is likely to effect the corals at Kapit I, possibly reducing calcification rates (Marubini and Atkinson, 1999). In Marubini and Atkinson's (1999) study, calcification rates halved when pH levels were reduced from 8 to 7.2. However, their study was undertaken in laboratory conditions without dilution with seawater. In addition to decreased pH, metal levels at Oanolam Creek are higher than those sampled from Pikira Creek, particularly soluble Al, Cu, Zn, Co, Ag and Fe. Methods of metal uptake and assessment of contamination in corals is still an unresolved issue (Bastidas and Garcia, 1999), although several studies found higher metal levels in coral tissues than skeletons (e.g. Bastidas & Garcia, 1999; Harland & Brown, 1989, see also Chapter 2, Section 2.2.3.1.). One study found that the zooxanthellae within coral tissues took up the highest levels of metals (Reichelt-Brushett and McOrist, 2003). Even though some studies found significant effects of metal pollution on corals, for example increased iron concentration leading to a loss of zooxanthellae (Harland and Brown, 1989), it was also found that this response diminished in areas of chronic metal pollution, which may be due to adaptation of corals to increased metal levels. Possible effects of the increased metal concentration of Oanolam Creek on Kapit I corals, are therefore, uncertain.

Kapit I is also the most turbid area where corals survive on Lihir Island (Thomas, 2003). However, this does not explain why corals at Kapit III also had lower tissue than corals at Kapit II. Total Potassium (K), an essential nutrient, was almost twice as high at Pikira Creek compared with Oanolam Creek. Increases in K may indicate increases in nitrogen and phosphate

(Salisbury and Ross, 1992), both known to be used as food source by corals (e.g. Anthony, 1999b; Ferrier-Pages *et al.*, 2003). Kapit II corals might, therefore, be 'fed' by high levels of essential nutrients from Pikira Creek, leading to abnormally high tissue thicknesses.

4.6.4. Can tissue thickness patterns found in relation to turbidity stress be replicated over time? Tissue thickness showed a linear, negative response to the turbidity gradient along the eastern coast of Lihir Island in 2001. With additional study sites, however, outliers to the general pattern appeared (such as Kapit II, see discussion above). In general, the pattern of reduced tissue thickness in areas with increased turbidity was apparent in all years (see Fig. 27 and 28). However, varying tissue thicknesses over the years were found at several study sites within turbidity zones. Even though there was no significant difference in tissue thickness between years, there was a significant difference between study sites and years ($F_{(11)} = 5.374$, $p < 0.000$; see Table XX). The most obvious patterns are discussed here.

The approximately 30% increases in tissue thickness in Lakunbut shallow and Kunaiye shallow and deep sites between 2001 and 2002 probably reflect a recovery from a severe bleaching event in 2001 (Rotmann, 2001b). True (*in review*) found that bleached corals have thinner tissues and/or lower lipid levels, compared with unbleached colonies. Corals at Kunaiye and Lakunbut were affected most severely along Lihir Island, with up to 90% of corals bleached on the reef slope at Kunaiye. The high tissue thickness levels at Kunaiye (on average 5.7 +/- 0.5 mm in shallow and 4.5

+/- 0.3 mm in deep water), compared with other study sites (on average 4 +/- 0.3 mm in shallow and 3.1 +/- 0.2 mm in deep water), are likely due to the low levels of turbidity at this site (Thomas, 2003, see above). Kunaiye probably has higher levels of tissue thickness than control sites at Mali and Masahet Island due to differences in current, wave and natural discharge regimes between the locations. The great water clarity and lack of terrestrial run-off, particularly on Masahet and Mali Island, may lead to more oligotrophic (i.e. nutrient-poor) conditions for the corals. This could explain naturally lower levels of tissue thickness than at sites with higher levels of nutrients, similar to the inshore-offshore gradients found on the GBR (e.g. Barnes and Lough, 1992; Anthony and Fabricius, 2002).

Sanambiet Island and PutPut #2 increased in tissue thickness by about 20% between 2001/02 and 2003. The increase in tissue thickness at both sites may be related to increased intensity of average solar radiation from August 2002 to December 2002 (Fig. 30). As Sanambiet Island is a naturally turbid regime, increased solar radiation may have increased effective depth (see discussion in Section 4.6.3), thus aiding the corals to accumulate more energy reserves in the form of tissue thickness. PutPut #2 is located directly in front of a creek, which transports sediment run-off from an unused quarry located behind PutPut #2, also leading to increases in turbidity. In areas without increased turbidity, the same increase in solar radiation may have caused the ~ 25% decrease in tissue thickness at deep sites at PutPut, PutPut Point, Kapit IV and V and Kunaiye (e.g. Fitt and Warner, 1995).

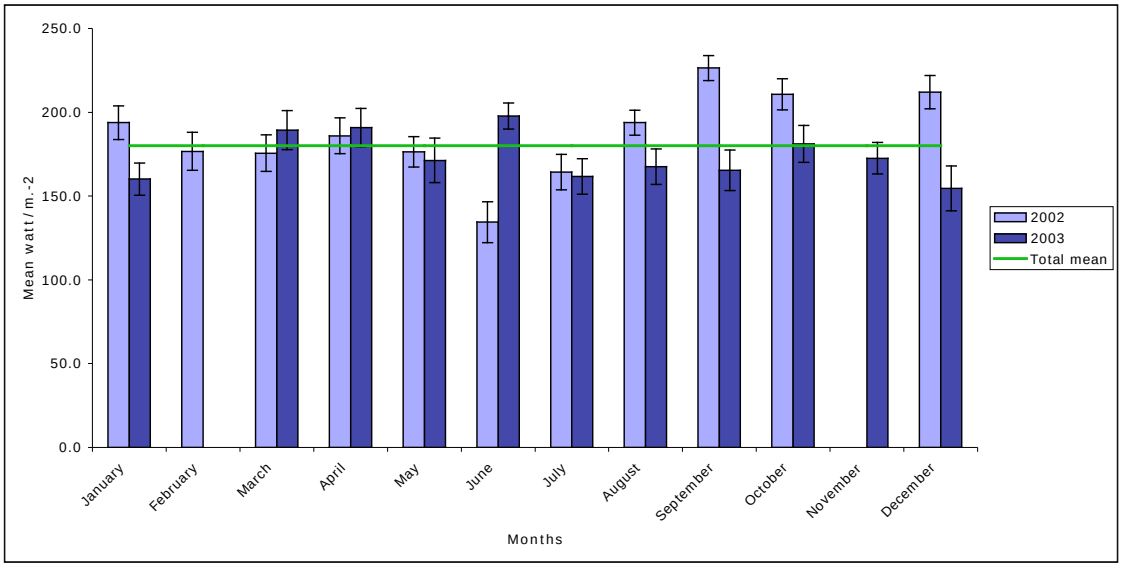



Figure 30. Average monthly solar radiation on Lihir Island between 2002 and 2003.

Increased UV radiation has been known to be a potential stressor of corals, inhibiting photosynthesis and increasing respiration as well as resulting in a greater release of planulae and decreased skeletal growth (Shick *et al.*, 1995). Lyons *et al.* (1998) discuss damaging effects of UVR on coral DNA. Shallow colonies were found to be about twice as tolerant to harmful radiation than deeper conspecifics (Shick *et al.*, 1996). This is thought to be linked to shallow corals possessing 5-10 folds higher concentrations of mycosporine-like amino acids (MAAs), which are the first line of defence against solar UVR, providing protection for zooxanthellae (Shick *et al.*, 1995). Coral transplantations have also shown the effects of UVR being more damaging than decreases in light regime. Corals that were transplanted to shallow depths died, whereas shallow corals transplanted to deeper depths could photoadapt, although they exhibited decreases in growth rates (Yap *et al.*, 1998; Rosenfeld *et al.*, 2003). The corals at deep Kapit V, which dropped in tissue thickness by 1/3 between 2002 and 2003,

also exhibited increases in bleaching on their upper surfaces, which can lead to decreased tissue thickness (True, *in review*). Hence, increased solar radiation may have caused the localised patterns of decreased tissue thickness found on Lihir Island in deep corals in 2003. Thus, on the one hand, increases in solar radiation may have been benefitial for corals by increasing their effective depth in shallow sites with some turbidity. On the other hand, the same increases in solar radiation may have stressed corals in deep, clear water. There are many large-scale environmental factors, acting alone or in synergy which can either positively or negatively affect tissue thickness. In addition, a whole range of small-scale, localised environmental changes may have also driven the between-yearly changes in some study sites. It will never be possible to account for all environmental factors affecting individual corals. The main objective, namely to use tissue thickness as a reliable method to assess relative turbidity stress, has been fulfilled, despite some local and yearly variability.

4.6.5. To what extent does water depth influence tissue thickness and does it have to be standardised? In some instances, tissue thickness varied with depth between different study sites (as expressed by significant depth*site interactions in ANOVA I in 2003, Table XVII and ANOVA III, Table XX). For example, corals at Masahet Island had similar amounts of tissue between their deep and shallow sites (on average 3.8 mm +/- 0.2mm), in contrast with sites such as Kapit IV, V, Lakunbut and PutPut Point which had twice as much tissue thickness in shallow compared with deep habitats (see Fig. 22). The lack of significant difference in tissue thickness of Masahet deep and shallow corals may be due to the deep site at Masahet Island being

shallower than other deep study sites (11.3-15.1 m, average: 12.8 m +/- 0.5 m, average of all other sites: 17.6 m +/- 1 m). In addition to being shallower than other sites, very clear water and oceanic conditions can be found at Masahet Island (Thomas, 2003). Therefore, differences in tissue thickness between shallow and deep sites, which are related to light levels, would have been smaller at Masahet Island than at other study sites.

Linear regressions of tissue thickness against depth for data from both shallow and deep water corals showed no significant relationships (all $r^2$ values were <0.3, often <0.1). Hence, depth does not have to be standardised to reduce natural variability in the data sets for corals from shallow and deep water. Depth may, however, have an effect on tissue thickness if corals are sampled at greatly different depths, particularly in areas with high turbidity (like Kapit II, see above). It should always be tried to sample for tissue thickness at similar depths in order to avoid such unnecessary variability. Decreases in coral growth with increasing depth are common in the literature (Bosscher and Meesters, 1992; Yap *et al.*, 1998) and usually related to decreasing light reaching the corals. Similar patterns have also been found in skeletal growth data on Lihir Island (see Chapter 5). Depth effects on coral growth and the relationship of growth form with light and substrata slope are examined in more detail (Ch. 5).

4.6.6. Adjusting tissue thickness for time of sampling. This study showed that some patterns in tissue thickness variability could be accounted for by the effect of the lunar month. Examples were the decrease in tissue thickness in Kapit II and Kapit IV deep corals between 2002 and 2003 and

the increase in deep Kapit III colonies over the same time period (Fig. 24). Other patterns in tissue thickness were unaffected or became even more significant by accounting for lunar influence. This reliable indicator of regular, monthly tissue thickness variability, should always be used to ameliorate effects of additional, natural 'noise', as found between years and study sites. Tissue thickness should either be sampled at the same time during the lunar month, or potential variability should be adjusted for. As tissue thickness is generally lower on Lihir Island (average of 4.3 +/- 0.25 mm in non impacted sites) compared with corals from similar depths at the GBR (average of 7.31 mm, see Table 4 Lough *et al.*, 1999), daily values of increase quoted here may not be applicable for other areas. Therefore, monthly variability of tissue thickness should also be quantified in other locations in order to adjust large datasets, such as the ones collected from the GBR by Barnes and Lough (1992).

## 4.7. SUMMARY OF RESULTS:

- Tissue thickness responded to both, natural and anthropogenic turbidity impacts. This was shown by a significant decrease in tissue thickness in areas of high turbidity compared with less turbid locations.
- Tissue thickness decreased by a third when turbidity increased to 15-30mg $l^{-1}$ SSC. Hence, a distinct cut-off boundary of turbidity impact could be identified in Luise Harbour.
- Tissue thickness showed variability between study sites, some of which could be explained by different environmental conditions between study sites, including different depth gradients sampled.

- Tissue thickness was always lower in deep, compared with shallow water corals. However, depth effects within the same depth regimes did not need to be adjusted for.
- General patterns of change in tissue thickness with turbidity and water depth were similar between years.
- Tissue thickness data was improved when corrections were made for changes in tissue thickness over a lunar month.

Summary of aims of studies, importance of studies, methods, predicted and actual outcomes and final comments.

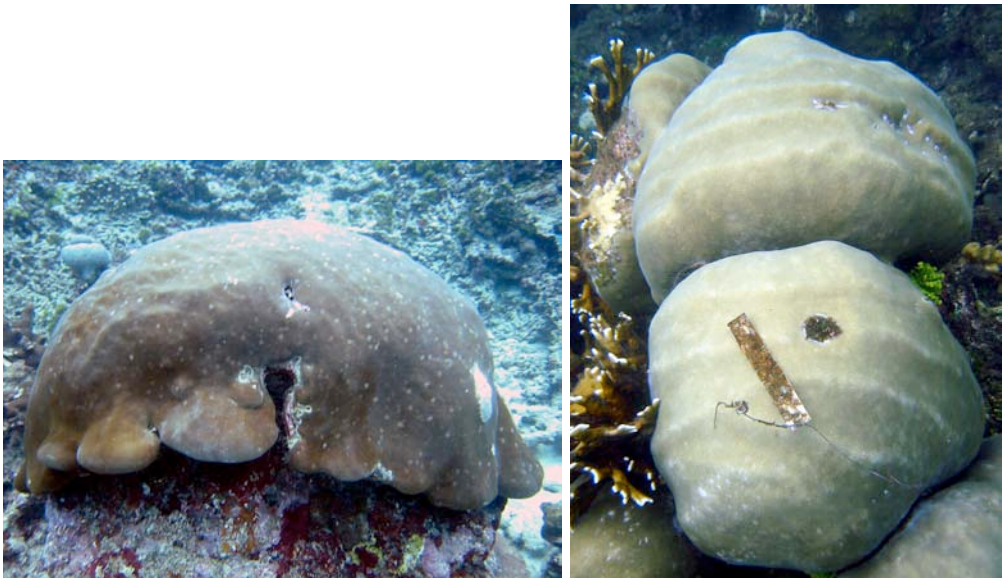
| AIM | IMPOR-TANCE | METHOD USED | PREDICTED OUTCOME | ACTUAL OUTCOME | COMMENTS, FUTURE WORK |
|---|---|---|---|---|---|
| To examine if ttl changes with turbidity gradients – both natural & anthropogenic | To be able to use ttl as a monitoring tool for turbidity stress in remote areas | Sampled ttl at 8 sites in 3 impact zones. 1 site had natural turbidity | ttl responds by decreases to different turbidity gradients. (from Barnes & Lough, 1999) | ttl decreased in areas of high turbidity > 10mg/l not in minor or control areas | First study that showed ttl decreases to both, natural and anthropogenic turbidity levels. Need to assess other stressors too |
| To assess natural variability of ttl with water depth, study sites and years | Natural variability may decrease usefulness of ttl as turbidity stress response | All ttl data measured in 2 depths, 8-13 sites and between 3 years | The ttl stress response to turbidty is greater than natural ttl variability. (Barnes & Lough, 1999) | Some variability with study sites, depth and years but ttl was always less in impact zone | Care should be taken not to include locations with extreme variability. Longer-term temporal changes in ttl should be assessed |
| To assess if depth needs to be calibrated | To reduce extra 'noise' in the data set | Depth vs ttl regressions | Linear decrease in ttl with depth offers adjustment value | No relationship between ttl and depth | No depth calibration needed. But: 2 sites differ due to depths |
| To find boundaries of turbidity impact on Lihir Island | For manage-ment, extent of coral stress to mining needs to be known | Measured 5 additional sites within 'impact' zone > 10mg/l | Distinctive cut-off boundary of turbidity stress is shown by ttl. | Boundary reached from Kapit III in north to PutPut Point in south of Lihir | Re-assessed sediment impact zones predicted by NSR. Only 2 instead of 4 and within 4 km rather than 8 km |
| To assess if ttl measurements correspond to live coral cover and turbidity | To assess sensitivity of ttl against more common monitoring tools | Compared ttl with coral cover (NSR) and turbidity (Thomas) | Different methods show different impact zones (from NSR, 2000) | Live coral cover & ttl significantly decreased where turbidity > 10mg/L | First study comparing ttl to other monitoring methods. Can be early warning tool before coral cover changes |
| To compare adjusted and unadjusted ttl results | To assess if adjusting for time of sampling works | Did all analyses on both data sets | Adjusted data sets are different to raw data (from Chapter 3) | some differences adjusting smoothed out some variability | ttl should be adjusted for time of sampling. But: different values may be needed in other areas |

NB: ttl= tissue thickness; references refer to speculations in the literature which these studies addressed. Arrows denote links between studies.

# 5.0 TISSUE THICKNESS AND COLONY MORPHOLOGY

5.1. INTRODUCTION: Tissue thickness variability in response to external environmental influences has been examined in previous chapters. Intrinsic factors, such as colony size, shape and intracolonial variability, may also result in variable tissue thicknesses. These factors could further reduce the usefulness of tissue thickness as a stress response monitoring tool and will have to be accounted for. Barnes and Lough (1992) found that tissue thickness increased with colony size and decreased from summits to sides of colonies. Here, colony diameter was used as the primary measure of colony size (Ch. 1, 1.5), in addition, colony height was also measured and a morphological classification developed. Four distinct and 2 intermediate growth forms of massive *Porites* were found on reefs around Lihir Island. These growth forms were rounded, round-encrusting, pyramidical, pyramidical-encrusting, encrusting and vertical encrusting ( Plates 7-12).

1) ROUNDED (R): Rounded colonies largely resembled hemispheres



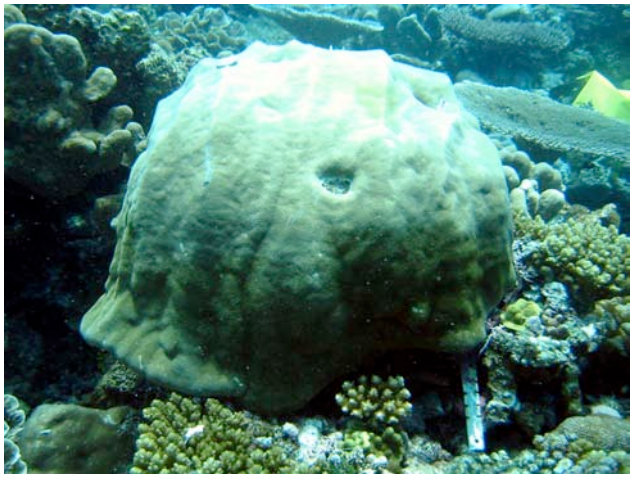


Plate 7. Examples of rounded morphologies on Lihir Island.

2) PYRAMIDICAL (P): Colonies were classed pyramidical when their summits were obviously narrower then their bases (Plate 8).

Plate 8. Examples of pyramidical morphologies on Lihir Island

3) ROUNDED-ENCRUSTING (R-E): These colonies were rounded but flatter than a hemisphere and often had slightly encrusting edges (see Plate 9)

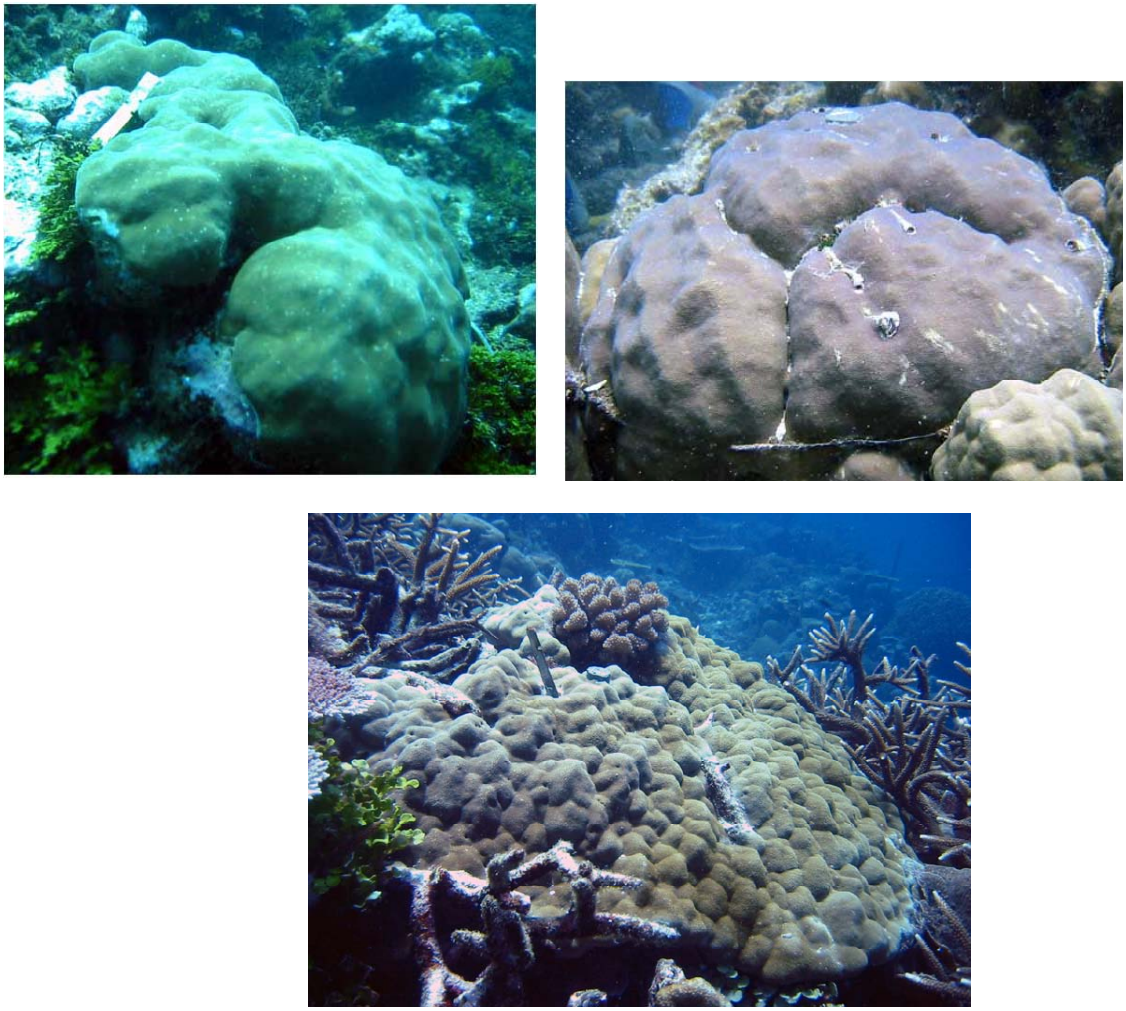


Plate 9. Examples of round-encrusting morphologies on Lihir Island.

4) PYRAMIDICAL-ENCRUSTING (P-E): Colonies in which growth was mainly directed laterally but for which there was significant upward growth. These were often seen as colonies encrusting on steeply sloping surfaces but in which higher parts of the colony had grown upwards and outwards (see Plate 10)

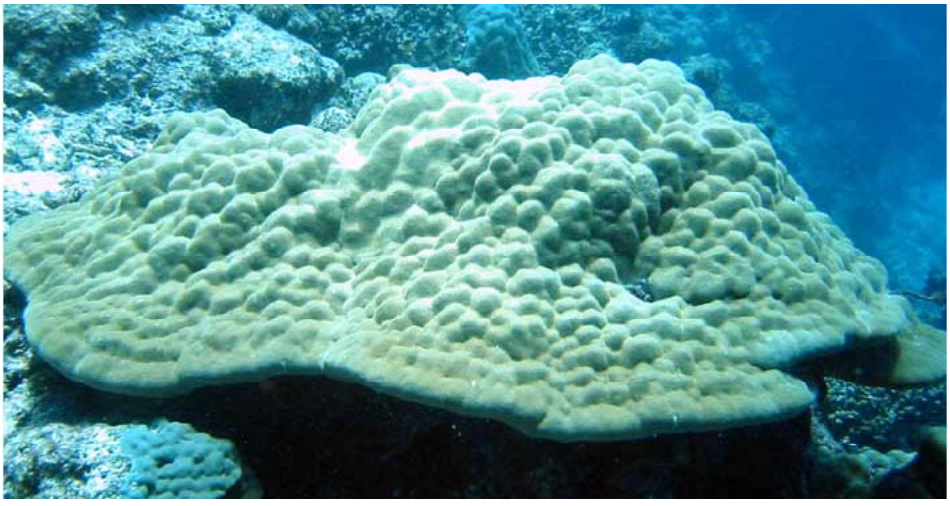
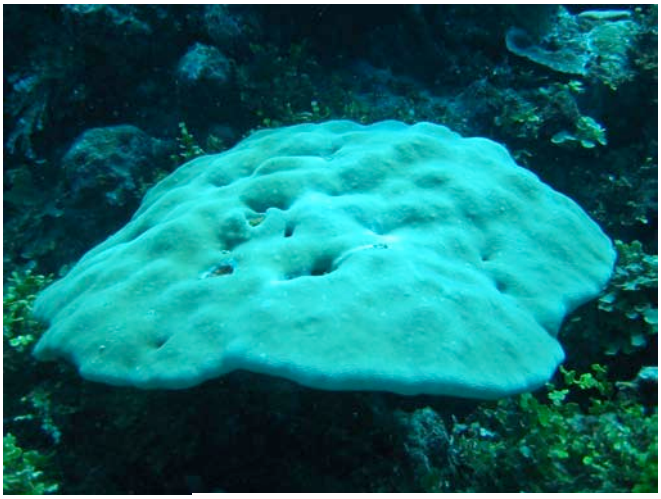


Plate 10. Examples of pyramidical-encrusting morphologies.

5) ENCRUSTING (E): Colonies that were horizontally flattened (Plate 11)



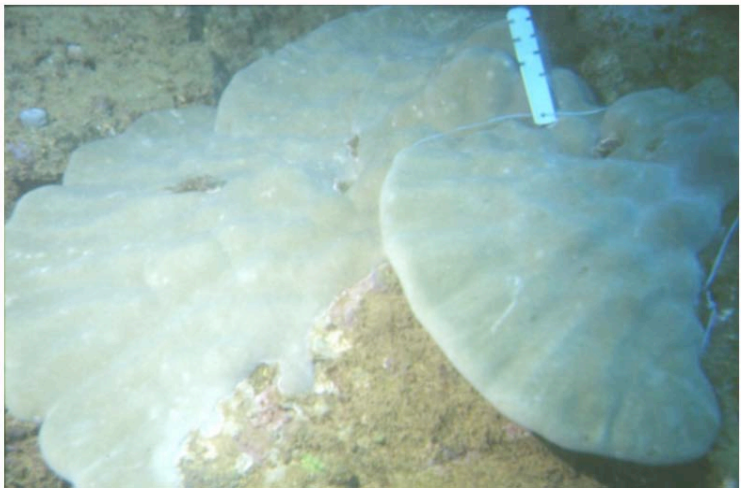


Plate 11. Examples of encrusting morphologies on Lihir Island.

6) VERTICALLY ENCRUSTING (VE): Colonies that were vertically flattened and growing on slopes without thickening of their upper regions, cf. (4), Plate 12.

Plate 12. Examples of vertical-encrusting morphologies on Lihir Island.

5.1.1. Intracolonial variability of tissue thickness between rounded and flattenend colonies: All previous studies on tissue thickness have been undertaken on approximately hemispherical colonies. Here, intra-colonial

tissue thickness variability between rounded and flattened growth forms was assessed by three separate studies:

1) Tissue thickness variability between the summit and sides of rounded and flattened colonies;
2) Tissue thickness variability between summits of bumps and valleys of both growth forms;
3) Tissue thickness variability every 20 mm on both growth forms.

1) Flattened corals result from a strong tendency for radial (edge) rather than vertical extension (Hughes, 1992). The form of the corallum could also be due to two separate growth processes: skeletal accretion, which is dependent on light and tissue growth, which is independent of light (Barnes, 1973; Brakel, 1976). If, at low light, calcification can not keep up with tissue growth, it could result in the lateral proliferation of 'excess' tissue, forming a flat colony (Brakel, 1976). Polyps were found to be added almost exclusively along the seaward edge of a flattened colony (Barnes, 1973; Dustan, 1975), and the edges of flat colonies were found to grow downwards (Dustan, 1979). If the main axis of growth changes from vertical to horizontal, maximum tissue thickness might also change from being greatest at the summit of a rounded colony (e.g. Barnes and Lough, 1992) to being greatest at the edge of a flattened colony. Consequently, it might not be appropriate to compare the tissue thickness at the summit of rounded colonies with tissue thickness at the centre of flattened colonies. Tissue thickness was therefore examined between summits and sides of skeletal slices from rounded and flattened *Porites* skeletons. To gain further understanding on what could drive possible variability of intracolonial tissue

thickness patterns, major skeletal growth parameters were also assessed for both morphologies.

2) Bumpy growth surfaces develop when skeleton no longer provides the necessary increase in surface area to accommodate tissue growth (Darke, 1991). Darke (1991) found new corallites being initiated on the summit of bumps, whilst older corallites were compressed and ultimately occluded at the bottom of valleys formed between bumps. Possible variability in tissue thickness between the summits of bumps and valleys, in both rounded and flattened colonies was examined as well.

3) Tissue thickness can differ over short distances on a coral slice due to bumps and valleys but also if the slice has not been cut perfectly perpendicular to the coral calices (M Devereux, *pers. comm.*). Cuts which are not perpendicular to the surface of a colony can appear to increase tissue thickness. Bumps are also likely to have a much bigger effect on slices cut a few milimetres out from the centre line of a rounded colony. A section that passes vertically through the summit of a bump will give a measure of the true tissue thickness, i.e., the depth of skeleton occupied by tissue in a direction normal to the surface of the skeleton. A section through the side of a bump will not be normal to the surface of the skeleton. Measurements of tissue thickness in this situation are greater than measurements taken normal to the colony surface. To assess this variability, and if it differs between rounded and flattened colonies, tissue thickness was measured every 20 mm along skeletal slices.

5.1.2. Tissue thickness variability with colony size and shape: Increasing tissue thickness was positively correlated (correlation 0.4, $p < 0.01$) with

increasing colony height (Barnes and Lough, 1992). Colonies of different sizes could, therefore, affect tissue thickness measurements. As it was not possible to find ten same-sized colonies at each study site, it is assessed here if size effects influence tissue thickness measurements enough to warrant standardization for colony size.

Similar to tissue thickness, the morphology of *Porites* colonies also changes with increasing colony size (Done and Potts, 1992). Van Veghel and Bosscher (1995) found tissue thickness to be significantly higher in 'bumpy' (7.3 mm) compared with 'massive' (6.8 mm) and 'columnar' (6.9 mm) morphotypes. According to Barnes (1973), hemispherical colonies with individual polyps cannot increase in size indefinitely without changing shape because it becomes increasingly difficult to add new polyps, i.e. new tissue, as colony size increases. Hence, massive colonies with individual polyps change shape from hemispherical to columnar, to bumpy (the latter of which consists of many small, low columns), to flattened with increasing depth. Change in morphology is a way of balancing differences in tissue and skeletal growth – and tissue thickness may not vary in a simple fashion between differently shaped colonies of the same species. Here, I explore the possibility that a decrease in tissue thickness with increasing depth (as found in Chapters 3 and 4) results from changes in colony shape with increasing depth. It is important to account for possible additional factors which could mask known environmental influences, such as water depth.

5.1.3. Quantifications of qualitative descriptions of colony morphology: One of the major challenges when discussing intra-specific morphological

variability is describing the various growth forms in a numerical way. It is necessary to go beyond imprecise verbal descriptions to quantify colony shape, although it can often be difficult to achieve (Hubbard and Scaturo, 1985; Stafford-Smith, 1992). Brakel (1976) argued that classifying corals as 'massive' and 'branching' resulted in an arbitrary categorization of shapes into two groups that represent the extremes of a continuous, intergrading series of possible forms. Most studies examine morphological differences on the polypal level (e.g. Beltrantorres and Carricartganivet, 1993; Amaral, 1994) and usually discuss gross morphological changes on the colony-level only qualitatively. One study described massive morphologies as having one vertical branch so that they could be compared with branching colonies when assessing mechanical impacts (Marshall, 2000). He was, however, unable to quantify flattened morphologies with those geometrical approximations. Riegl (1995) described the morphology of massive corals by their degree of sphericity, i.e. how close their height/diameter ratio approached a hemisphere (which he identified to have a ratio of 0.5). However, Brakel (1976) showed that the height to width ratio of massive colonies varied markedly: between 0.07 and 0.7 and with a mean of only 0.28. Brakel (1976) expressed complex morphological concepts by sets of quantitative measurements such as size (maximum and minimum width and height), total volume (length*width*height) and symmetry (length/width). Similar colony size parameters were used here to numerically describe the six morphologies of massive *Porites* (see 5.1.). Tissue thickness variability with qualitative and quantitative descriptions of the six morphologies found on Lihir Island was examined as well.

5.1.4. Environmental variables influencing colony morphology: Modification of colony shape in response to environmental influences has been termed phenotypic plasticity (Bruno and Edmunds, 1997). Transplant experiments have supported the importance of phenotypic plasticity in coral morphology, as transplanted colonies were found to alter their shapes over time (e.g. Foster, 1979; Bruno and Edmunds, 1997; Muko *et al.*, 2000). Many studies have found colonies to adopt a flattened habit with increasing depth by increasing their surface area to maximise interception of light (Done, 1983; Acevedo *et al.*, 1989; Bosscher and Meesters, 1992). Flattening could also be due to the need to maintain tissue growth with a lower resource for producing skeleton (Barnes, 1973). Flattening of corals with depth is a general, although not universal trend (Dustan, 1979). Although light is generally regarded as the most limiting factor in coral distribution, being most commonly implicated in inducing morphological changes with depth (e.g. Dustan, 1975), it is not the only factor discussed in the literature. For example, Dustan (1979) also suggested flattening as an adaptation to resist downslope travel. This study examined substrata slope as another possible environmental factor influencing distribution of different *Porites* morphologies on Lihir Island.

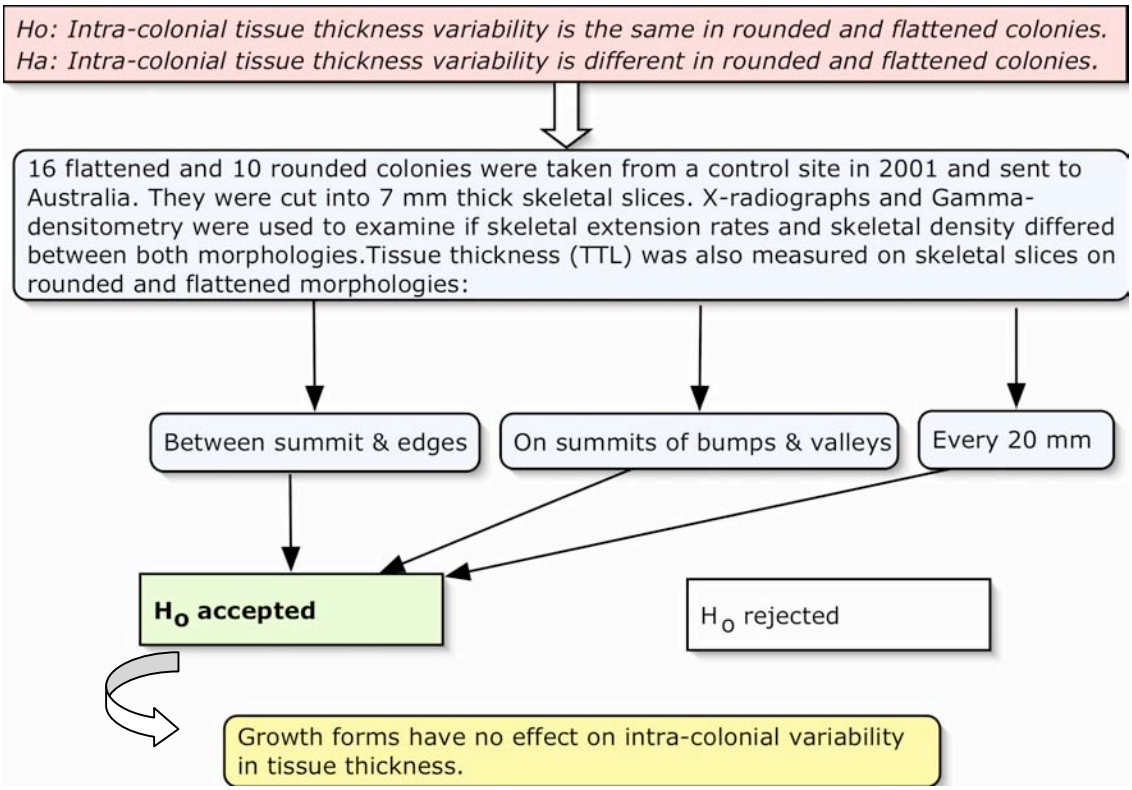
## 5.2. AIMS OF THIS STUDY:

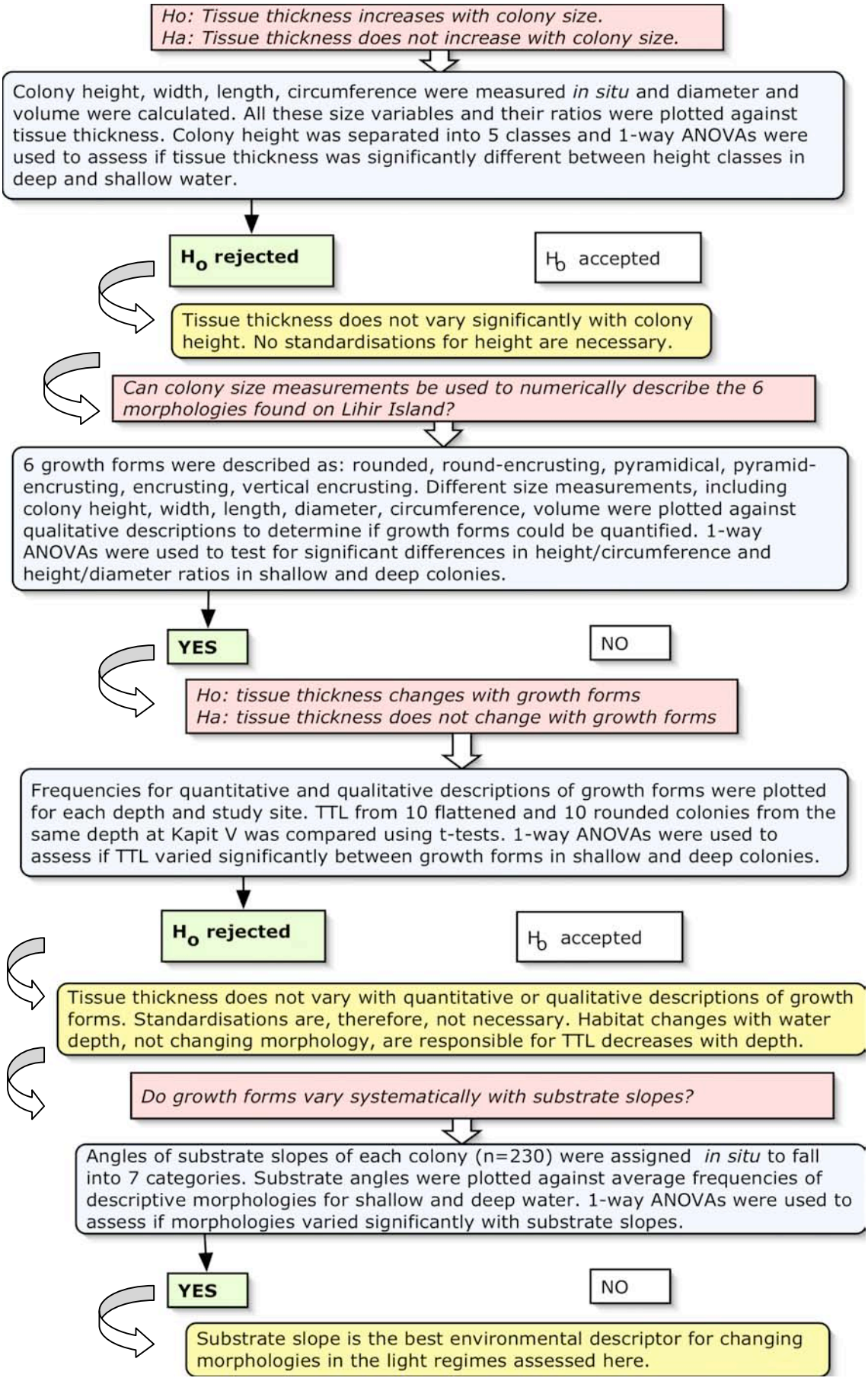
1) To examine how tissue thickness varies over the surfaces of rounded and flattened colonies;
2) To determine if tissue thickness was related to colony size and morphology at Lihir Island;

3) To determine if qualitative descriptions of growth forms could be quantified using colony size measurements;
4) To examine if different distributions of colony morphology (described qualitatively and quantitatively) in different water depths masked depth effects on tissue thickness found in Chapter 3 and 4;
5) To determine if morphological plasticity in colonies of *Porites* at Lihir Island could be linked with one or more environmental variables.

## 5.3. FLOWCHART:

This flowchart describes the various study questions, the methodology used to answer each question and the links between studies.




Ho: Tissue thickness increases with colony size.
Ha: Tissue thickness does not increase with colony size.
Colony height, width, length, circumference were measured in situ and diameter and volume were calculated. All these size variables and their ratios were plotted against tissue thickness. Colony height was separated into 5 classes and 1-way ANOVAs were used to assess if tissue thickness was significantly different between height classes in deep and shallow water.
Ho rejected
Ho accepted
Tissue thickness does not vary significantly with colony height. No standardisations for height are necessary.
Can colony size measurements be used to numerically describe the 6 morphologies found on Lihir Island?
6 growth forms were described as: rounded, round-encrusting, pyramidical, pyramid-encrusting, encrusting, vertical encrusting. Different size measurements, including colony height, width, length, diameter, circumference, volume were plotted against qualitative descriptions to determine if growth forms could be quantified. 1-way ANOVAs were used to test for significant differences in height/circumference and height/diameter ratios in shallow and deep colonies.
YES
NO
Ho: tissue thickness changes with growth forms
Ha: tissue thickness does not change with growth forms
Frequencies for quantitative and qualitative descriptions of growth forms were plotted for each depth and study site. TTL from 10 flattened and 10 rounded colonies from the same depth at Kapit V was compared using t-tests. 1-way ANOVAs were used to assess if TTL varied significantly between growth forms in shallow and deep colonies.
Ho rejected
Ho accepted
Tissue thickness does not vary with quantitative or qualitative descriptions of growth forms. Standardisations are, therefore, not necessary. Habitat changes with water depth, not changing morphology, are responsible for TTL decreases with depth.
Do growth forms vary systematically with substrate slopes?
Angles of substrate slopes of each colony (n=230) were assigned in situ to fall into 7 categories. Substrate angles were plotted against average frequencies of descriptive morphologies for shallow and deep water. 1-way ANOVAs were used to assess if morphologies varied significantly with substrate slopes.
YES
NO
Substrate slope is the best environmental descriptor for changing morphologies in the light regimes assessed here.

5.4. METHODS:

5.4.1. Intracolonial variability of tissue thickness in rounded compared with flattened colonies:

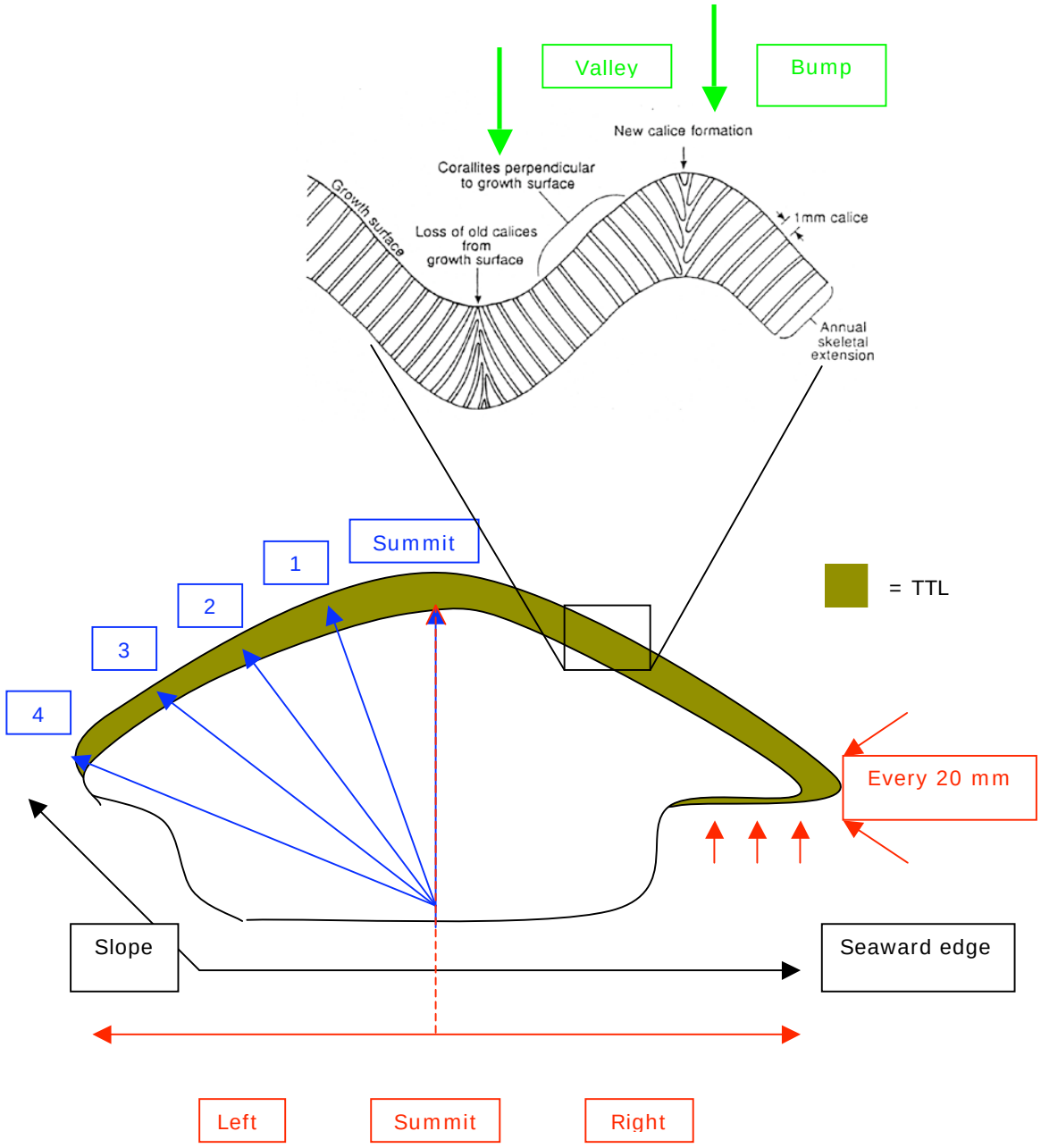
*5.4.1.1. Skeletal growth analysis:* In 2001, sixteen colonies from deep and eleven colonies from shallow water were collected at Masahet Island (see Chapter 1, Section 1.5.). Colonies collected from deep habitats comprised encrusting, pyramidical and pyramid-encrusting shapes and were categorised as 'flattened' (see Plates 8, 10 and 11 above). Shallow colonies were mainly hemispherical and were considered to be 'rounded' (see Plate 7). Skeletal slices of 7 mm thickness were cut from each colony (see Chapter 1). X-radiography and $\gamma$-densitometry were used to determine average yearly linear extension, density and calcification rates (see e.g. Lough and Barnes, 1992; see Chapter 1). The results for each growth parameter were averaged and compared between flattened and rounded colonies using one-way ANOVA. Due to the large variability of skeletal growth parameters within colonies and between years only average data could be tested (J. Lough, *pers. comm.*). In addition, several measurements of tissue thickness were undertaken on slices of each colony to examine intra-colonial variability in tissue thickness:

*5.4.1.2. Does tissue thickness vary from summit to sides of rounded and flattened morphologies?* To determine if tissue thickness variability between summits and sides of colonies is the same in rounded and flattened morphologies, each coral slice was divided into four segments on each side of the summit (see Fig. 31). Tissue thickness was measured at the summit

of bumps in each segment and compared between rounded and flattened morphologies using ANOVAs.

*5.4.1.3. Does tissue thickness vary between summits of bumps and valleys in rounded and flattened colonies*? Tissue thickness was measured at the summit of every bump and in each valley between bumps in all skeletal slices (Fig. 31). One-way ANOVA was used to assesse if tissue thickness differed between bumps and valleys and if these differences varied between rounded and flattened morphologies.

*5.4.1.4. Does tissue thickness vary every 20 mm along skeletal slices of rounded and flattened colonies?* Tissue thickness was examined every 20 mm along slices cut from rounded and flattened colonies (see Fig. 31) and plotted with line graphs for both growth forms. Differences in tissue thickness between each neighbouring point were calculated to obtain average intra-colony variability for both morphologies. In order to establish major patterns of tissue thickness variability, all data was averaged into three segments from where it was measured: left of summit, summit and right of summit. The 95% confidence limits were calculated for each colony using the formula 1.96+/- Standard Error (Sokal and Rohlf, 1996) to assess average intra-colony variance for both rounded and flattened skeletal slices.




The green arrows refer to measurements taken in 5.5.1.3)
The diagram was taken from Darke (1991)
The blue arrows refer to measurements taken in 5.5.1.2)
The red arrows refer to measurements taken in 5.5.1.4)
The black arrows refer to substrata inclination.

Figure 31. Diagram of tissue thickness measurements taken to determine intra-colonial variability in flattened and rounded colonies. (Diagram of bumps and valleys modified from Darke, 1991).

5.4.2. Does tissue thickness vary with colony size? To identify possible relationships of tissue thickness with colony size, tissue thickness was plotted against colony height, width, length, circumference, diameter (=length*width/2), volume (=height*width*length), height/diameter and height/circumference, in both deep and shallow colonies (50 scatterplots overall). These colony size parameters were chosen for ease of measuring size underwater. $R^2$ values were used to describe how well linear trendlines fit the data. Colonies of average height (=250 mm +/- 80mm) and average diameter (=440 mm +/- 100 mm) were sampled in this study. However, not all study sites had ten *Porites* colonies of similar sizes (at all sites, the colonies sampled for tissue thickness ranged from 80 – 640 mm in height and 200 – 1000 mm in diameter). Tissue thickness is known to increase with colony height (Barnes and Lough, 1992), thus potential height effects on tissue thickness measurements had to be examined. Colony height was measured vertically from the basal attachment of a colony to its highest point. All colonies were separated into five height classes. Tissue thickness changes between the five height classes were examined with a one-way ANOVA for colonies from deep and shallow habitats. The tests were undertaken on colonies from control sites only (Chapter 4). This was done to avoid committing Type II errors as tissue thickness is known to decrease with turbidity (Chapter 4).

5.4.3. Does tissue thickness change with quantitative and qualitative descriptions of colony morphology? The objective of this research was to assess if the significant links between tissue thickness and depth and between tissue thickness and study sites (Chapter 4) were related to

differences in colony morphology between depths and sites. First, it had to be assessed if the different growth forms could be quantified. Secondly, the distributions of different morphologies between different depths and study sites had to be examined.

*5.4.3.1. Quantifications of different morphologies:* Six different morphologies of corals growing on reefs around Lihir Island are shown in Plates 7-12, Section 5.1. Each colony sampled in this study was visually assigned to one of these six morphotypes. To be able to compare studies examining different morphologies of massive *Porites* it is important to find less subjective evaluation of growth forms than purely visual identifications. Therefore, it was assessed if the six qualitatively described growth forms could be quantified using the size measurements collected from each colony. These commonly used parameters describing colony size (height, length, width, circumference) were plotted for each morphotype. Also, diameter and volume were calculated and ratios of these different parameters (e.g. height/diameter) were plotted for each morphology. One-way ANOVAs for colonies from both deep and shallow water were used to test for statistically significant differences in height/circumference and height/diameter ratios. Growth forms that had three or less representatives at any depth were excluded from the analysis, due to insufficient replication.

*5.4.3.2. Links between tissue thickness and morphology:* Frequencies of quantitative and qualitative descriptions of growth forms were plotted for each depth and study site to examine their distribution in each habitat. Ten

flattened colonies were found at Kapit V shallow and their tissue thickness was compared with ten rounded colonies from the same depth and site using t-tests. One-way ANOVAs were used to test if tissue thickness varied significantly between growth forms in both, shallow and deep water corals. These tests were undertaken on both numerical (height/circumference) and descriptive morphological variables (the six shapes described above).

5.4.4. Links between environmental variables and colony morphology: Light is known to be a major factor determining morphological plasticity (e.g. Barnes, 1973; Bosscher and Meesters, 1992). The steep reef slopes on Lihir Island in which the deep habitat corals were exlusively located, result in different microhabitats with regards to light levels. As it was logistically unfeasable to attach light loggers on each colony, another potential indicator for varying light levels was examined, namely substrata slope. During sampling in 2003, the angle of the substrata slope of each colony was visually assigned to one of the following slope categories: $0^0$, $15^0$, $30^0$, $45^0$, $60^0$, $75^0$, $90^0$. These angles were plotted against average frequencies of descriptive morphologies for both deep and shallow habitats. One-way ANOVAs were used to assess if growth forms varied significantly with substrata slopes, in colonies from both deep and shallow habitats.

## 5.5. RESULTS:

### 5.5.1. Intra-colonial variability of skeletal growth and tissue thickness in flattened and rounded colonies:

*5.5.1.1. Skeletal growth data:* Average annual linear extension rates (cm $yr^{-1}$) and average annual calcification rates (g $cm^{-2}$ $yr^{-1}$) were up to 50%

lower in flattened, deep water colonies than in rounded, shallow water colonies (Fig. 32). Average annual density (g $cm^{-3}$), however, showed the opposite trend, with flat colonies having significantly greater density than round, shallow water ones (One-way ANOVA, $F_{(1)}=10.58$, $p<0.003$).

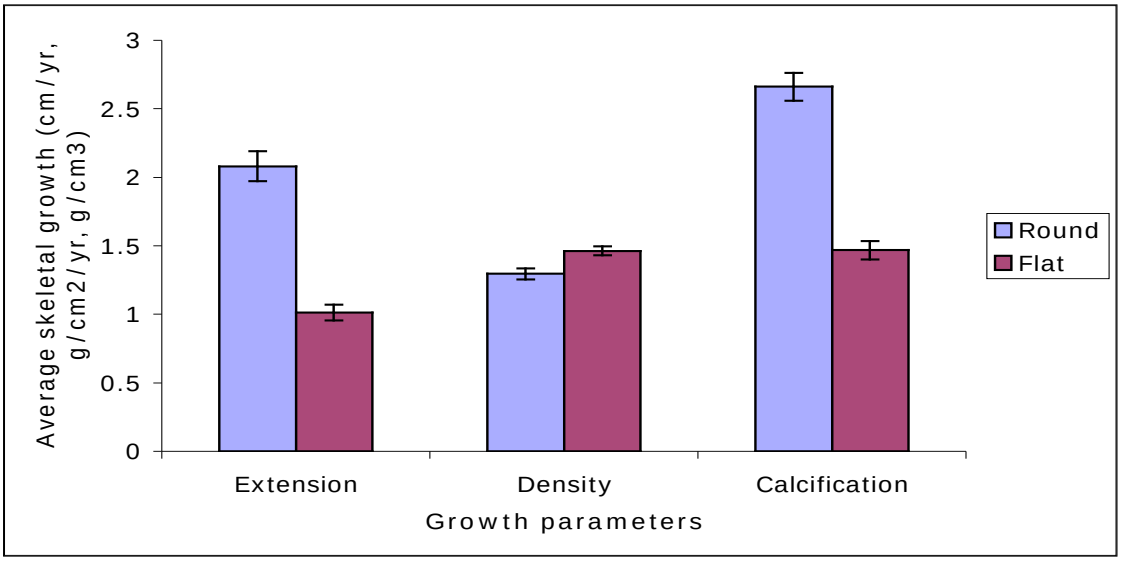



Figure 32. Average growth parameters in rounded (shallow) and flattened (deep) morphologies.

Average extension rates and average density had a negative relationship in both growth forms (Fig. 33 a). Calcification rate was positively correlated with extension rate in rounded and flattened colonies (Fig. 33 b) and there was no significant relationship between density and calcification rates in both morphs (Fig. 33 c).

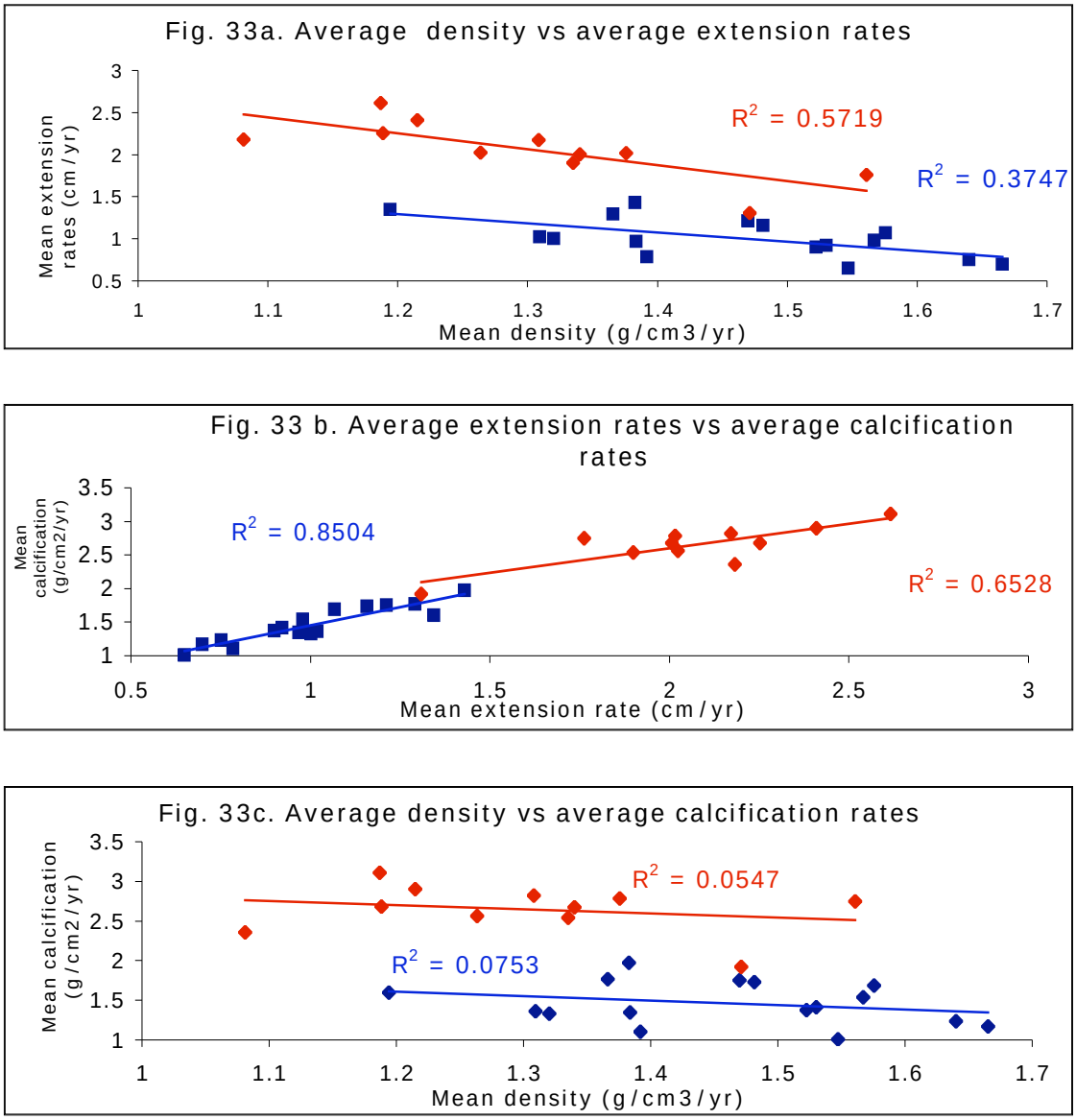



Figure 33. Scatterplots of average density vs average extension rates (Fig. 33 a); average calcification rates vs average extension rates (Fig. 33 b) and average density vs average calcification rates (Fig. 33 c) in both rounded (red) and flattened (blue) skeletal slices

*5.5.1.2. Tissue thickness variability from summits to sides of flattened and rounded skeletons*: There was no difference in tissue thickness between the first three segments either side of the colony summit in either flat and round colonies (see Fig. 35, One-way ANOVA for round $F_{(8)}=5.226$, $p<0.000$ and One-way ANOVA for flat $F_{(8)}=19.870$, $p<0.000$). Only the outermost edge (the last segment, Fig. 31) had significantly less tissue

than the other three (Tukey's post-hoc analysis, $p < 0.000$) and there was no significant difference between the two sides of the summit. The summit always had greater tissue thickness than the sides of a colony, regardless of morphology.

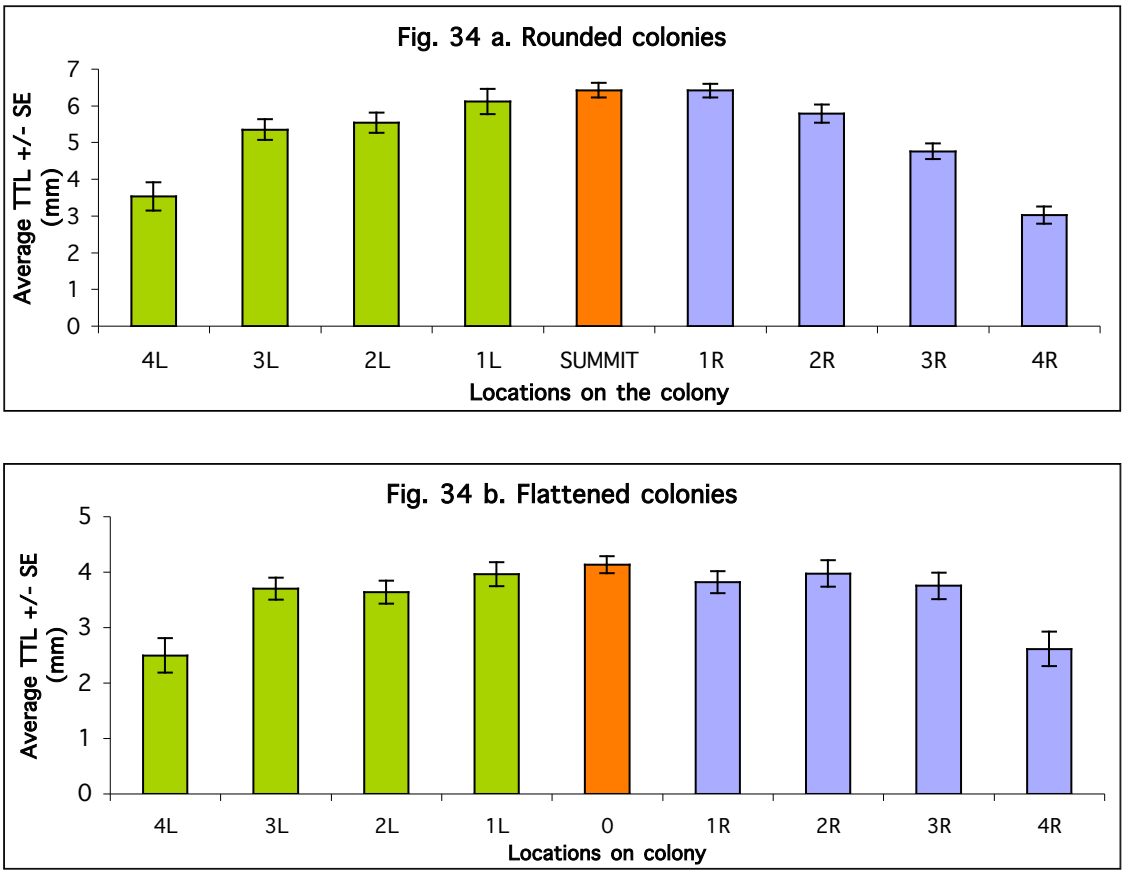



Figure 34. Average tissue thickness measurements from four segments either side of the summit (see Fig. 31) of rounded (Fig. 34 a) and flattened (Fig. 34 b) colonies

*5.5.1.3. Tissue thickness variability between summits of bumps and valleys in both morphologies*: Tissue thickness was significantly higher on the summits of bumps than in valleys between bumps in both, rounded and flattened growth forms (Fig. 34). A univariate ANOVA also showed that tissue thickness was significantly different between rounded and flattened colonies ($F_{(1)} = 280.599$, $p < 0.000$) and between bumps and valleys ($F_{(a)} = 38.034$, $p < 0.000$). There was no interaction between the two variables, indicating that tissue thickness from bumps was significantly

different from tissue thickness in valleys in both morphologies. On average, tissue thickness differed by 0.6 mm (+/- 0.025 mm) between bumps and valleys in both morphologies.

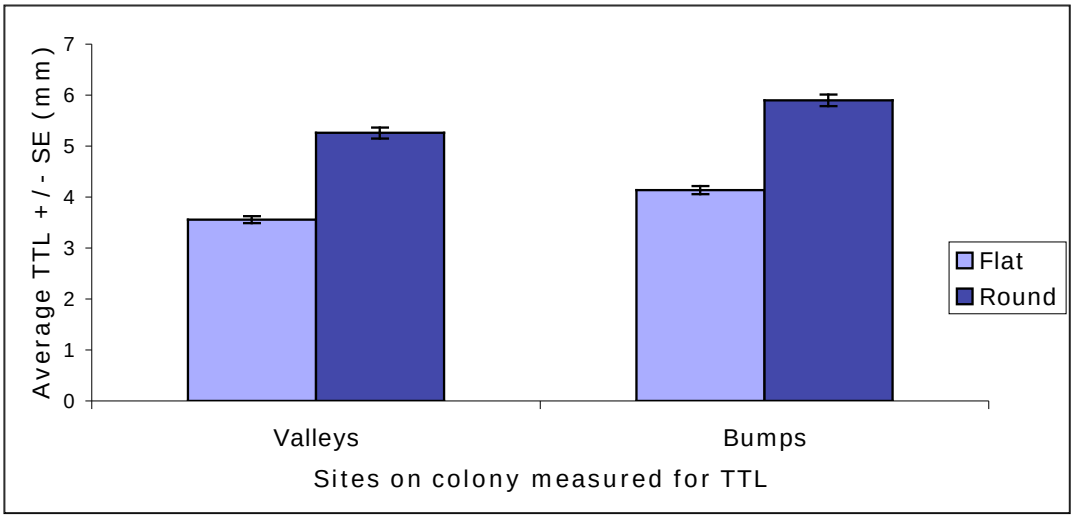



Figure 35. Average tissue thickness variability between bumps and valleys in rounded and flattened colonies

*5.5.1.4. Tissue thickness measurements every 20 mm along the surface of skeletal slices cut from rounded and flattened colonies:* Tissue thickness could change by up to 25% between points only 20 mm apart (e.g. Fig. 36). The average difference in tissue thickness between neighbouring points was 0.5 mm (+/-0.4 mm) across all skeletal slices from both morphologies.

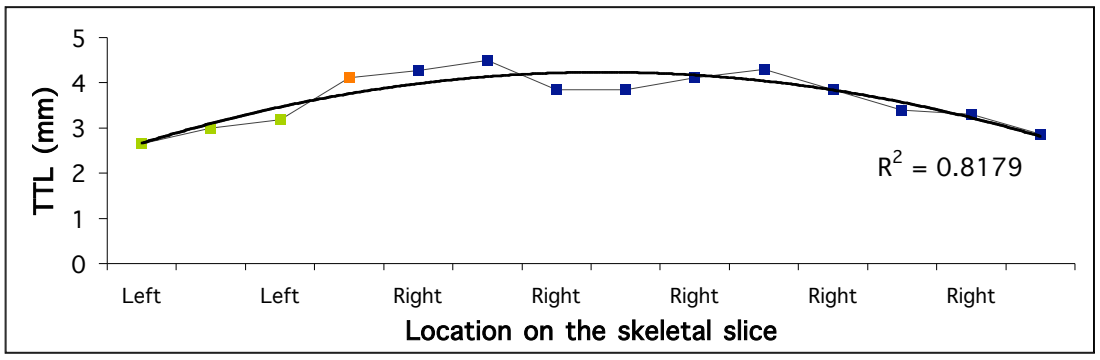



Figure 36. Example of tissue thickness measured every 20 mm along a skeletal slice of a flattened colony. Green=TTL measured left of summit, orange=summit, blue=right of summit

When averaging the measurements into three main locations on a skeletal slice, namely each side of the summit and the summit, the patterns were similar between both morphologies, with tissue thickness being highest on the summits (Fig. 37).

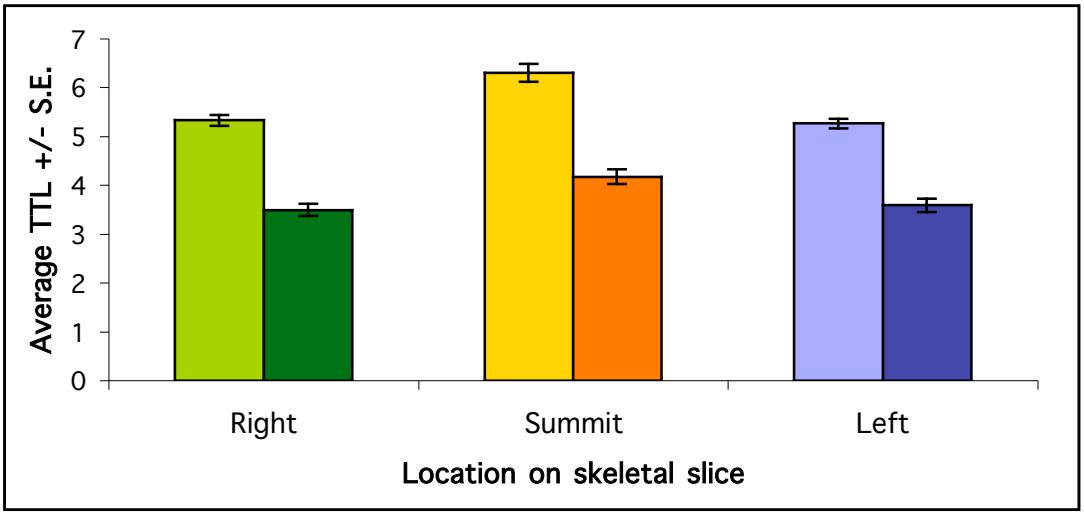



Figure 37. Tissue thickness measured every 20 mm then averaged for 3 areas on a skeletal slice in rounded (light bars) and flattened (dark bars) morphologies

The 95% confidence limits calculated as 1.96*Standard Error (i.e. the standard deviation of the mean) were, on average, 0.36 mm for rounded (mean = 5.3 mm) and 0.31 mm for flattened colonies (mean = 3.8 mm).

5.5.2. Links between colony size and tissue thickness: Linear regressions were used to examine potential relationships between colony size and tissue thickness measurements. No significant correlation was found between any of those size parameters and tissue thickness (all $r^2$ values were <0.1). Tissue thickness did not differ significantly between five different height categories in both shallow (One-way ANOVA $F_{(4)}=2.775$, $p=0.091$) and deep (One-way ANOVA $F_{(4)}=0.786$, $p=0.563$) colonies.

5.5.3. Links between colony morphology and tissue thickness:

*5.5.3.1. Qualitative and quantitative descriptions of growth forms:* None of the measured or calculated size parameters could be used to numerically describe all six growth forms. Two size ratios, however, separated different morphologies into a distinctive grouping (Fig. 38 and 39).

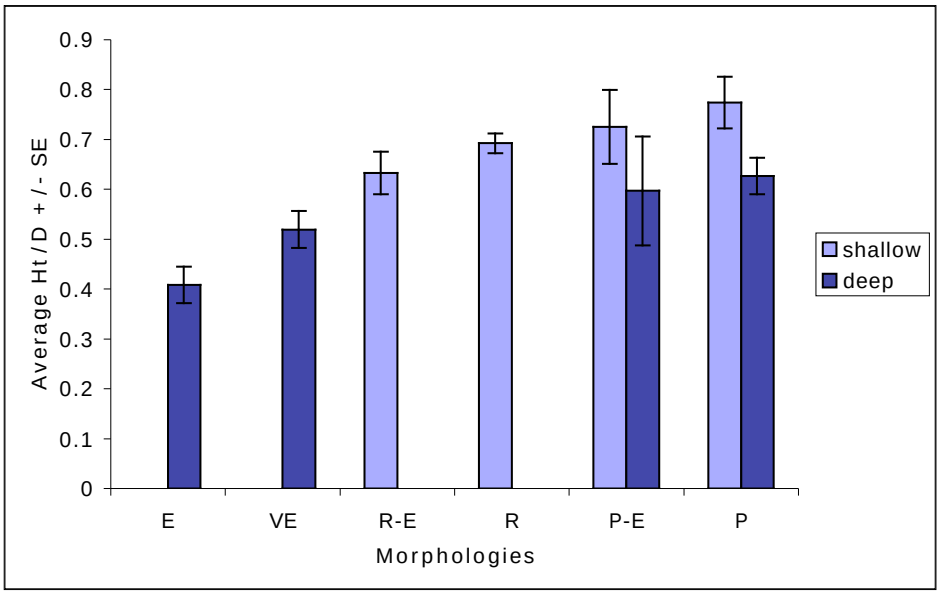



Figure 38. Average height/Diameter ratios in different morphologies and water depths.

NB for Fig. 38 and 39: E=encrusting, VE=vertical encrusting, R-E= round-encrusting, R=rounded, P-E= pyramid-encrusting, P= pyramid (see text for qualitative descriptions)

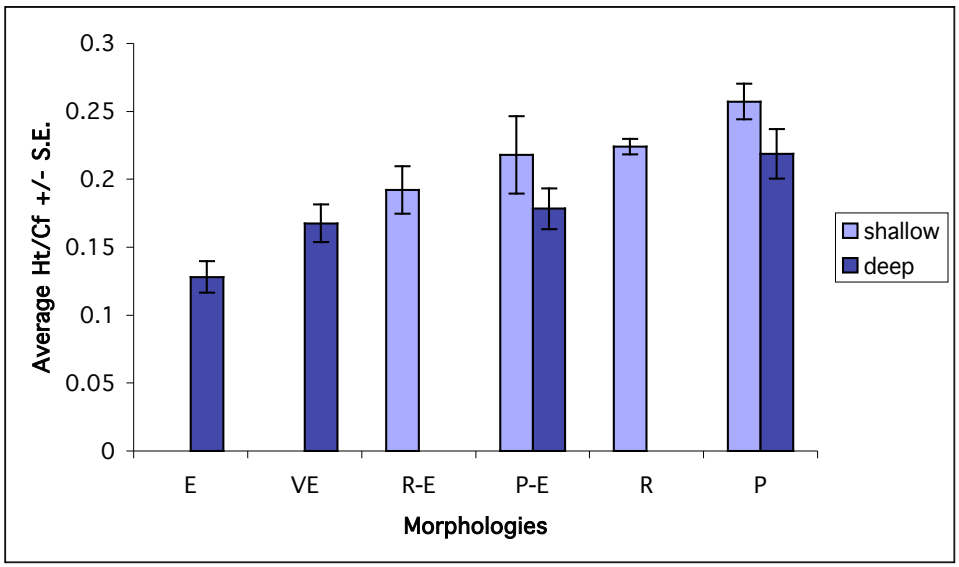



Figure 39. Average height/circumference ratios in different morphologies and water depths.

Morphological groupings into height/diameter and height/circumference ratios were: encrusting < vertical-encrusting < round-encrusting < rounded and pyramidical-encrusting < pyramidical. Not all growth forms could be found in shallow and deep water (Fig. 38 and 39) with encrusting and vertical encrusting morphs mainly found in deep (49% of deep water morphologies, only 4% of shallow water morphologies), and rounded and round-encrusting mainly found in shallow water (68% of all shallow water morphologies and only 8% of all deep water morphologies). The linear trend of decreasing height/circumference ratios with water depth is highly significant (Fig. 40) and can be related to changes in growth form from hemispherical to flattened with increasing depth (see below).

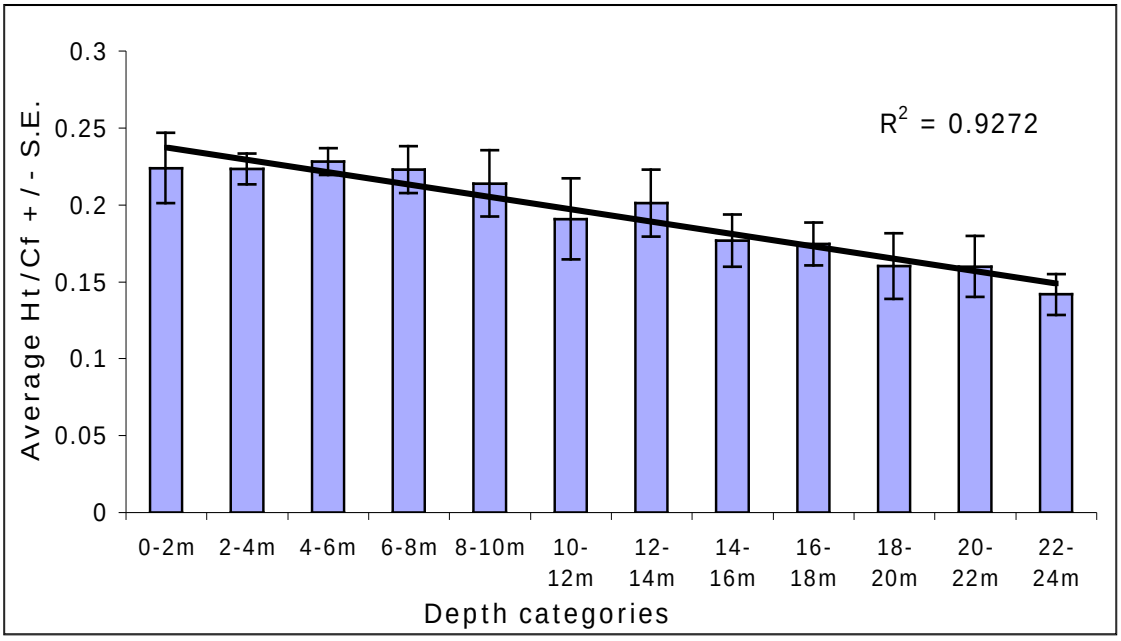



Figure 40. Average height/circumference ratios in different depth categories.

The main difference in growth forms as quantified by height/circumference and height/diameter is between encrusting and pyramidical corals in deep, and round-encrusting and pyramidical corals in shallow water (Fig. 38 and 39). Height/Circumference and height/diameter ratios were not significantly

different between shallow water growth forms at $\alpha=0.025$ ($F_{(3)}=1.588$, $p=0.196$). Height/circumference ratios in deep water colonies were significantly different between growth forms ($F_{(4)}=6.435$, $p<0.000$). Tukey's HSD post-hoc analyses showed pyramidical, rounded and pyramid-encrusting colonies to be significantly different from encrusting shapes ($p<0.000$), but not significantly different from each other ($p>0.05$). Vertically encrusting morphologies were not significantly different from any other shapes. Height/diameter ratios in deep water colonies were also significantly different between growth forms ($F_{(4)}=3.216$, $p<0.02$). However, post-hoc analysis revealed significant differences only between pyramids and encrusting morphologies ($p<0.03$). Height/circumference ratio, is therefore regarded as the best parameter to quantitatively describe different growth forms on Lihir Island.

*5.5.3.2. Links between qualititative and quantitative morphologies and tissue thickness in different water depths:* Tissue thickness was always found to be thinner in deep, compared with shallow water (see Chapter 3 and 4). The height/circumference ratios of coral colonies decreased with increasing water depth (Fig. 40) because colonies tended to become lower and more flattened as depth increased (Fig. 41). Encrusting and vertically-encrusting colonies dominated deep water habitats, rounded colonies dominated shallow water habitats with pyramidical and pyramid-encrusting forms occurring in both shallow and deep water. Tissue thickness was not significantly different in both visual descriptions of morphologies (One-way ANOVAs for shallow $F_{(4)}=1.073$, $p=0.373$ and deep $F_{(5)}=1.592$, $p=0.171$)

and numerical descriptions of morphologies (One-way ANOVAs for shallow $F_{(4)}=0.704$, $p=0.591$ and deep $F_{(5)}=1.204$, $p=0.315$).

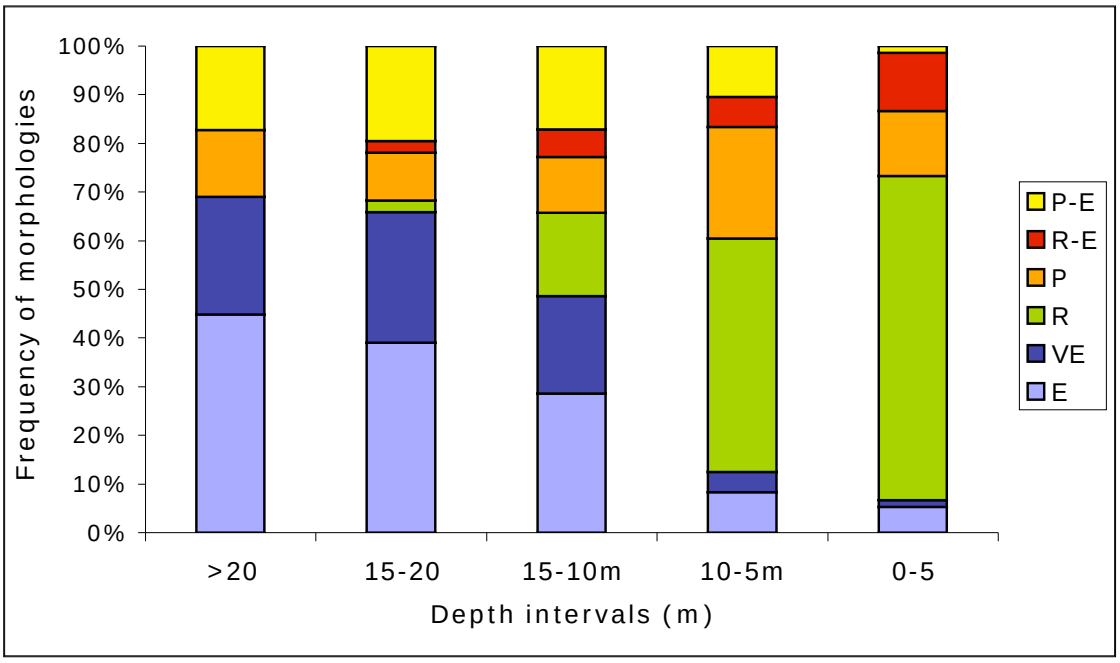



Figure 41. Percentage frequency distribution of growth forms over different depth intervals on Lihir Island. NB: E=encrusting, VE=vertical encrusting, R-E= round-encrusting, R=rounded, P-E= pyramid-encrusting, P= pyramid (see text for qualitative descriptions)

A One-way ANOVA showed that there was no significant difference in tissue thickness between rounded and encrusting colonies when sampled at the same depths at Kapit V ($F_{(1)}=0.086$, $p=0.773$).

5.5.4. Substrata slope and colony growth form: Tissue thickness did not vary amongst different growth forms growing at similar water depths (Section 5.5.3.2). Growth forms were found to distribute according to the angle of substrata slope (Fig. 42). The average slope angle was found to increase with increasing depth (Fig. 43).

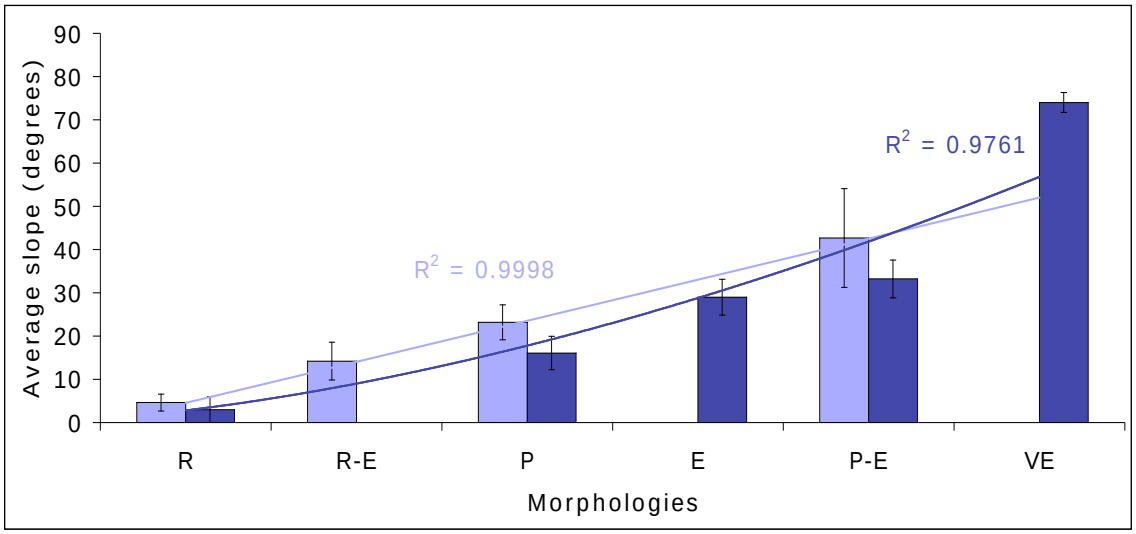



Figure 42. Distribution of growth forms over average slope angles in shallow (light bars) and deep (dark bars) water

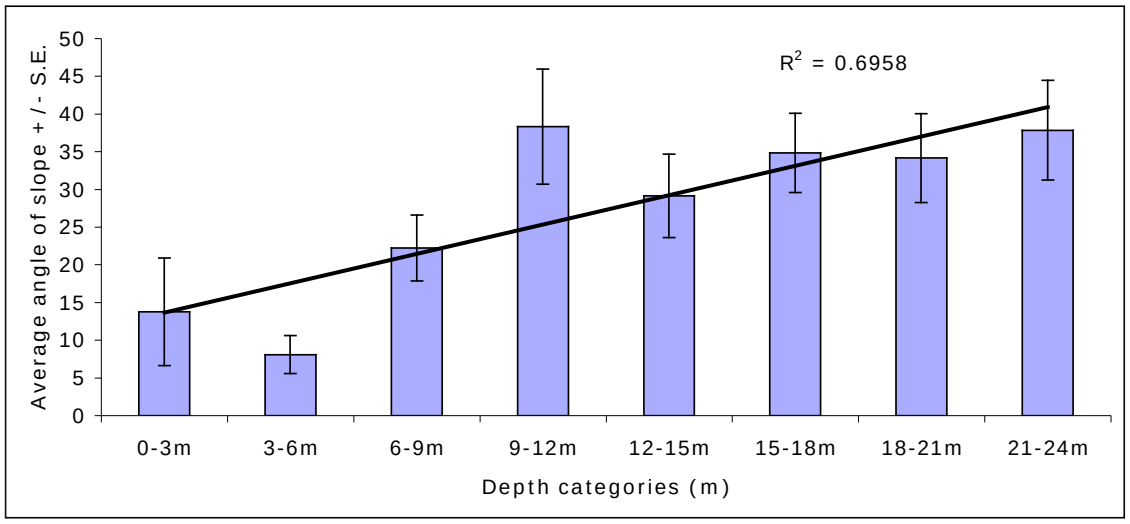



Figure 43. Changes of average slope angles with different depth categories.

The relationship of angle of substrata and growth forms is highly significant in both shallow ($r^2$=0.99) and deep ($r^2$=0.98) water. Morphologies distribute accordingly with increasing slopes (Fig. 42): round < round-encrusting < pyramid < encrusting < pyramid-encrusting < vertical encrusting. One-way ANOVAs examining slope effects on growth form in both water depths showed that these relationships were significant (shallow $F_{(3)}$=26.147, $p<0.000$; deep $F_{(4)}$=12.665, $p<0.000$). Post-hoc analyses grouped morphologies in the following way: in shallow water round colonies

were on significantly lower average slope angles than all other growth forms (Tukey's $p < 0.001$). Round-encrusting morphologies were on significantly less steep substrata than pyramid-encrusting colonies (Tukey's $p < 0.002$). In deep water, round and pyramidical colonies were similar with regards to their substrata slopes, as were pyramids with encrusting and pyramid-encrusting shapes. Vertical encrusting colonies were on significantly steeper substrata slopes than all other growth forms (Tukey's $p < 0.000$). The angle of slope seemed to be a better indicator for different coral shapes than any of the colony size variables examined above. However, tissue thickness did not change significantly with substrata slope (One-way ANOVA, $F_{6)} = 1.936$, $p = 0.084$).

## 5.6. DISCUSSION:

5.6.1. Intra-colonial variability of tissue thickness and differences in skeletal growth rates between rounded and flattened colonies: Skeletal growth rates in flattened and rounded colonies were examined for any possible features which could help explain possible intra-colonial differences in tissue thickness (there were none, see below). However, as flattened colonies were mainly found on steep slopes in deep water, comparisons between the two shapes were limited by the main effect of water depth and light levels driving the changes in skeletal growth patterns. This study found a strong positive correlation between extension rate and calcification rate ($r^2 = 0.65$ in shallow, 0.85 in deep water), which concurs with the findings of Lough and Barnes (2000). Density and calcification rate do not show a significant relationship, which again concurs with previous studies (Lough and Barnes, 2000). Extension rate and density are inversely

correlated, which means that extension is occurring at the expense of density increases (faster growing colonies are less dense, see also Lough and Barnes, 2000). Decreased growth rates with depth are commonly attributed to decreased light at depth (Barnes, 1973; Crabbe and Smith, 2003). Decreases in linear extension and calcification rates are, however, often accompanied with increases in skeletal density, but only if extension decreases relatively more than calcification (but see Guillaume, 1985 for studies that found no change in density with increasing water depth; Hughes, 1992). Other studies also found a non-linear increase of skeletal density with depth and an inverse relationship of linear extension and skeletal density (as seen here, see also Bosscher, 1993; Lough and Barnes, 2000). Hughes (1992) found massive corals to be the most porous and 'foliaceous' corals (which he described as flattened morphologies found in calm, deep waters) to be the most dense. In order to identify if water depth/light or growth form affect the differences in skeletal density between different water depths, skeletal growth rates of flattened colonies from shallow water should be examined in future studies.

This study found that tissue thickness was always thinnest on the edges of colonies and thickest on their summits, regardless of morphology or water depth (see Section 5.5.1.2, Fig. 34). Darke (1991) first mentioned decreasing tissue thickness from the summit to the sides of a colony. However, she examined mainly hemispherical, shallow water colonies. In totally flat colonies, no tissue increase is possible without peripheral budding which is mainly found on columnar and platey colony shapes (Graus and MacIntyre, 1976). Several studies have described the axis of

growth changing from vertical in rounded, to horizontal towards the seaward edge in flattened colonies (Dustan, 1975 and 1979; Hubbard and Scaturo, 1985). In this study it is shown that intracolonial patterns of tissue thickness remain the same, regardless of morphology, water depth or changes in growth axis. Other studies have also found differences between the summit and sides of coral colonies for various parameters: $\delta^{15}N$ (Heikoop *et al.*, 1998), micro-sporine amino acid (MAA) content (Muszynski *et al.*, 1998; Corredor *et al.*, 2000), and protein concentrations (Darke, 1991). The difference in protein concentrations between the summit and sides of a colony was thought to be related to differences in tissue thickness (Darke, 1991), which could also have driven the differences found in $\delta^{15}N$ and MAAs. To assess maximum values and retain consistency between samples in both, biochemical studies on tissue content and stress monitoring studies using tissue thickness, tissue should *always* be sampled from the upper summits of colonies.

Corallites become increasingly displaced into valleys as new corallites are initiated at the summit of a bump (Darke and Barnes, 1993). Tissue thickness was found to be significantly thicker at the summits of bumps than in valleys between bumps, where corallites became 'squashed' ($F_{(a)} = 38.034$, $p < 0.000$). At least one study found tissue thickness to remain the same between bumps and valleys of massive *Porites* colonies (Cohen and Hart, 1997). However, this could have been a remnant from sawing the colonies and tissue thickness falsely appearing thicker in colony valleys (see below). It has not previously been assessed if the pattern of changing tissue thickness with bumps and valleys differed between rounded

and flattened morphologies. Although tissue thickness differed significantly between bumps and valleys (by, on average 0.6 mm +/- 0.025 mm), both morphologies exhibited similar patterns of this variability. Tissue thickness should, therefore, always be sampled on top of a bump of a colony in order to reduce potential intra-colonial variability.

An additional problem when measuring tissue thickness on skeletal slices, is the large, up to 25% variability not only between bumps and valleys and between summits and sides, but also over very short distances over a skeletal slice. Skeletal architecture and differences in techniques and interpretations of dating skeletal slices were shown to introduce considerable errors into density banding studies (Barnes and Lough, 1990). In this study, large differences in tissue thickness were found between points separated by only 20 mm along skeletal slices, but the same relative variability was found in rounded and flattened morphologies. This large variability over small distances can mainly be attributed to not being able to cut a skeletal slice perfectly perpendicular to all axes of polypary growth (Monty Devereux, *pers. comm.*). A cut along a growth axis might give a tissue thickness of 5 mm. A cut 45 degrees from that growth axis will make tissue thickness appear to be nearly half as thick again – new thick = old thick*1/sin(45) = 5*1/.707 = 7.1 mm). This is why tissue thickness should be measured only where it seemed that a section passed close to the summit of a bump, which is a relatively easy visual judgement to make. Caution is needed if tissue thickness is measured from skeletal slices and several measurements should be taken to obtain an estimate of the intra-colonial variability of tissue thickness. If, however, small cores are drilled

from bumps of the summits of colonies and subsequently chiselled in half, they tend to break more perpendicularly to the growth surface than cuts and by sawing them. The sampling protocols used in this research are optimal to minimise intra-colony variability in tissue thickness due to sampling and measurement artifacts. These protocols should be adhered to in future studies using this tool in order to retain consistency in results and to enable comparisons between studies.

5.6.2. Colony size and tissue thickness: The difference in size classes examined in this study was not large enough to affect tissue thickness measurements. There was no correlation between tissue thickness and colony height under any circumstance. The correlation between tissue thickness and colony height in shallow round colonies (comparable to Barnes and Lough's (1992) colonies, see below) was less than 0.001. The height ranges examined by these authors, however, were significantly greater than those examined in this study (<99 mm to 8000 mm, versus 80-640 mm in this study). Also, in this study, reduced height was mainly associated with an encrusting morphology, which was largely found in deep water colonies. In all future tissue thickness studies, colonies of similar size classes should be chosen to reduce additional variability.

5.6.3. Colony morphology – links with tissue thickness and water depth. This study suggests that the ratio of colony height/colony circumference is the best quantitative descriptor of colony morphology. Both variables can be measured accurately and precisely *in situ*. It is, however, not a perfect value as it can not differentiate between all morphologies. It identifies only

encrusting forms to be significantly different from all other morphologies (Tukey's Post-Hoc HSD $p < 0.000$). A mathematical, quantitative descriptor for the large variety of morphological plasticity in massive *Porites* is still lacking. Separating different growth forms using qualitative descriptions was, however, sufficient to identify major patterns between environmental variables and the distribution of different shapes (e.g. Fig. 41). Tissue thickness did not vary with either qualitative or quantitative descriptions of different morphologies found on Lihir Island (see 5.5.3.2.). It also did not vary between rounded and encrusting growth forms at the same water depth and study site. Tissue thickness variability between water depths and study sites (as found in Chapter 4), is therefore, not related to different distributions of morphologies. It was important to exclude possible additional effects of morphological distributions on tissue thickness patterns. This was the first study that has examined the potential effects of the large phenotypic plasticity of massive *Porites* on tissue thickness.

5.6.4. Substrata slope as an indicator of colony morphology: In this study, growth form changed with substrata slope (see Section 5.5.4., Fig. 42) and both variables changed with water depth (Fig. 41 and 43). Hubbard and Scaturo (1985) also found high correlations between bottom slope and water depth. However, neither substrata slope nor growth form were responsible for changes in tissue thickness with increasing water depth (One-way ANOVA, $F_{(6)} = 1.936$, $p = 0.084$; see Fig. 44). Hence, although light seems to be the main factor driving tissue thickness changes, it may not be the only factor driving changes in colony morphology (see Fig. 44).

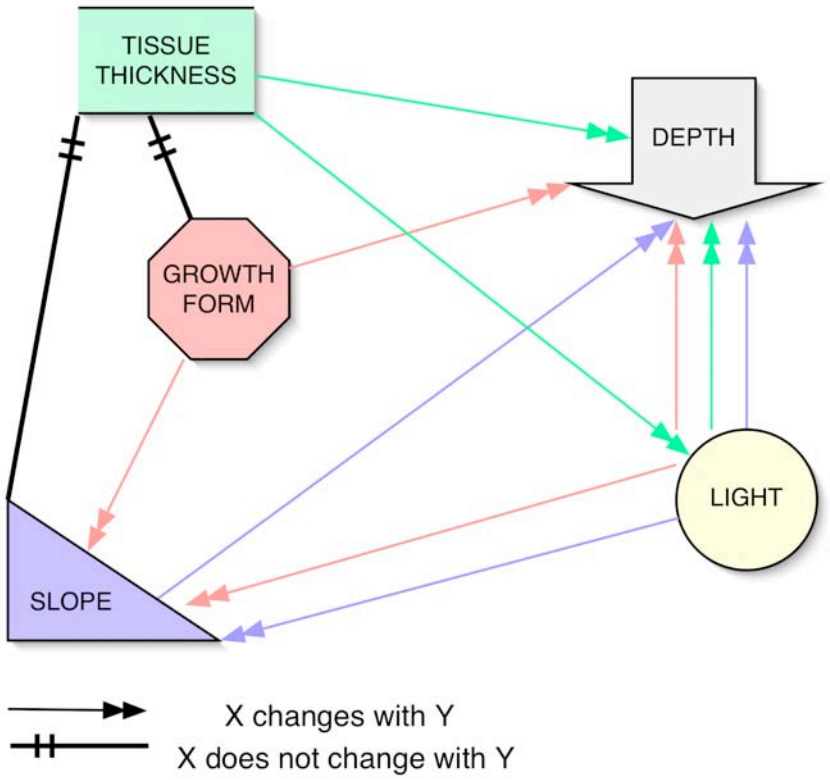



Figure 44. Diagram showing complexities of relationships between variables assessed in this study.

Water depth is known to be a dominant gradient over coral reefs, with associated changes in environmental variables such as turbulence, light and predation (Bak and Nieuwland, 1995). Coral colonies were often flatter with increasing depth (Bosscher and Meesters, 1992), which was usually linked to decreases in ambient light levels, rather than water depth (e.g. Barnes, 1973). However, light, although a dominant control, is not the only factor influencing morphological changes with depth (see Fig. 44; Bosscher and Meesters, 1992). Light is assumed to be stressful to corals from 0-15 m and only to become limiting around 40 m in clear waters (Chappell, 1980; Yentsch *et al.*, 2002). On the other hand, a sharp drop-off in growth rate was found to occur at 15 m depth by Hubbard and Scaturo (1985).

The flattened shape of massive colonies on deeper reefs could also be a growth response to limit chances of falling downslope (Brakel, 1976; Dollar, 1982; Done and Potts, 1992). Several studies found substrata slope to have an effect on both, colony growth rate and morphology (Hubbard and Scaturo, 1985; Edmunds, 1999). In addition, colonies on horizontal substrata were found to change their morphologies with increasing depth, whereas colonies on vertical substrata did not (Helmuth and Sebens, 1993). It may be physically impossible for colonies growing on vertical or steeply sloped substrata to grow into hemispheres or pyramids. First, their centre of gravity would topple them off the slope once a certain size is reached. Meroz *et al.* (2002) examined changes in polyp morphology with direction and intensity of the gravitational force and concluded that scleractinian corals can sense gravity, and that they adjust their morphology according to its direction and intensity (Meroz *et al.*, 2002). However, their research was undertaken on coral polyps and its implications have not yet been examined in adult colonies. Secondly, the undersurfaces of pyramids or hemispheres would not receive any light on steep slopes, leading to tissue death on undersurfaces and thus more encrusting shapes. In addition, increasing substrata slope is related to decreases in light levels (e.g. Heikoop *et al.*, 1998). Hence, these two environmental variables are intrinsicly linked and both should be examined as potential driving forces for phenotypic plasticity (see Fig. 44). This is particularly true where morphological variety has been found in depth regions where photoadaption occurred and nutritional needs were fulfilled (Sheppard, 1982). In this study, encrusting colonies were found at the same water depth but on greater substrata slopes than rounded shapes

(see 5.5.4). In clear water, in depths below 20 m, changes in morphology might therefore not exclusively result from the effect of diminished light and decreased photosynthesis (see also Vermeij and Bak, 2002), but also from self-shading and gravitational forces associated with increased substrata slopes. Additionally, the angle of the substrata slope was found to be the best indicator of changes in morphology (see 5.5.4). Problems comparing verbal morphological descriptions between studies may be reduced by providing substrata slope measurements for different morphologies. The relationship between substrata slope and coral morphology should be assessed in other locations and coral species to find a more comparable way of describing phenotypic plasticity in different studies.

## 5.7. SUMMARY OF RESULTS:

- Tissue thickness had large intra-colonial variability: between the summit and edges of a colony, between bumps and valleys of a colony and over small areas on a colony slice due to sawing artifacts. This variability did not differ in rounded and flattened colonies from different water depths.
- Skeletal extension and calcification rates were lower in flattened deep water than rounded shallow water skeletons. Skeletal density, however, increased with water depth and flattened morphology.
- Tissue thickness did not change with the colony sizes measured on Lihir Island.
- Tissue thickness did not change with either qualitative or quantitative descriptions of colony morphology.

- Colony morphology changed with water depth and was best described by the angle of the substrata slope. Tissue thickness did not change with substrata slope.
- Tissue thickness changes with depth and turbidity are mainly related to changes in light availability. Morphological changes with depth may be due to a combination of light levels and substrata slope.

Summary of aims of studies, importance of studies, methods, predicted and actual outcomes and comments.

| AIM | IMPOR-TANCE | METHOD USED | PREDICTED OUTCOME | ACTUAL OUTCOME | COMMENTS, FUTURE WORK |
|---|---|---|---|---|---|
| To examine natural intra-colonial ttl variability in rounded & flattened corals | If ttl variability differs between growth forms, can't compare ttl results of various shapes | Measured ttl in 2 shapes: Summit vs sides, bumps vs valleys, every 20 mm | Intra-colonial ttl differ due to different growth axes in round & flat shapes (from Dustan, 1975) | Intra-colonial variations in ttl were always the same | First study that compared intra-colonial ttl variability in different morphologies. Care needed when measuring ttl on skeletal slices |
| To assess natural variability of ttl with colony size | Size needs to be included as covariate or adjusted for if ttl changes with varying sizes | Size vs ttl regressions | ttl increases with colony height (from Barnes & Lough, 1992) | No relationship between ttl and the colony size classes measured on Lihir | No calibration necessary to avoid 'noise' due to coral size. But: always need to sample similar size classes |
| To assess if colony size can quantify various morphologies | To compare with other studies need quantifications of morphology | Plotted all sizes and size ratios vs qualitative morphologies | It will be hard to find a numerical value for all different shapes (Marshall, 2000) | Couldn't describe all 6 shapes. Height/ circumference best indicator | Found one quantitative indicator grouping some morphologies. Need to find way to quantify all different shapes |
| To assess natural variability of ttl with different morphologies | Depth effects on ttl maybe masked by changing coral shapes with depth | ttl vs all morphologial variables; ttl from round & flat colonies at same site & depth | ttl changes with colony morphology as shapes change with reduced light & ttl decreases with reduced light (from Chapter 4) | No relationship with ttl and all morphological variables. ttl of different shapes the same at same depth | Depth, rather than differing distributions of morphologies with depth is responsible for ttl changes with depth. No need to standardise for colony shapes |
| To examine the effect of substrata slope on colony morphology | To find another way describing different shapes to compare b/w studies | Estimated slopes of each colony. Plotted with depth, shapes & ttl | Substrata slope will drive changes in colony morphology (e.g. Hubbard and Scaturo, 1985) | Different shapes highly related to substrata slope. Slope increases with increasing depth | Substrata slope as best description for colony shape. Slope, depth and light have complex, interconnected relationship |

NB: ttl= tissue thickness; references depict speculations in the literature which these studies addressed. Arrows denote links between studies.

# 6.0. GENERAL DISCUSSION, CONCLUSIONS AND FUTURE RESEARCH

6.1. GENERAL DISCUSSION: The main aim of this project was to develop tissue thickness as a reliable tool to monitor coral stress response to turbidity gradients on Lihir Island, PNG. To achieve this end, several objectives had to be fulfilled:

1) the amount of natural variability in tissue thickness had to be determined;
2) the extrinsic and intrinsic factors influencing this variability had to be identified;
3) sampling procedures minimising or avoiding tissue thickness variability had to be devised.

The three previous studies fulfilled all these premises (for overview see Diagram below; for detailed descriptions see Table XXI). The extent of natural variability in tissue thickness was assessed and related to several extrinsic (the lunar month, water depth, study sites, time of year and year, turbidity, substrata slope) and intrinsic (intra-colonial variability between morphologies; colony size and shape) factors. The sampling protocols developed in this study minimised natural tissue thickness variability and maximised the value of tissue thickness as a tool to quantify turbidity stress response of massive *Porites*. The main factors which could not be accounted for by sampling protocols were large-scale climatic events over time, or localised physical, biological or chemical events which had different effects on individual colonies or study sites.

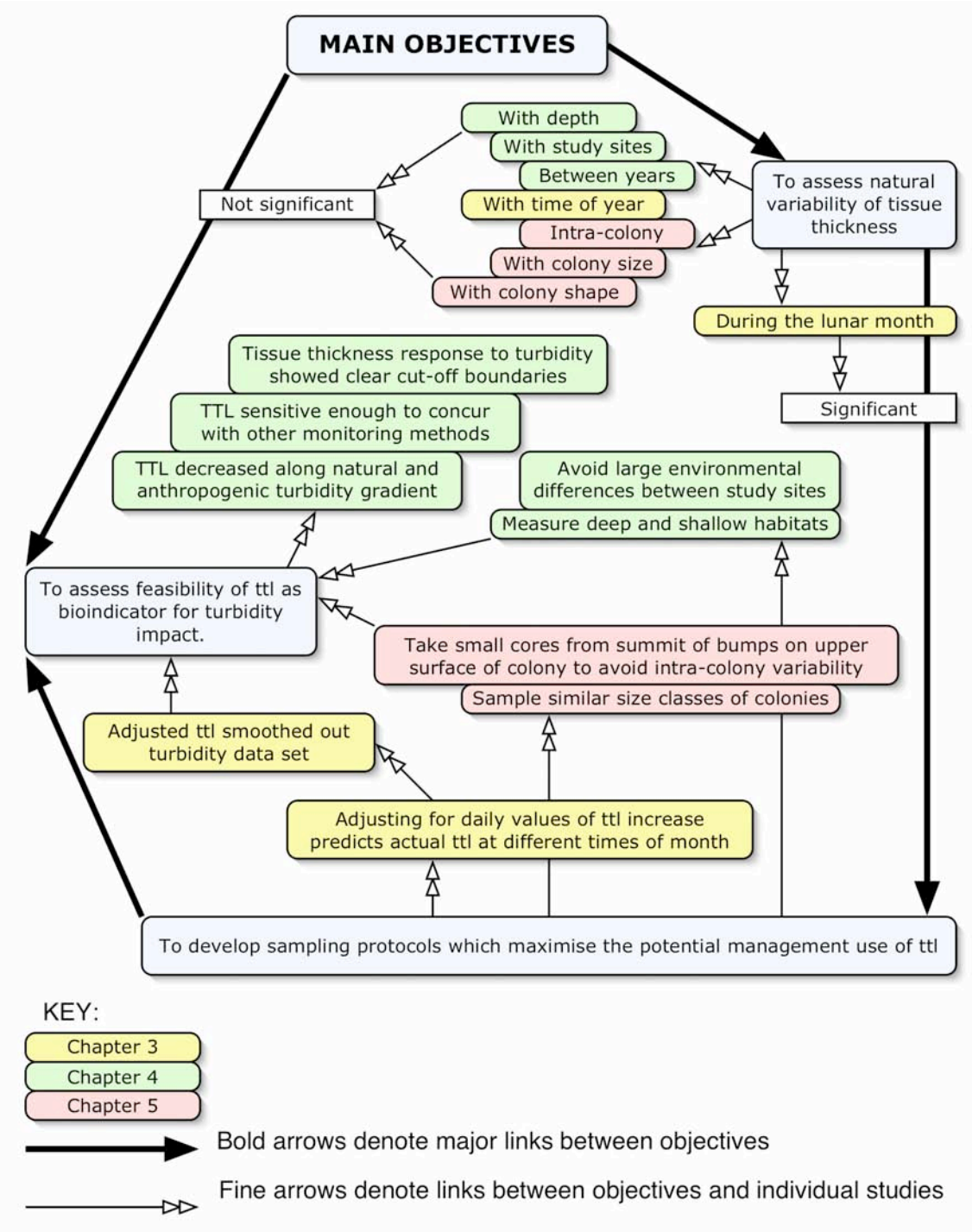



Diagram showing the main objectives of this project and how the three studies were linked to achieve each objective.

Table XXI. Detailed description of tissue thickness variability, factors responsible for the variability, sampling procedures used here to minimise natural variability, comments on the procedures and recommendations for future studies using this tool.

| AMOUNT OF TTL VARIABILITY | FACTORS RESPONSIBLE | SAMPLING PROCEDURE | OUTCOME, COMMENTS | FUTURE RECOMMENDATIONS, GAPS |
|---|---|---|---|---|
| 10-30% | Tissue uplift after full moon | Daily value of increase used to calibrate for time of sampling | Calibration tested; used successfully on large dataset. Very important to account for monthly variability | Calibration value may be different in other locations due to different growth rates. Should be assessed before starting any large-scale ttl sampling |
| 10-30% | Cessation of tissue uplift to preserve energy (due to stress, seasons or reproduction) | Corals with < 2.2 mm were not adjusted for monthly variability. | No uplift when ttl was lower than 2.2 mm. No seasonal variability on Lihir. No spawning during time of sampling | Reproductive periods for *Porites* have to be known, as tissue uplift is likely to stop. Large seasonal variability will also likely affect tissue uplift. Need to know both before using calibration |
| 30% | > 10mg/l turbidity, from natural and anthropogenic sources | Sampled different turbidity zones, identified impact boundaries | Turbidity impact identified by ttl corresponded well with turbidity and live coral cover indices | ttl is sensitive and real-time measure to indicate sediment impact. Its sensitivity to other stress factors stil needs to be assessed |
| Up to 40% | Water depth | Shallow and deep sites have to be distinct. But: depth gradients within sites have to be similar to reduce depth*site interactions | Depth calibration not needed as ttl did not change with depth within same depth regimes. Some study site variability when depth regimes were too different | Corals from similar depths need to be compared to avoid additional site variability. Deep water corals should always be studied as early warning indicators. Should examine ttl stress response to too much light, as suggested in 4 deep sites between 2002 and 2003 |
| Up to 40% | Time | Sampled ttl in same corals over 3 years | General patterns similar, turbidity response similar. But some localised variability | It will never be possible to assess all environmental influences on individual study sites and colonies. Background knowledge on large environmental changes needed |
| Up to 50% | Summit to Sides | Always sampled on summits | Important finding that large intra-colonial dfferences did not change with morphologies | Any study assessing tissue content or ttl needs to sample from coral summits for maximum values. If using skeletal slices, ttl variability over small areas due to sawing artifacts needs to be accounted for |
| ~ 20% | Bumps and Valleys | Always sampled on top of bumps | | |
| Up to 25% | Sawing artifacts | Took cores and chiselled them | | |
| Not significant | Colony size and shape | Sampled similar size classes. Quantified growth forms | Although growth form distributions differ with study sites and depths, they don't affect ttl | Complex relationships between slope, light and depth and how they effect phenotypic plasticity still needs to be unravelled |

Reduction in tissue thickness mobilises tissue and energy reserves. Hence, tissue thickness above the required minimum may be seen as a resource that can be used in times of stress. Monthly average tissue thickness may indicate the relative performance of a coral colony in any given month, making it a powerful monitoring tool for the assessment of relative impacts of stressors on corals. Monitoring of *Porites* for tissue thickness by

removing small skeletal cores is, essentially, a non-destructive technique since concrete plugs used to fill the core hole were quickly overgrown by coral tissue. In comparison with other monitoring methods for sediment stress on coral reefs, tissue thickness is simpler, cheaper and indicates that changes are occurring. Most other monitoring procedures used on reefs detect change only after it has been damaging or fatal. Tissue thickness monitoring is a procedure suitable for use in developing countries because it does not require specialist equipment or expertise. In addition, local communities can easily be taught how to use tissue thickness to assess the status of their surrounding reef. Tissue thickness has immense potential to function as a universal indicator of coral and reef response to a variety of anthropogenic and natural environmental concerns.

## 6.2. SUMMARY OF RESULTS:

1. In studies at Lihir Island, PNG, tissue thickness decreased, on average, by 20% immediately after the full moon. This was due to uplift of the base of the tissue layer.
2. Tissue uplift after the full moon occurred at different times of the year, in different years, at different water depths and different locations.
3. Tissue uplift ceased when tissue thickness decreased to around 2.2 mm. It resumed when tissue depth increased above this level.
4. The average daily increase in tissue thickness after tissue uplift was ~0.3 µm per day.
5. Tissue thickness was reduced by a third at Lihir Island when turbidity increased above 10 mg $l^{-1}$.

6. Tissue thickness was significantly reduced by naturally and anthropogenically elevated turbidity. There was no evidence for increased sedimentation on coral reefs around Lihir Island.
7. Changes in tissue thickness indicated that mining activities affected coral communities over smaller areas than predicted in the environmental impact statement (NSR, 1989).
8. Tissue thickness was up to 40% thinner in deep than in shallow water.
9. Tissue thickness was highest on top of bumps at the summits of colonies. This pattern was similar in different morphologies.
10. Tissue thickness varied between 20 mm distances along a colony slice, mainly due to sawing artifacts.
11. Tissue thickness did not change with colony size, colony morphology or substrata slope.
12. Variations in morphology were best described by angles of substrata slopes.

## 6.3. FUTURE RESEARCH:

- Detailed analyses of changes in biochemistry and histology with tissue uplift following the full moon should be undertaken to determine the exact processes involved.
- The exact connection of tissue thickness and dissepiment formation should be assessed by investigations of procedures by which tissue thickness can be recovered from the internal structure of coral skeletons. This would allow recovery of past values of tissue thickness in modern and fossil corals. This would make possible studies of natural and unnatural variations in environments over

time scales from months to centuries. It would also make it possible to carry out “before and after” studies after an event has occurred.

- Investigations of the links between skeletal extension rates and amounts of tissue uplift should be undertaken.
- Assessment of what happens to colonies once tissue thickness has been reduced to a minimum level and how long it takes until sufficient energy is available for resumption of tissue uplift. In addition, once corals reach minimum tissue levels, a stressor’s cut-off level between colony death or survival, should be quantified.
- Daily values of tissue increase during a lunar month in other localities should be determined to see if calibration values need to be adjusted for different areas. Tissue uplift response to gametogenesis and seasonal variability have to be assessed.
- Tissue thickness should also be examined in species other than massive *Porites*, preferably in more sediment intolerant genera in order to get even earlier warning of stress factors affecting the corals.
- Tissue thickness was found to respond to shading (True, 1995), sediment accumulation and burial (Barnes and Lough, 1999) and natural and anthropogenic transitional levels of turbidity (this study). The response of tissue thickness to other natural and anthropogenic stressors should also be assessed in order to determine the universal usefulness of this method.

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# APPENDIX A.

# Study site descriptions and photographs

NB on all following pages:

TSS = total suspended solids

SSC = suspended sediment concentration

★ = Approximate location of study site

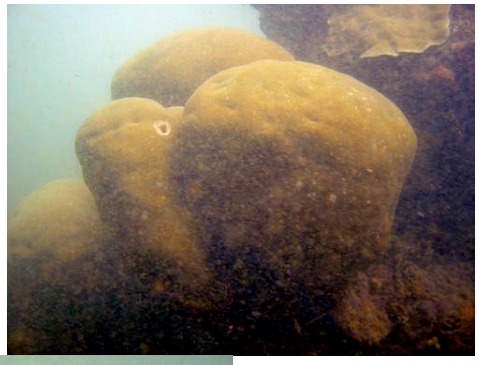
## KAPIT I
(measured in 2002 & 2003)

Impact zones: Predicted by NSR (1989): Severe (median TSS 100mg/L)
Actual measurement (Thomas, 2003): Transitional (15-30mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): Impact

Visual observations: Even on a sunny day without obvious surface plume, very bad visibility (<1.5m), large amounts of sediment particles in the water column, thin layer of sludge and rubble on bottom. Main coral genera found were *Millepora* and massive *Porites spp*. Fair amount of algal cover, but not much accumulated sediment on dead coral surfaces. Patchy coral cover but several large bommies of massive *Porites*. Corals measured between 8.6-4m depth.

Location/Topography: Approximately 50m from road, directly in front of Kapit 6 creek outfall, first bit of continuous reef on north side of Luise Harbour. Gentle sandy slope, bottoms out at around 10m depth. Severine Thomas' nephelometer unit is deployed here. Faces SE.

Kapit 6 creek outfall with processing plant



## KAPIT II
(measured in 2002 & 2003)

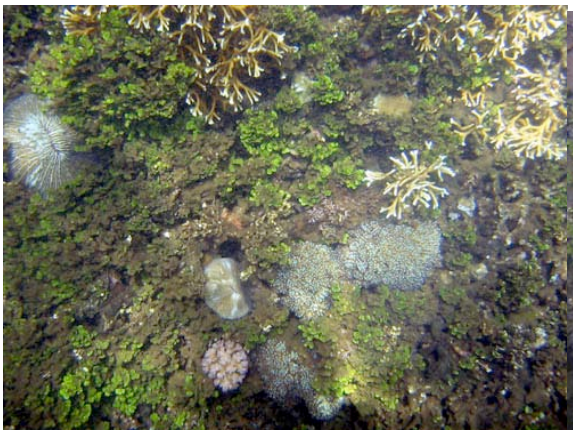
Impact zones: Predicted by NSR (1989): Severe (median TSS 100mg/L)
Actual measurement (Thomas, 2003): Transitional (15-30mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): No Impact
measured but regarded as 'impact zone' in analysis

Visual Observations: approximately 2m visibility with apparent surface plume, fair amount of sediment in water column and thin layer of sludge on the bottom. Many massive *Porites* bommies, a lot of them overturned (anchor damage?), lots of *Millepora*, several fungiids and bubble corals, algae. Corals measured between 9-3.7m depth.

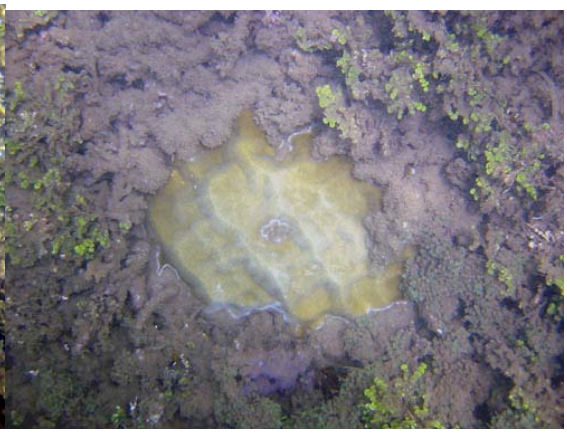
Location/Topography: Approximately 80m from road, directly in front of Kapit 5 creek outfall and situated on the outer border of a sacred site. Kapit village is located in front of this reef. Gentle sandy slope, bottoms out around 9m depth. Faces SEE.

View towards Kapit village, visible plume

Kapit 5 creek outfall, view to processing plant



Bubble corals, *Millepora*, fungiids and algae



Massive *Porites* with surrounding sediment

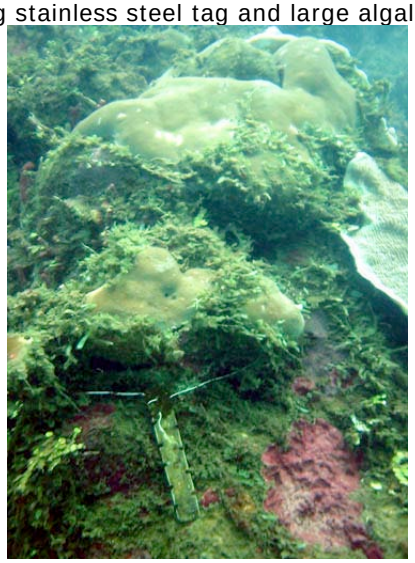
## KAPIT III
(measured in 2001, 2002 & 2003)

Impact zones: Predicted by NSR (1989): Severe (median TSS 100mg/L)
Actual measurement (Thomas, 2003): Transitional (15-30mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): Impact

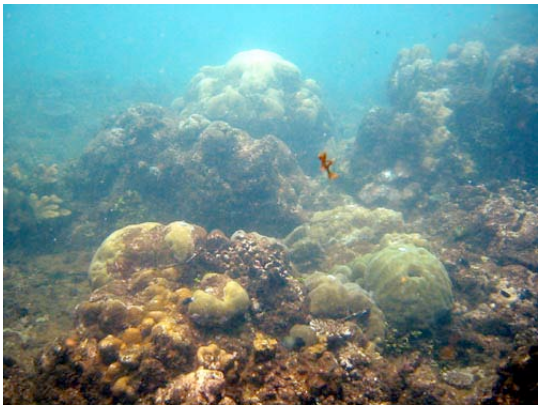
Visual observations: SHALLOW: without plume around 10m viz, little sediment in the water column, right next to NSR coral transect starpicket, quite a lot of algae. Colonies measured between 5-4.2m depth.
DEEP: very steep slope, poor viz (5m), many algae, dead corals and branching coral rubble. Healthy-looking fungiids, foliose corals and flattened *Porites.* Sediment on dead corals. Colonies measured between 20-14.5m.

Location/Topography: Approximately 150m from road, on sediment and coral monitoring site. Approximately 75 degree slope from 5m depth. Faces E. NSR coral monitoring and Severine Thomas sediment monitoring site.

Kapit III deep showing stainless steel tag and large algal cover



Location of Kapit III reef, NSR monitoring site



Both Kapit III shallow sites showing several species of corals, but large partial mortality, algal cover and sediment particularly on dead coral surfaces.

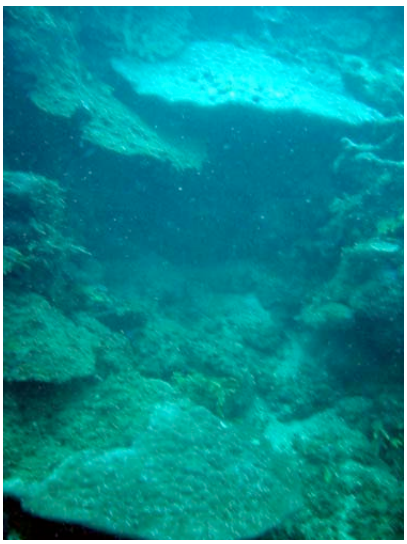
## KAPIT IV
(measured in 2002 & 2003)

Impact zones: Predicted by NSR (1989): Severe (median TSS 100mg/L)
Actual measurement (Thomas, 2003): Minor (SSC ≤ 10mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): No impact

Visual Observations: SHALLOW: little sediment in water column, around 10m viz, very patchy reef - very diverse parts with high live coral cover interspersed by patches of dead corals and algae. Measurements between 11-5.5m depth.
DEEP: Around 10m viz without surface plume, some sediment particles in water column, lots of sediment, algae and dead corals, not many *Porites*.

Location/Topography: Approximately 100m from little point, ~60 degree slope, faces NEE.

Location of site just opposite small point



Deep water site showing sediment

Shallow water sites showing different coral species but algal cover and some partial bleaching

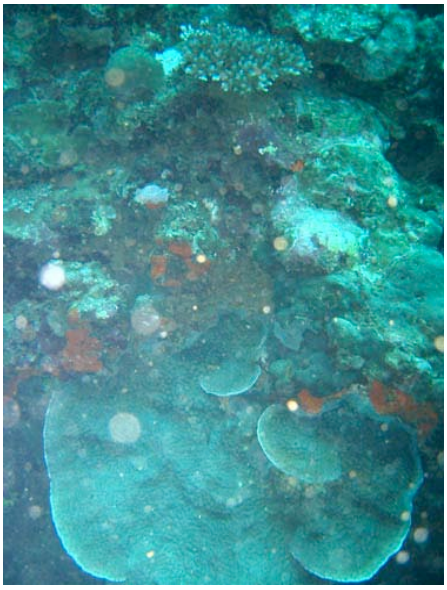
## KAPIT V
(measured in 2002 & 2003)

Impact zones: Predicted by NSR (1989): Severe (median TSS 100mg/L)
Actual measurement (Thomas, 2003): Minor (SSC ≤ 10mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): No impact

Visual observations: SHALLOW: 20m viz below surface plume (only about 5m in 0.5m depth), large stands of branching acroporids, no sediment, very few algae. Measurements between 5.3-4.6m depth.
DEEP: few sediment particles, fair amount of sediment on slope, about 15m viz. Measurements between 24-14m depth.

Location/Topography: Extremely steep drop-off around 90 degrees. Approximately 80m in front of small village. Severine Thomas nephelometer and light meter deployed here. Faces NE.

Deep Kapit V sites showing steep drop-off, vertically flattened morphologies and sediment cover



Kapit V shallow reef with great visibility and large diversity of species and live coral cover

## KUNAIYE
(measured in 2001, 2002 & 2003)

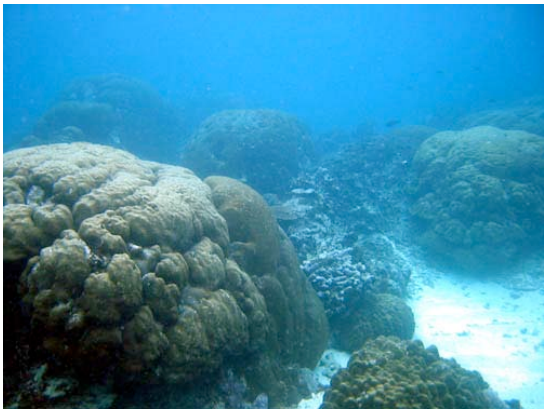
Impact zones: Predicted by NSR (1989): Minor (median TSS <5mg/L)
Actual measurement (Thomas, 2003): Background (SSC 3mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): No impact

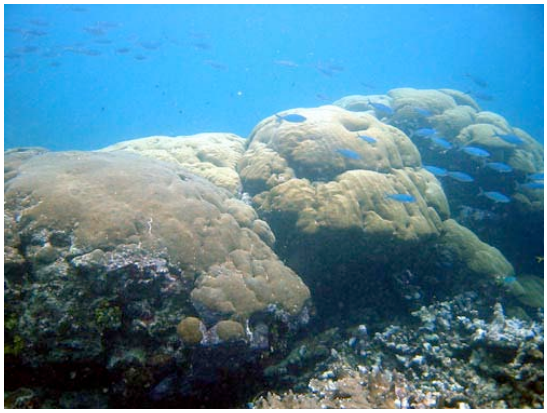
Visual observations: SHALLOW: Lots of rubble and branching corals, no *Porites* than there is a big sandy patch where very large massive *Porites* bommies are concentrated. Very strong swell between bommies, good viz ~20m. Measurements between 5.4m and 3.6m depth.
DEEP: ~20m viz, many massive colonies not that many *Porites*, lots of milleporids and *Halimeda* algae. Measurements between 24m and 16m.

Location/Topography: Very wide gentle sloping reef flat, only around 30 degree slope towards deep site, steep drop-off at around 25m. Site right in front of Kunaiye church and school. Faces E.

Kunaiye study site in front of church

Kunaiye deep with sandy slope





Kunaiye shallow massive *Porites* bommies around sandy patch

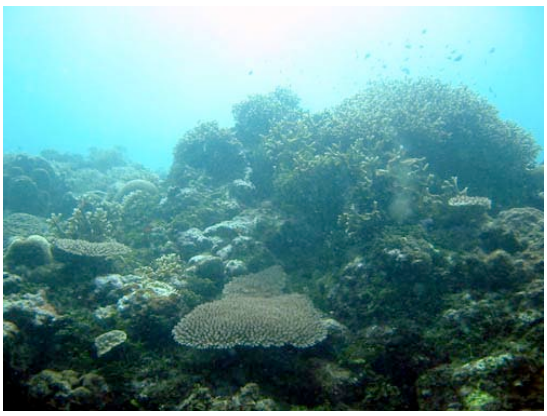
## LAKUNBUT
(measured in 2001, 2002 & 2003)

Impact zones: Predicted by NSR (1989): Minor (median TSS 10mg/L)
Actual measurement (Thomas, 2003): Minor (SSC ≤ 10mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): No impact

Visual observations: SHALLOW: Good coral reef, first metre bad viz due to freshwater run-off from creek, not too many particles in water column. Measurements between 3.4m and 2.6m depth.
DEEP: not much sediment in water column, good viz ~20m. Sewage outfall at 35m depth. Measurements between 23m and 11m depth.

Location/Topography: situated in small bay near sewage outfall. Extremely sharp drop-off at 4m depth, another drop-off at 25m depth. Faces E.

Lakunbut study site looking towards hotel on top of cliff



Lakunbut deep reef looking up steep slope

Lakunbut shallow reef flat

MALI ISLAND (NSR control site)
(measured in 2001, 2002 & 2003)

Visual Observations: SHALLOW: 25m viz, strong swell in shallow regions from about 10m upwards, reef quite sparse on upper flat but very good on crest and slope, therefore fairly deep measurements from 8.2m-7.3m
DEEP: *Halimeda* algae make up main part of sediment, some particles in water column, some rubble, 15m viz. Lots of fungiids on slope. Measurements from 22-14m depth.

Location/Topography: On NSR monitoring site, very narrow reef flat only about 25m wide, really steep 80 degree slope, faces SW.

Mali Island study site

Shallow reef flat with NSR star picket

Deep slope at Mali Island

## MASAHET ISLAND
(measured in 2001, 2002 & 2003)

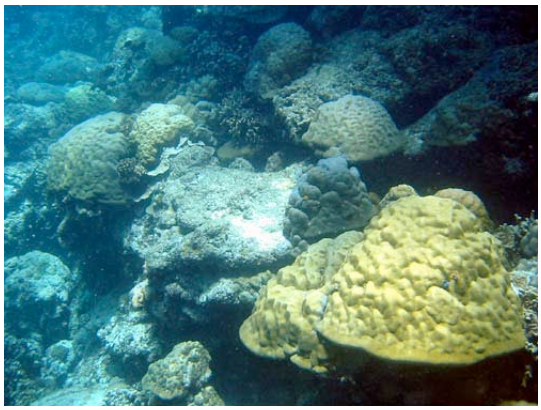
Impact zones: Predicted by NSR (1989): Control (median TSS <5mg/L)
Actual measurement (Thomas, 2003): Oceanic (SSC ~3mg/L)
Biological impact on *Porites* tissue thickness: No impact

Visual Observations: SHALLOW: Very good viz 25m+, very good reef, some rubbish on sand slope next to reef. Measurements between 6.4-4.8m.
DEEP: Lots of rubble, foliose and branching corals, some soft corals, hardly any sediment in water column, some reef slips with sandy patches. Measurements between 15-11.5m depth.

Location/Topography: Situated in little cove called Lamue, very sheltered, narrow reef flat, steep slope of 75 degree angle. Deep site further east from shallow side on point of cove. Faces SWW.

Lamue cove on Masahet Island

Deep reef at Masahet Island



Shallow site with many massive *Porites*

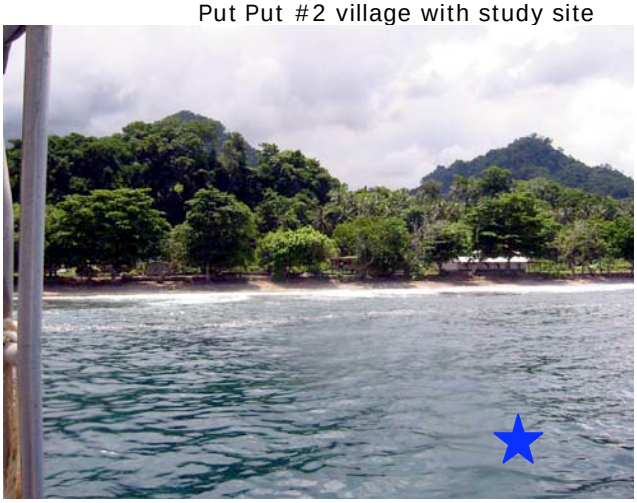
## PUT PUT #2
(measured in 2001, 2002 & 2003)

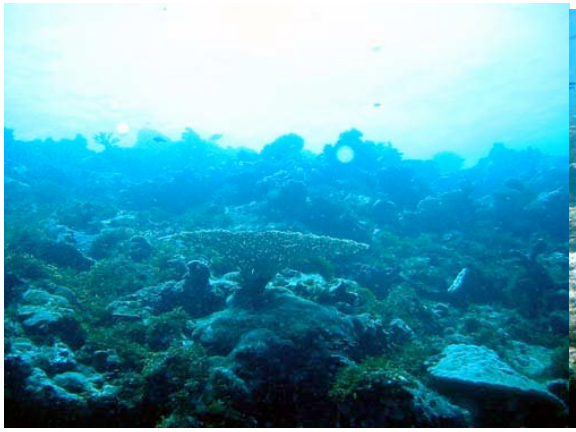
Impact zones: Predicted by NSR (1989): Minor (median TSS 10mg/L)
Actual measurement (Thomas, 2003): Minor (SSC ≤ 10mg/L)
Biological impact on *Porites* tissue thickness: No impact

Visual Observations: SHALLOW: Visibility around 20m, some sediment in water column, lots of dead substrata and some algae, many massive corals but not many *Porites spp.* Measurements between 10-5.2m depth.
DEEP: Many *Porites*, many acroporids, big ridge and sudden large patches of *Halimeda* algae. Extremely good visibility of around 30m+. Measurements between 23m to 14m depth.

Location/Topography: In front of PutPut #2 village, about 50m from beach. Reef flat slightly sloping, then steep drop-off around 75 degrees. On NSR sediment monitoring site. Faces E.

Put Put #2 village with study site





Deep site looking up slope

Shallow reef flat, some algae good coral cover

## PUT PUT POINT
(measured in 2001, 2002 & 2003)

Impact zones: Predicted by NSR (1989): Severe (median TSS 100mg/L)
Actual measurement (Thomas, 2003): Minor (SSC ≤ 10mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): Impact

Visual observations: SHALLOW: Bad visibility <5m with surface plume, 10m+ on days without plume, good reef flat, lots of acroporids, table, branching and foliose growth forms not that many massive *Porites*. Not much sediment in water column, not much sediment accumulated on bottom. Corals measured between 4.8-3.7m depth.
DEEP: Lots of rubble, sand and algae, many dead corals. Huge vase like sponges, fungiids and many small, flattened *Porites*. Steep slope about 75 degrees. Viz ~5m. Corals measured between 19.4-14m depth.

Location/Topography: Large reef flat, approximately 500m wide before sloping off. Shallow site on NSR monitoring site, deep site a little further down the reef edge. Very strong tidal swell in shallow study site. Faces NNE.

*Porites* corals at PPP deep study site, note algae encroaching and some sediment

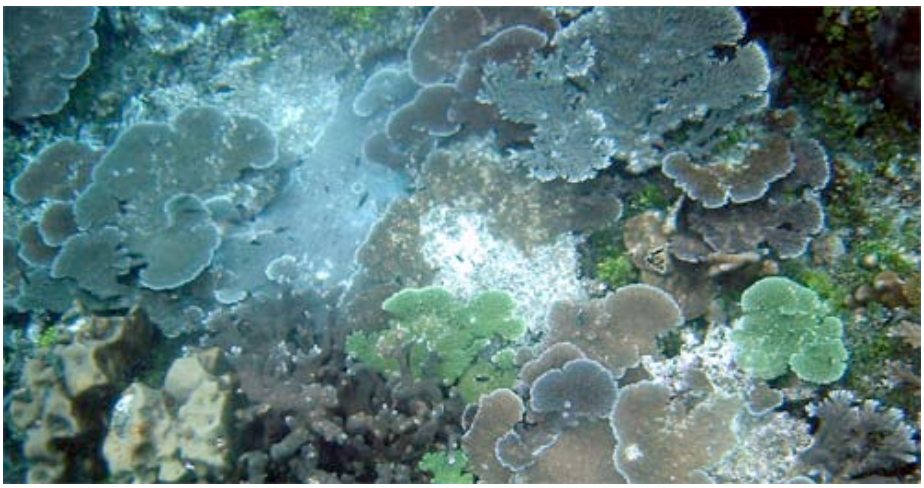
PPP shallow reef

## PUT PUT
(measured in 2002 & 2003)

Impact zones: Predicted by NSR (1989): Transitional (median TSS 25mg/L)
Actual measurement (Thomas, 2003): Minor (SSC ≤ 10mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): No impact

Visual observations: SHALLOW: 25m visibility, not many particles in water column, good variety of corals, corals measured between 10.5m and 6m depth.
DEEP: 25m viz, no sediment in water column, corals measured between 23.5m and 13m depth.

Location/Topography: very steep 70 degree slope, reef flat about 40m wide. Between PutPut Point and PutPut #2, study site in front of PutPut village. Slope bottoms out to sandy flat around 35m depth. Faces E.



Put Put deep reef with foliose and branching acroporids.

Put Put shallow reef flat

## SANAMBIET
(measured in 2001, 2002 & 2003)

Impact zones: Predicted by NSR (1989): Control (median TSS <5mg/L)
Predicted by Thomas (2003): Background (SSC 3mg/L)
Biological impact on *Porites* tissue thickness (Chapter 4): Impact

Visual observations: On first part of reef all *Porites* were dead and buried in sediment. Occasional small bommies on sand bank, some branching acroporids. <10m viz, sediment in water column. Measurements between 4.4m-3.4m depth

Location/Topography: situated in lagoon between Sanambiet and Mali Island. Large sand bank, long, gentle slope bottoms out at around 9m depth. Faces S.

Sanambiet lagoon

Shallow reef with many massive *Porites* bommies

# APPENDIX B:

# Table I: Examples of studies of lunar effects on marine animals

**Table I. Summary of literature from 1985-2002 with regards to lunar effects on various marine animals.**

| LUNAR EFFECT | SPECIES STUDIED | COMMON NAME | LUNAR PHASE | REFERENCE |
|---|---|---|---|---|
| COMMUNITY LEVEL<br><br>Increased abundance | *Penaeus plebejus* | Eastern king prawns | New Moon | (Griffiths, 1999) |
| | several | Reef fishes | New & Full Moon | (Kingsford and Finn, 1997) |
| | | | Full Moon | (Letourneur, 1996) |
| Increased larval abundance | several | Reef fishes | New Moon | (Rooker *et al.*, 1996) |
| | *Loimia meduas* | Polychaetes | | (Seitz and Schaffner, 1995) |
| REPRODUCT-ION & RECRUITMENT | *Montastrea cavernosa* | Scleractinian coral | Full Moon | (Acosta and Zea, 1997) |
| | *Pocillopora verrucosa* | | New Moon | (Fadlallah, 1985) |
| | *Porites astreoides* | | | (McGuire, 1998) |
| | 85 species | | Full Moon | (Hayashibara *et al.*, 1993) |
| Sexual Reproduction | *Fungia scutaria* | | | (Kramarsky-Winter and Loya, 1998) |
| | *Bohadschia argus*<br>*Euapta godeffroyi*<br>*Actinopyga lecanora*<br>*Bohadschia graffei* | Sea cucumbers | Lunar periodicity | (Babcock *et al.*, 1992) |
| | *Polycheira rufescens* | | Full & New Moon | (Kubota and Tomari, 1998) |
| | *Globigerinoides sacculifer* | Planktic foraminifer | Full Moon | (Bijma and Hemleben, 1994) |
| | *Tenulosa macrura* | Tropical shad | New & Full Moon | (Blaber *et al.*, 1999) |
| | *Centrostephanus rodgersii* | Sea urchin | Lunar periodicity | (Byrne *et al.*, 1998) |
| | *Evechinus chloroticus* | | Full Moon | (Lamare and Stewart, 1998) |
| | *Paramuricea clavata* | Gorgonian coral | Full Moon | (Coma *et al.*, 1995) |
| | *Xestospongia bergquistia*<br>*X. exigua*<br>*X. testudinaria* | Sponges | Lunar phase | (Fromont and Bergquist, 1994) |
| | *Dascyllus aruanus* | Damselfish | Full & New Moon | (Mizushima *et al.*, 2000) |
| | *Chaetodon trifasciatus* | Butterflyfish | | (Yabuta, 1997) |
| | *Helice tridens* | Mud-flat crabs | Semilunar | (Omori *et al.*, 1997) |
| | *Parozanthus parasiticus* | Zoanthid coral | Full Moon | (Ryland, 1997) |
| Brooding & larval eclosion | *Chasmagnathus granulata* | Crabs | Lunar cycle | (Greco and Rodriguez, 1999) |
| Increased gonadal development | *Porites lobata* | Scleractinian coral | Full & New Moon | (Glynn *et al.*, 1994) |
| Settlement | *Stegastes spp*<br>*Chromis spp* | Damselfish | Lunar periodicity | (Booth and Beretta, 1994) |
| | 46 families | Reef fish | | (Dufour *et al.*, 1996) |
| | *Collinectes sapidus* | Blue crabs | | (Morgan *et al.*, 1996) |
| | *Thalassoma bifasciatum* | Pelagic fish | | (Robertson, 1995) |
| | *Merluccius bilinearis* | Silver hake | | (Steves and Cowen, 2000) |
| GROWTH<br>Sub-bands within statoliths | *Ancistrocheirus leseurii* | Squid | Lunar cycle | (Arkhipkin, 1997) |
| Fine density bands | *Porites spp* | Massive corals | Full Moon | (Barnes and Lough, 1989) |
| Dissepiment uplift | *Porites spp* | Massive corals | Full Moon | (Barnes and Lough, 1992; Barnes and Lough, 1993)<br>(Taylor *et al.*, 1993)<br>(True, 1995) |
| Migrogrowth banding pattern | *Semimytilus algosus* | Chilean mussel | Spring-neap lunar cycle | (Abades *et al.*, 2000) |
| BEHAVIOUR | | | | |

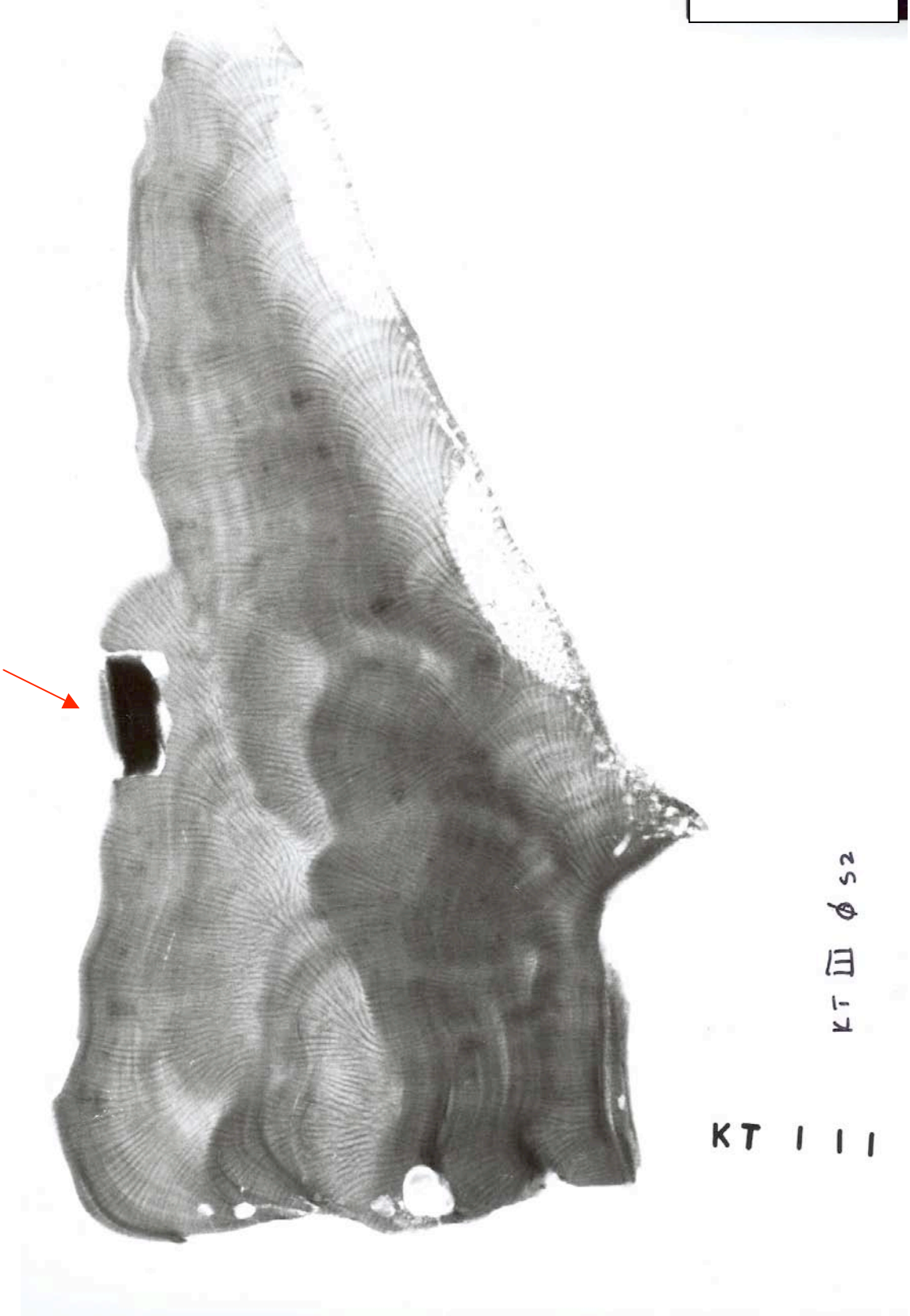
| | | | | |
|---|---|---|---|---|
| Mucus sheet production | Porites furcata | Scleractinian coral | Full Moon | (Coffroth, 1985) |
| Reduced risk of predation | *Panuliris argus* | Spiny lobster | New Moon | (Acosta and Butler, 1999) |
| Decreased diving activity and body mass losses | | Galapagos fur seals | Full Moon | (Horning and Trillmich, 1999) |
| Greater activity | *Oronectes virilis*<br>*Oronectes propinquus* | Crayfish | New Moon | (Mitchell and Hazlett, 1996) |
| Spatial aggregations | *Holothuria scabra* | Sea cucumber | Full Moon | (Mercier *et al.*, 2000) |
| Less vertical migration | 5 *Hygophym* species | Lanternfish | New Moon | (Linkowski, 1996) |

# APPENDIX C:

## Photographs of X-ray positives from 5 corals from Kapit III deep

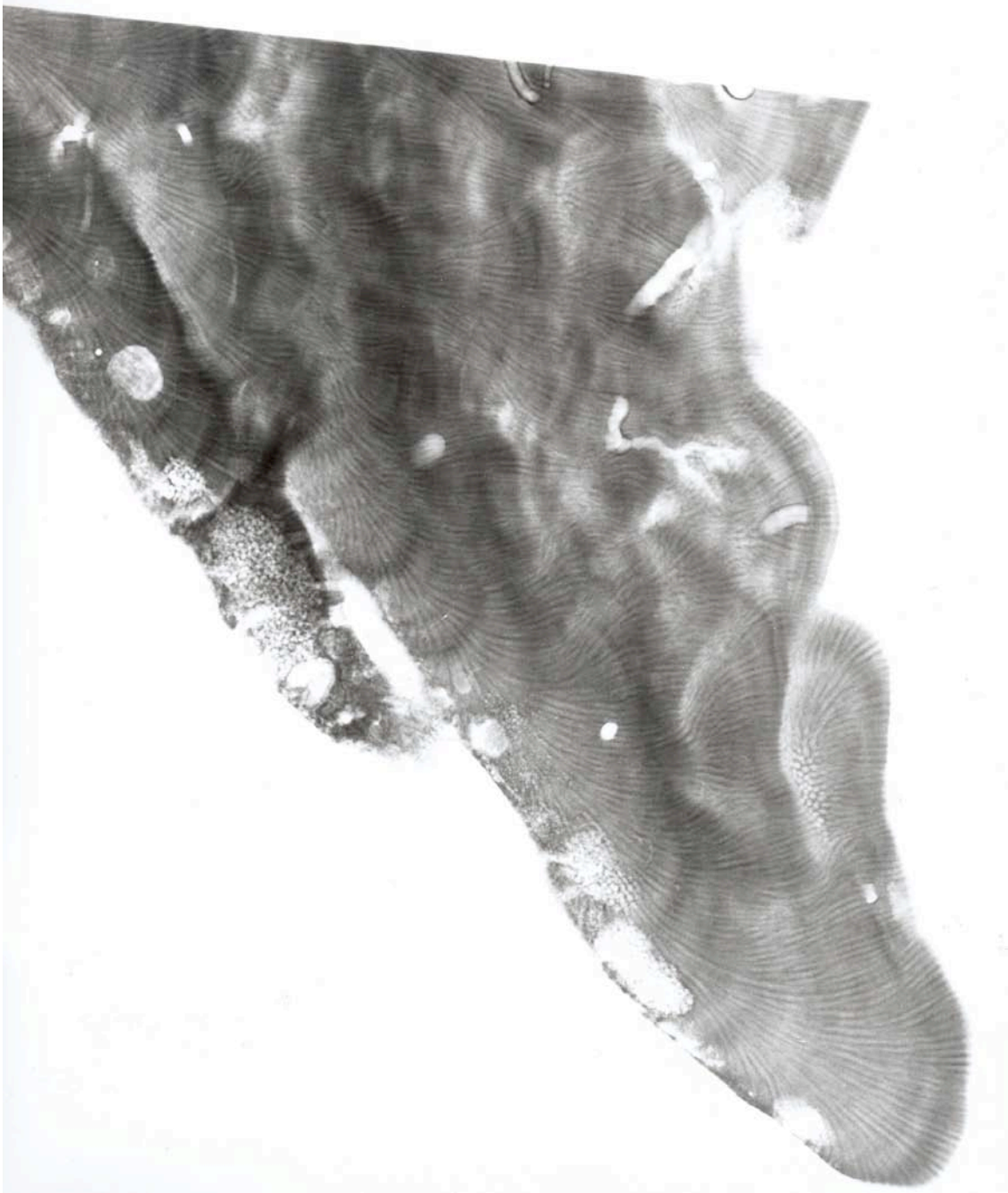
## (KT III 0, 3, 4, 7 and NKT III)

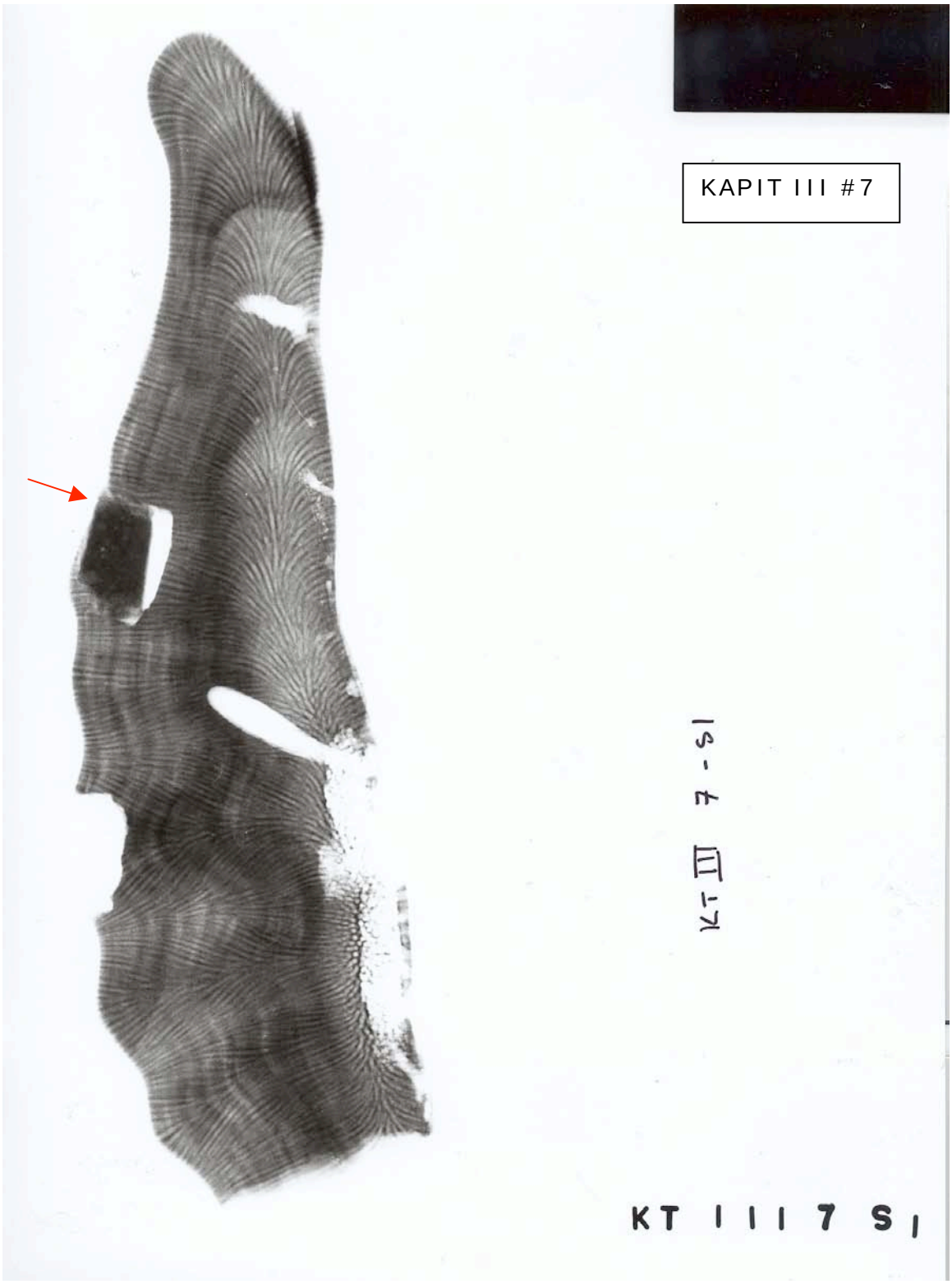
NB: The numbers following abbreviations for study sites are the identifications of colonies studied over time. ‘N’ identifies new colonies, which had not been sampled for tissue thickness earlier in this project.

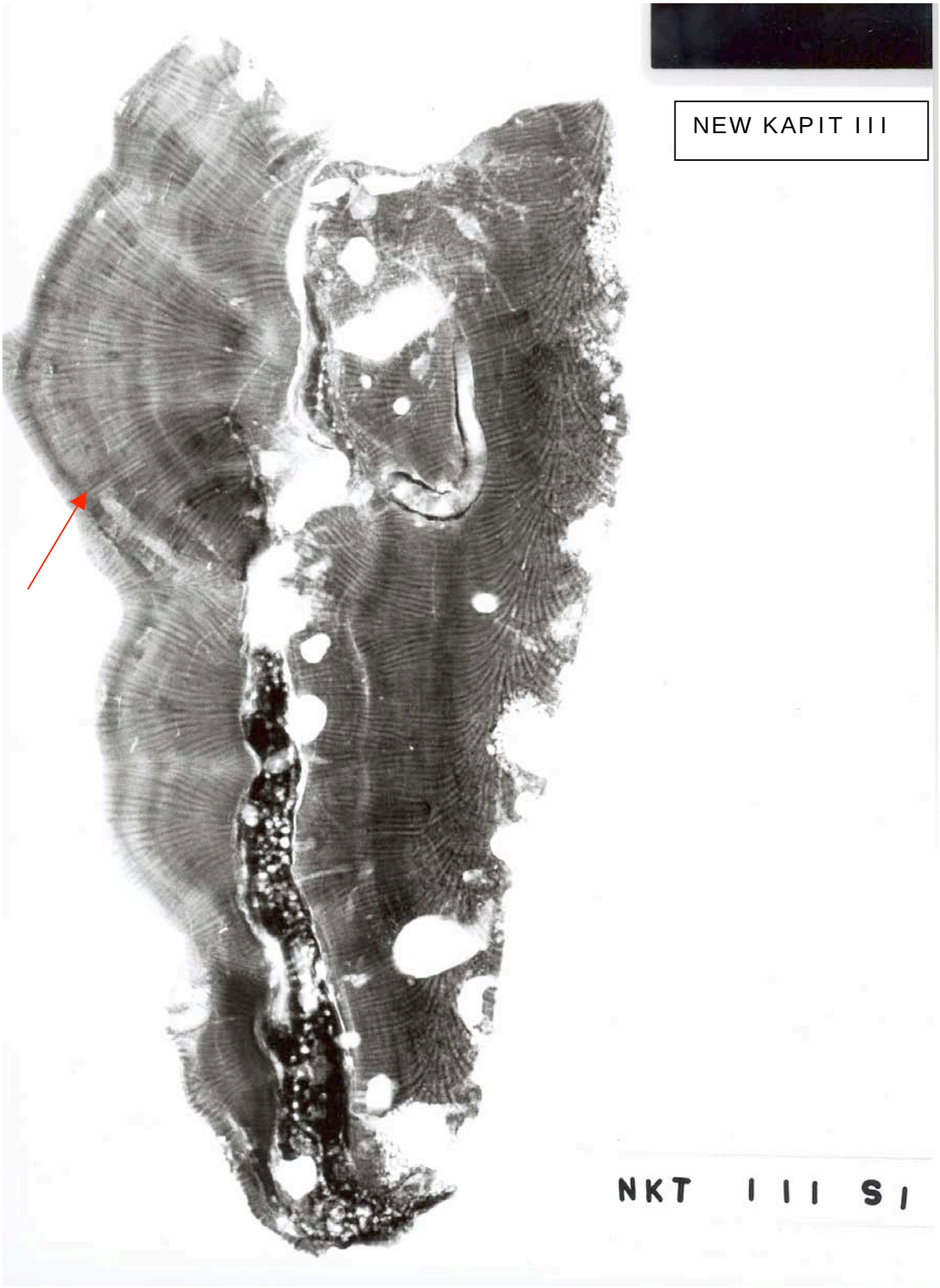

KT III Φ S2
KT III


KAPIT III #3

KAPIT III #4




KAPIT III #7
KT III 7 - s1
KT III 7 S1


NEW KAPIT III
NKT III S1

# APPENDIX D:

# Sample size calculations

From: Marine Ecology Handbook, MB 2060. 1996. Department of Marine Biology, James Cook University. Lab 3, Tute 3. Compiled by Uschi Kaly. 51pp.

FORMULA USED FOR CALCULATING SAMPLING SIZE TO A PRECISION VALUE OF p=0.05:

$$p = S.E. / \chi$$

p=precision

S.E. = Standard error calculated from (Standard deviation(tissue thickness of 10 colonies)/Square root (10))/$\chi$

$\chi$= Mean