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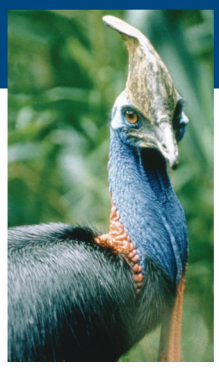
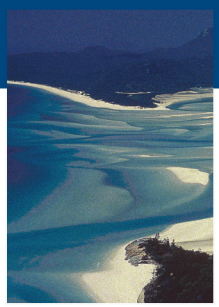
Candidate Bioindicator Measures to Monitor Exposure to Changing Water Quality on the Great Barrier Reef

Katharina Fabricius, Sven Uthicke, Tim Cooper, Craig Humphrey, Glenn De'ath and Jane Mellors

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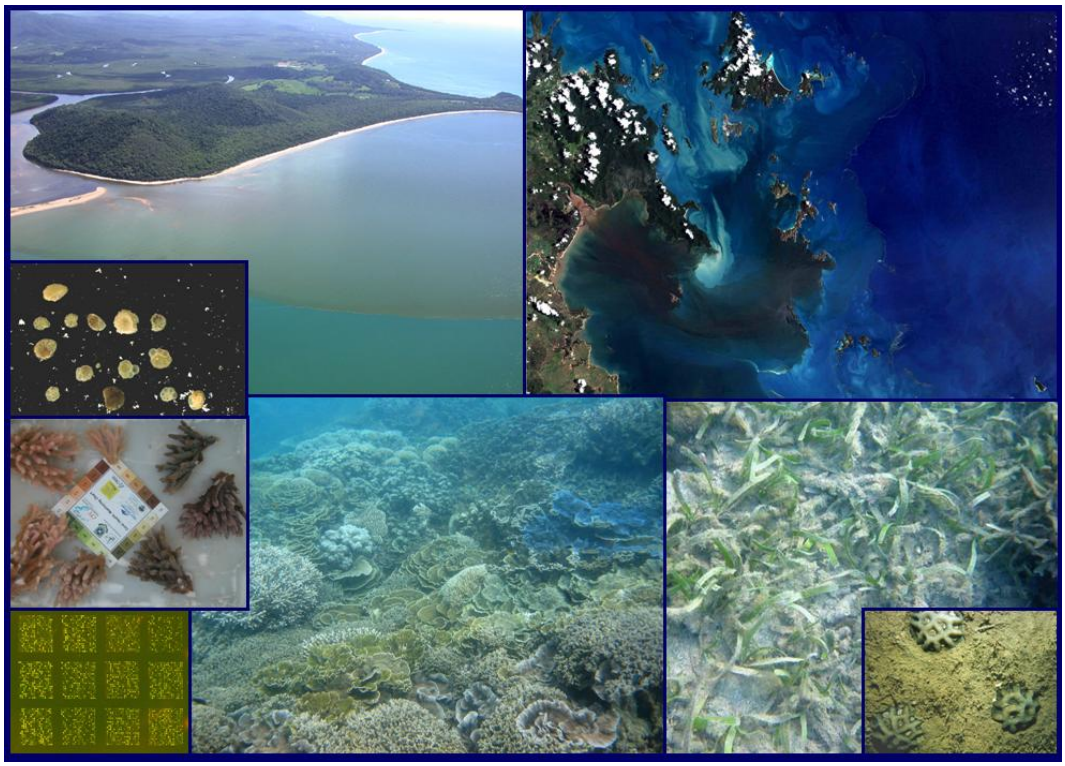
INTERIM REPORT



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Preface

This Interim Technical Report summarises research results aimed at identifying sensitive and cost-effective indicators to monitor changes in biota in the inshore Great Barrier Reef (GBR) in response to changing water quality from altered catchments.

Through the Great Barrier Reef Water Quality Protection Plan, the National Action Plan (NAP) for Salinity and Water Quality and National Heritage Trust (NHT2), the Commonwealth and Queensland Governments proposed to assist landholders in the Great Barrier Reef catchment to reduce terrestrial runoff of sediment and nutrients to the reef. The main aim of the 'Reef Plan' is to 'halt or reverse the decline in water quality entering the GBR' by 2013. As rivers are the most important sources of new nutrients and sediments entering the lagoon, a reduction of river loads should, in the long term, prevent further deterioration of the water quality within the GBR lagoon. The importance of the actions proposed through the 'Reef Plan' have recently been further emphasised by new models that show that dissolved nutrients discharged from the Burdekin river mouth may be retained in the GBR lagoon by physical processes alone for up one year. Biological uptake could further slow down dissipation, resulting in exposure times of reef organisms to land-sourced materials that are ecologically relevant.

Developing the capacity to reliably monitor the status in nearshore marine ecosystems in response to changing water quality is an essential part of the Reef Plan. This Report presents preliminary results of research aimed at identifying the most suitable biophysical indicators to identify and track such changes. It was conducted as a Task of the 'Catchment to Reef Program' (January 2004 - June 2006), a supplementary program to the Cooperative Research Centre for the Great Barrier Reef World Heritage Area (CRC Reef) and the Rainforest CRC. This Interim Report also builds on and incorporates elements of previous work carried out through the CRC Reef Task 'Terrestrial Runoff: Inputs and Impacts (July 2000 – June 2006), and ongoing research activities at AIMS, which produced a review of a number of related studies assessing the effects of terrestrial runoff on individual groups of ecosystem properties (e.g. Fabricius and De'ath 2004; Brodie *et al.* 2005; Harrington *et al.* 2005; Negri *et al.* 2005; Wolanski *et al.* 2005; DeVantier *et al.* 2006; Fabricius 2006; Weber *et al.* 2006).

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Acronyms Used In This Report

CRC Reef..... Cooperative Research Centre for the Great Barrier Reef World Heritage Area
DEW..... Commonwealth Department of the Environment and Water Resources
GBR ..... Great Barrier Reef
MTSRF..... Marine and Tropical Sciences Research Facility
Rainforest CRC..... Cooperative Research Centre for Tropical Rainforest Ecology and Management
RRRC..... Reef and Rainforest Research Centre Limited
WTWHA..... Wet Tropics World Heritage Area

Acknowledgements

This research project was jointly funded by the Catchment-to-Reef Program (a supplementary program to the Cooperative Research Centre of the Great Barrier Reef World Heritage Area [CRC Reef], and the Rainforest CRC), and the Australian Institute of Marine Science (AIMS). Many thanks to Jon Brodie, Miles Furnas, Dan Alongi, Eric Wolanski, Britta Schaffelke, Miriam Weber and Christian Lott for discussions throughout the study. We are grateful to Michele Skuza and Margaret Wright for processing the chlorophyll and nutrient samples, and Stephen Neale for processing the video transects for benthic analyses. We thank Laurence McCook, Emre Turak and David Williams for their contributions as co-authors to the reef community chapter, which started as a product of the Reef CRC Task “Effects of terrestrial runoff on inshore reefs”. Jon Brodie and Arnold Dekker provided the aerial photograph of the Whitsundays flood plume used on the front cover. Many thanks also to all volunteers during field and lab experiments for their great help in the field and laboratory during this project, especially Katharina McGuire, Danika Tager, Nadine Koch and Christopher Shellbourn. The skippers and crews of the research vessels "Lady Basten" and "Cape Ferguson" were of continued great company and support. Some of the work presented in the biofilm chapter was part of two honours projects, and Chapters 2 and 5 will be part of a PhD Thesis by Tim Cooper:

1) Diatoms: Steffi Gottschalk, 2005. Tropical benthic microalgal communities and the effect of regional and seasonal enhanced nutrient levels on their distribution in the Great Barrier Reef. Diplomarbeit, University of Rostock, 132pp.

2) Foraminifera: Kirsti Nobes, 2006. Growth, distribution and ecology of benthic symbiontic foraminiferal assemblages along a turbidity gradient on the Central Great Barrier Reef. Honours Thesis, James Cook University, Townsville, 105pp.

3) Coral Indicators: Tim Cooper (to be submitted) Coral based indicators of the trophic status of nearshore reefs on the Great Barrier Reef. James Cook University, School of Marine Biology and Aquaculture.

Executive Summary

This Interim Report summarises baseline data and research results identifying measures of changes in coral reefs that are specifically related to recent and past exposure to changing water quality from altered catchments.

The objective of the study is to develop methods that allow time-integrated measures of exposure to changing water quality, and detect the effects of changing exposure in inshore reefs of the Great Barrier Reef (GBR). Such measures could become sensitive, specific and cost-effective monitoring tools. To achieve this goal, we tested a range of potential indicators including physical and chemical properties of the water column and sediments (Chapter 2), genetic and physiological sublethal measures (Chapters 3-5, and 9), and population, communities, recruitment and biodiversity-based measures (Chapters 3, and 7-9). We also reviewed the main properties essential for the development of an indicator system (Chapter 1, and T. Cooper, unpub. results), and the main effects of changing water quality on the ecological condition of inshore reef ecosystems (Chapter 6).

The research focused on three groups of indicator organisms: biofilms, corals and seagrasses. For biofilms and corals, we assessed changes in genetic, physiological, population and community-based properties along *in situ* water quality gradients and in controlled experimental conditions. These were investigated in the context of varying levels of light from turbidity, particulate and dissolved nutrients and chlorophyll in both the water column and sediments. For seagrasses, we focused on temporal changes in tissue nutrients and biomass in response to changing sediment properties.

A priori, we identified a number of steps that are essential in the process of indicator development, namely:

a) Define the function and role of the proposed indicators;
b) Assess many potential indicators in the field;
c) Prioritise based on temporal and spatial variability, specificity and ease of measurement through review of own and published data;
d) For priority indicator candidates, conduct laboratory tests and undertake field verification, develop dose-response relationships, and identify threshold concentrations; and
e) Develop rating system / index and form an indicator system.

In this Interim Report, we present the main findings of our research that has so far focused on topics A, B and parts of C. A summary of the main findings is presented below and details are presented in Chapters 2-9. A comparative review of the numerous coral and bioindicators tested, resulting in a prioritisation of these measures, is forthcoming (T. Cooper, in prep.; Uthicke, in prep.). Another important objective of the study was to develop a better understanding of inshore ecosystem processes and functions, especially reef resilience and biodiversity, in response to exposure to altered conditions of water quality, and some of the main findings of this topic are also included here.

Chapter 1: Introduction

Impact-specific biomarkers and bioindicators are being increasingly used to monitor biotic responses to environmental change. We define an ecological indicator as a metric, at all levels of organisation, which is designed to inform about spatial and temporal changes in the condition of relevant ecosystem properties. Chapter 1 provides a brief overview of the main issues involved when attempting to measure the effects of changing water quality around

coral reefs, and a brief overview of previous work on ecological indicators proposed for coral reefs and other aquatic ecosystems exposed to changing water quality.

Chapter 2: Physico-chemical characteristics of the water column and sediments, Whitsunday Islands

Spatial variation in water column characteristics, sediment and irradiance on coral reefs was examined in the Whitsunday region of the GBR. A number of water column parameters including chlorophyll a, total suspended solids, total organic carbon and particulate nutrients, irradiance and turbidity strongly changed along a gradient towards the coast and the mouths of two rivers. For example, concentrations of chlorophyll a and total suspended solids increased two- and three-fold, respectively, while Secchi and optical depth decreased three-fold. Many of the water column variables were highly correlated, and the relative influence of distance from the coast and to the river mouths were confounded and could not be resolved. Water column chlorophyll *a*, sediment colour, and the irradiance variables Secchi and optical depth, all showed strong relationships with distance from the coast and rivers, and were strongly related to benthic processes (see below). If resources are limited, this suite of relatively simple measures could be used as best 'surrogate indicators' to monitor changes in water column characteristics.

Light is a key resource for benthic organisms on coral reefs. We highlight the usefulness of 'optical depth' (a measure of the transparency of the media through which light is passing), as a parameter to quantify water column characteristics relevant for coral reefs. It can be obtained from field measurements as well as from satellite imagery. Further, our data show that in the Whitsunday Islands, reef development generally extended to a depth of ~6-8% of surface irradiance. This 'irradiance threshold depth' is the water quality specific critical depth where zooxanthellate corals are so light-limited that photoadaptation and heterotrophy can not compensate for the lack of light, preventing reef growth. In the Whitsunday Islands, the critical irradiance threshold depth declined along the water quality gradient from ~22 m on the outer Whitsunday Islands to ~6 m on Repulse Island.

Chapter 3: Benthic biofilms

Biofilms develop on sediment surfaces, hard substratum and artificially deployed surfaces within a few days in response to prevailing environmental conditions. Biofilms have been previously used as indicators for water quality conditions in other aquatic environments, as they respond quite rapidly to changes in water quality conditions. In this project, we investigated three groups of biofilms, namely foraminifera, bacteria and diatoms, for their suitability as indicators for changing water quality in the GBR. All three groups have provided important leads towards a future practical application as bioindicators. Some of the main results from the three groups are summarised here.

Foraminifera: Benthic foraminifera exhibited gradual changes in community composition along water quality gradients. Several species were associated with either high nutrient/high turbidity or low nutrient/low turbidity conditions. In general, large foraminifera that bear algal symbionts were more characteristic for clear water, low nutrient environments, while more turbid high-nutrient environments only house small and heterotrophic taxa. This is similar to previous findings in the Caribbean, but not all species followed this pattern on the GBR. An application of the Caribbean FORAM index showed significantly increasing values along the Whitsunday Islands water quality gradient. We conclude that it will be possible to apply the FORAM index to GBR reefs, after adaptations and fine-tuning of the index based on a better understanding of the physiology and ecology of specific GBR species. Pilot experiments showed that light was an important factor influencing the growth and carbonate production in four of the large symbiont bearing species, and their specific tolerance ranges agreed with

the distribution patterns recorded *in situ* for these species. These experiments will now be expanded to investigate the specific responses of key individual GBR species to changing nutrient and light conditions.

Benthic bacteria: Genetic analyses confirmed that the diversity in benthic bacteria on the GBR is so high that estimates on taxonomic richness can not yet be attempted. However, the analyses showed that two major groups of benthic bacteria (Acidobacteriaceae and δ-proteobacteria) were more common on the inshore reefs surveyed, while a third group, Cyanobacteria, were most abundant offshore. This indicated that water quality could play an important role in affecting bacterial abundances, with far-reaching consequences: the different groups of marine bacteria greatly determine rates of nutrient cycling in the system, and they also contribute to shaping ecological processes such as settlement induction in larvae from corals and other invertebrates. Further work will focus on the development of rapid genetic methods to identify benthic bacteria, and on controlled experiments to better understand the responses of these important communities to changing light, nutrients and organic enrichment of sediments.

Benthic microalgae: Benthic microalgae growing on sediment surfaces (microphyto-benthos) are among the most important primary producers in the reef system. Their photophysiology and community composition changed strongly along inshore-offshore gradients. The benthic community adapted to low light at inshore locations by increasing their efficiency of light usage. Benthic diatoms were investigated in detail, and >200 species of diatoms were identified. Diatom communities were more diverse and had higher densities on inshore reefs compared to offshore reefs. A number of species were restricted to inshore reefs, or certain regions within the inner GBR, while others were only recorded on outer shelf reefs. Therefore, a large variety of putative indicator species for water quality exist in the benthic diatom community. We have also initiated the development of genetic markers to identify diatoms. In future, putative indicator species will have to be cultivated as pure cultures for experimental work to establish their specificity, and to obtain DNA to develop genetic methods for their identification and quantification.

Chapter 4: Coral genetics

A series of pilot studies has shown that the ratio of RNA to DNA in corals is sensitive to differences in depth, light and location. Our data on three candidate coral species, *Pocillopora damicornis, Acropora millepora* and massive *Porites*, combined with other published studies indicate that the RNA:DNA ratio may be a useful marker for detecting the effects of environmental change in some but not all species of corals. We have developed a new, simple and time effective technique for measuring the RNA:DNA ratio in a large number of samples. Despite the promise this research holds out for this indicator a number of difficulties in interpreting the data remain, due to the complex interaction between the coral host and algal symbionts. To further develop this indicator, research is required to test for natural seasonal variation in the RNA:DNA ratio, and to better understand how the coral - symbiont interactions change in response to environmental change. To clarify some of these issues, samples have been collected from two reefs for the past ten months, as well as from along a water quality gradient in the Whitsunday Islands region.

Chapter 5: Coral physiology

Physiological responses in scleractinian corals were investigated to determine their suitability as bioindicators of changes in water quality on nearshore coral reefs of the GBR. The study assessed physiological variables in massive *Porites* spp. and *Pocillopora damicornis* along a water quality gradient in the Whitsunday Islands, and by both laboratory and field experiments. In the field, all of the physiological variables tested in massive *Porites* and *P. damicornis* changed significantly along the water quality gradient in the Whitsunday Islands.

As nutrient and turbidity levels increased toward the coast, massive *Porites* became progressively darker in colour, while tissue thickness decreased. Similarly, in *P. damicornis* the concentrations of chlorophyll *a* and the density of symbionts per cm^{-2} increased, but skeletal density decreased, on coastal reefs compared with conspecifics from clean-water outer reefs. In the laboratory experiment, responses in massive *Porites* to changes in water quality occurred within days to weeks: corals darkened by up to 2 colour chart scores within 20 days of exposure to suspended particulate matter and nutrients coupled with reduced light regimes but did not change colour in clear water at high light. A coral colour chart was used to quantify colour saturation of corals in differing nutrient and light conditions. The colour difference was also measurable as a significant difference in concentrations of chlorophyll *a*. In the field, nubbins of *Porites* were transplanted within and across different zones of water quality in the Whitsunday Islands. Despite a moderate bleaching event and the mortality of almost half of the nubbins as a result of grazing by Parrotfish, corals relocated from the outer shallow (low nutrients, high irradiance) to the inner deep depth (elevated nutrients, low irradiance) increased their saturation of colour (measured using colour charts, chlorophyll *a* concentrations, and spectral reflectance). They were noticeably darker after three months exposure compared with nubbins in the other experimental treatments. Both the field gradient study and the manipulative experiments suggest that the physiological indicator with the greatest potential for incorporation into monitoring programs is a change in the saturation of coral colour. It can be measured with a range of different tools, the simplest being a coral colour chart developed for monitoring bleaching events. This study is the first to show that such a chart can also be used for detecting the physiological effects of changes in water quality on scleractinian corals.

Chapter 6: Review of the effects of changing water quality on inshore coral reefs

This study is now published as: Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50: 125-146.

The study reviewed and evaluated the current state of knowledge on the direct effects of terrestrial runoff on (1) the growth and survival of hard coral colonies, (2) coral reproduction and recruitment, and (3) organisms that interact with coral populations (coralline algae, bioeroders, macroalgae and heterotrophic filter feeders as space competitors, pathogens, and coral predators). The responses of each of these groups were evaluated separately against the four main water quality parameters: (1) increased dissolved inorganic nutrients, (2) enrichment with particulate organic matter, (3) light reduction from turbidity and (4) increased sedimentation. This separation facilitated disentangling and understanding the mechanisms leading to changes in the field, where many contaminants and many responses co-occur. The review also summarised geographic and biological factors that determine local and regional levels of resistance and resilience to degradation. It provides a conceptual aid to assess the kind of change(s) likely to occur in response to changing coastal water quality.

The literature review showed that four fundamentally different processes have to be distinguished when assessing the effects of terrestrial runoff on coral reefs:

1. Dissolved inorganic nutrients can reduce coral calcification and fertilisation rates, and increase macroalgal abundances. In the field, dissolved inorganic nutrients are taken up rapidly, so their main role may that of organically enriching benthos, sediments and suspended particulate organic matter.
2. Enrichment with particulate organic matter enhances feeding rates and growth in some corals, providing a growth advantage that can partly or fully compensate for light reduction, especially in high-flow environments. However, while some corals can benefit

from particulate organic matter, heterotrophic filter feeders will benefit even more than corals do, hence the competitive advantage shifts from corals that can grow at extremely low food concentrations to simpler, more heterotrophic communities. A promotion of the growth and survival of filter feeding larvae of *A. planci* also has profound negative consequences for coral populations.

3. Turbidity-related light limitation reduces gross photosynthesis. Light limitation increases with depth and under macroalgae, but will not occur in shallow water, even in very turbid environments. The effects of light limitation are more severe for phototrophic than mixotrophic species, while heterotrophic species such as filter feeders may be promoted. Light limitation also greatly reduces coral recruitment.
4. Sedimentation represents a severe disturbance for coral reefs. It reduces growth and survival in a wide range of coral species, although responses differ substantially between species and also between different sediment types. Smothering by sedimentation or sediment-trapping macroalgae is the main factor affecting recruitment and the survival of early life stages in corals: settlement rates are near-zero on sediment-covered surfaces, and sedimentation tolerance in coral recruits is at least one order of magnitude lower than for adult corals. Some of the bioeroding and space-competing groups of organisms are also sensitive to sedimentation by fine silt, and so are crustose coralline algae, with negative consequences for coral recruitment.

Responses to terrestrial runoff therefore depend on whether changes occurred predominantly in sedimentation, turbidity, particulate organic matter or dissolved inorganic nutrients. In most places, reduced recruitment success in corals, together with the promotion of macroalgae and *A. planci*, arguably represent the most significant direct effect of terrestrial runoff on coral reefs. In severe conditions, the overall outcome is reduced reef calcification, shallower photosynthetic compensation points, changed coral community structure, and greatly reduced species richness. Hence reef ecosystems increasingly simplify with increasing exposure to terrestrial runoff, compromising their ability to maintain essential ecosystem functions at the presently increasing frequencies of human-induced disturbances.

The type and severity of response to terrestrial runoff at any particular location also depends on the physical, hydrodynamic, spatial and biological properties of a location. Reefs that are surrounded by a shallow sea floor, reefs in poorly flushed bays or lagoons, deeper reef slopes, and frequently disturbed reefs are likely to experience changes even at low levels of pollution, in particular when populations of herbivores are low. In contrast, well-flushed shallow reef crests surrounded by deep sea floors or in areas of moderate tides are likely to have the highest level of resistance and resilience, especially when inhabited by healthy populations of herbivores that protect against overgrowth by sediment-trapping macroalgae.

Chapter 7: Changes in algal, coral and fish communities and abundances of potential indicator species along water quality gradients

This study is now published as: Fabricius KE, De'ath G, McCook L, Turak E, Williams DMcB (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin* 51: 384-398.

The study summarises surveys of macroalgae, hard corals, octocorals, and fish on 10 to 13 inshore coral reefs of the Great Barrier Reef, along a water quality gradient in two regions with contrasting agricultural land use. A water quality index was calculated for each reef based on available data of particulate and dissolved nutrients, chlorophyll and suspended solids. Strong gradients in ecological attributes occurred along the water quality gradient. Macroalgae of the divisions Rhodophyta and Chlorophyta increased with increasing nutrients, while Phaeophyta remained similar. Octocoral richness and abundances of many hard coral and octocoral taxa decreased, and none of the hundreds of species increased. At

reefs in higher nutrient environments, hard coral and octocoral assemblages were composed of subsets of the many species found in lower nutrient environments, whereas fish and macroalgal assemblages consisted of contrasting suites of species. The study identifies species groups that are likely to increase or decrease in abundance with changing water quality.

A similar study has now been conducted along the water quality gradient in the Whitsunday Islands, summarised in Chapter 8.

Chapter 8: Coral benthos composition, taxonomic richness and recruitment along a water quality gradient in the Whitsunday Islands

We quantified changes in the benthic community composition, taxonomic richness and juvenile densities in hard corals and octocorals along a water quality gradient in the Whitsunday Islands (described in Chapter 2). Coral and algal cover and taxonomic richness significantly changed along the water quality gradient. Hard coral cover declined five-fold (from ~50% to ~10%) along the gradient from clear to turbid sites, while octocoral cover declined from ~25% to 3%. The taxonomic richness of hard corals and octocoral communities declined towards the most turbid sites to about a third of those of the cleaner-water sites (from 11.5 to 4 hard coral taxa, and from 6.5 to 1.5 octocoral taxa per transect). In contrast, total macroalgal cover, especially the cover of brown macroalgae (Phaeophyta) strongly increased along the water quality gradient, from near-absence in clear-water reefs to a coverage of >50% of all substratum on the most turbid reefs. Red macroalgae (Rhodophyta) also increased from zero to an average of 7%, with two of the most turbid sites being occupied by 20-25% red macroalgae.

Juvenile densities and taxonomic richness of juveniles also strongly declined along the water quality gradient. Juvenile densities in hard corals on reefs in the most turbid waters were around a quarter of those in cleaner water, and in octocorals less than a tenth of those in cleaner waters. Similarly, the taxonomic richness in hard coral and octocoral juveniles in the most turbid waters were around half to a third of those in cleaner water. This shows that the ability of reefs to recover from disturbances is severely compromised, with reefs potentially taking twice to four times as long to re-establish cover, and resulting in a lower taxonomic richness than on reefs in consistently cleaner waters.

The strength and consistency in response in (1) the abundances of brown and red macroalgae, (2) the taxonomic richness of octocorals, and (3) the density and taxonomic richness of both hard coral and octocoral juveniles all indicate that these basic community measures represent specific, robust and relevant measures of ecosystem status in coral reefs, reflecting prolonged exposure to water quality and other environmental conditions.

We will now compare patterns in the Whitsunday Islands to those found in the Wet Tropics and Princess Charlotte Bay regions of the GBR (Chapter 7), to assess how the ecological responses compare across regions, and to test whether the indicators identified apply across GBR regions or whether specific indicators are required for each region.

Chapter 9: Temporal variation in seagrass biomass and tissue nutrients in relation to sediment nutrient contents

This study assessed temporal changes in seagrass biomass and tissue nutrients in relation to pore water and adsorbed nutrients in sediments at five sites bi-monthly over a period of 22 months. Two of the sites were occupied by the species *Halophila ovalis*, the other three sites were occupied by *Halodule uninervis*. The data represent the most detailed time series of

sediment and seagrass properties in these two structurally small species of seagrasses, available to date.

Changes over time were complex, and appeared to be dominated by disturbances and recovery from disturbances, obscuring any seasonal patterns in this <2 years data set. Spatial patterns remained stronger than temporal patterns, despite some pronounced changes both in sediments and in seagrass properties over time. The individual patterns observed across these meadows may suggest that these meadows are all in different stages of recovery, and therefore the time frame of this study was not long enough to evaluate a meadow in full recovery displaying seasonal dynamics. Examination of individual locations demonstrating meadow stability (beyond the scope of this study) to tease out the subtleties of seasonal change would be desirable.

Once Location had accounted for the majority of variance within the data set, porewater NH_4^+ was the best predictor of biomass and tissue N. Porewater NH_4^+ was positively related to plant tissue N and negatively related to biomass. This may indicate that as NH_4^+ increases plant tissue N also increases, but that the acquisition of NH_4^+ within the seagrass plant is not being translated into an increase in biomass – on the contrary, some factor is limiting seagrass growth where and when NH_4^+ is high. It is possible that light may be the limiting factor along this highly turbid coastline, with its seasonal terrestrial freshwater, nutrient and sediment inputs and wind generated sediment resuspension.

Most seagrass biomass was stored underground but the correlation between above- and belowground biomass was high suggesting that total biomass provides almost as much information than separate assessments of leaves, rhizomes and roots. Changes in seagrass biomass were much greater than changes in tissue nutrient concentration. Tissue nutrients were only slightly elevated at times of low biomass, suggesting that only a small proportion of the seagrass nutrients is being stored in the remaining biomass when biomass declines. As a result, differences in biomass strongly determined the standing stock of nutrients bound within seagrasses per unit area.

Tissue nutrient N may be used as an indicator of water quality, although it has to be emphasised that tissue nutrient contents do not signify ecological health of a seagrass meadow. A combination of variables is required to report on the health of a meadow: species presence or absence, its nutrient requirements for growth, the nutrient and light history of the location, and the age or stage of development of the meadow as dictated by its disturbance regime.

There is a need for a better understanding of seagrass responses with respect to the interaction between light and nutrients in relation to meadow development. Experimentation on the interaction between light, nutrients and temperature in controlled systems is required. Coupling this with varying degrees of exposure would enable us to better model intertidal plant responses. There is also a need to categorise seagrass meadows according to sediment type and sediment nutrient state and to have the ability to classify seagrass meadows by development stage. To be able to classify development stage/age of a meadow a diagnostic tool is required. Internode length of rhizomes looks promising, however this needs to be tested on species other than *Halophila ovalis* and on a larger number of meadows.

This study highlights the uniqueness of location with respect to seagrass meadow dynamics and behavior. Supporting programs such as Seagrass-Watch and the Reef Water Quality Protection Plan (RWQPP) Seagrass Monitoring program will increase the number of meadows being examined across a broader geographical scale and varied disturbance regimes. These programs are limited in their approach though as they focus on intertidal meadows of structurally small seagrass. There is a need to extend our knowledge of

seagrass meadows to include intertidal meadows of structurally large seagrasses (possibly reef top meadows) and shallow sub-tidal area meadows; areas that have logistical challenges.

Based on the evidence presented in this study, we suggest that structurally small seagrasses in this region are not primarily nutrient limited but are limited by one or more of the other factors that affect their growth. We also suggest that in this region, the disturbance regime of a location, that is, the localised aspects of exposure to predominant winds, tidal exposure, turbidity and hence light availability, and to a lesser degree the frequency and intensity of herbivory (particularly dugong grazing) dictates abundance and temporal signal of these intertidal seagrass meadows. There is a need to encompass the variability inherent in the different seagrass meadows within each habitat type that occurs within the Great Barrier Reef World Heritage Area (GBRWHA). For each meadow/habitat type it is important to recognise the different species, their relative form and function, and the disturbance history/ stage of development of these meadows. This type of approach will foster community and managerial understanding that not all seagrass meadows are the same, and that differences exist between meadows because of their geographical setting, species composition and abundance, sediment mineralogy, stage of meadow development and past nutrient history.

Chapter 10: Conclusions

A brief revision of the lessons learned from this research, and an outlook of how the many measures tested will now be used to prioritise indicators and combine them to form an indicator system that will specifically measure recent and past exposure to changing water quality from altered catchments in inshore ecosystems of the Great Barrier Reef.

References

Brodie J, Fabricius K, De'ath G, Okaji K. 2005. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. Marine Pollution Bulletin 51: 266-278

DeVantier L, De'ath G, Done T, Turak E, Fabricius K. 2006. Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. Coral Reefs 25: 329–340

Fabricius K, De'ath G, McCook L, Turak E, Williams DM. 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Marine Pollution Bulletin 51: 384-398

Fabricius KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50: 125-146

Fabricius KE. 2006. Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: Implications for coral bleaching? Limnology and Oceanography 51: 30-37

Fabricius KE, De'ath G. 2004. Identifying ecological change and its causes: A case study on coral reefs. Ecological Applications 14: 1448-1465

Harrington L, Fabricius K, Eaglesham G, Negri A. 2005. Synergistic effects of diuron and sedimentation on photosynthetic yields and survival of crustose coralline algae. Marine Pollution Bulletin 51: 415-427

Weber M, Lott C, Fabricius K. 2006. Different levels of sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, geochemical and organic properties. Journal of Experimental Marine Biology and Ecology 336: 18–32

Wolanski E, Fabricius K, Spagnol S, Brinkman R. 2005. Fine sediment budget on an inner-shelf coral-fringed island, Great Barrier Reef of Australia. Estuarine and Coastal Shelf Science: 65:153–158

Chapter 1: Introduction

1.1 Water quality and coral reefs

Around the world, water quality in coastal areas is changing in response to rapidly increasing land clearing, soil erosion and fertilizer use (Vitousek *et al.* 1997; Tilman *et al.* 2001; Smith *et al.* 2003). Globally, land clearing continues at a rate of 1% of the earth's surface per year, leading to extensive soil losses ((GESAMP 2001)). The use of Nitrogen fertilizer has also increased globally more than six-fold since 1960 (Matson *et al.* 1997), and coastal urbanisation is expanding disproportionally to human population growth. Marine coastal ecosystems, including coastal coral reefs, are therefore exposed to increasing amounts of terrestrially derived nutrients, sediments and pollutants.

Models of the global scale of pollution around coral reefs estimate that 22% of all coral reefs worldwide are classified as at high (12%) or medium (10%) threat from inland pollution and soil erosion (Bryant *et al.* 1998). The global models also classify 12% of reefs at threat from marine pollution (distance from ports, oil tanks, oil wells and shipping areas), and 30% of reefs as threatened from coastal development such as cities, mines and resorts (Bryant *et al.* 1998). Terrestrial runoff, pollution and coastal development are therefore a growing concern for most of the 104 nations endowed with coral reefs, ~100 of which are located in nations with developing economies (Bryant *et al.* 1998; Spalding *et al.* 2001). At a global scale, these factors are rated a threat similar in severity and scale to coral bleaching, overfishing and destructive fishing (Spalding *et al.* 2001). At regional scales, the percentage of reefs at risk is a function of the extent of land clearing, with up to 50% of reefs at risk in the countries with most widespread land clearing, and at local scales, it can be the single most significant pressure on coastal and inshore coral reefs (Bourke *et al.* 2002).

The Great Barrier Reef (GBR) represents the most extensive coral reef system on earth. Coral reefs of the GBR are highly diverse ecosystems, built by ~405 species in 78 genera of hard corals (DeVantier *et al.* 2006) that house many tens of thousands of other reef-associated species from other groups. The economic value of the GBR to Australia has been estimated as AU$5 billion annually (Hoegh-Guldberg and Hoegh-Guldberg 2004), derived from a highly profitable tourism industry, and other reef-related industry sectors such as commercial and recreational line and harvest fisheries. Additional invaluable ecosystem services provided by reefs include coastal protection and the storage of libraries of bioactive substances that are still to be investigated for potential pharmaceutical benefits. Because of their ecological and economic value, and their amazing beauty, coral reefs are generally treated as the 'poster child' ecosystem within the Great Barrier Reef World Heritage Area (GBRWHA). This report focuses predominantly on the effects of changing water quality on these coral reefs; the effects of changing water quality on the 95% of inter-reefal area including subtidal seagrass meadows remain largely unknown.

Field studies have provided a large body of information showing that sedimentation, nutrient enrichment and turbidity can degrade coral reefs at local scales (reviewed in Rogers 1990; Fabricius 2005). At regional scales, it has often been difficult to assess causal relationships between terrestrial runoff and reef degradation, because pollution effects and other disturbances are often confounded, historical data are often missing, and reef communities change naturally along gradients from terrestrially influenced conditions (fluctuating salinity, more variable or higher silt and nutrient levels, more variable or reduced water clarity) to oceanic conditions (low siltation, high water clarity, generally low nutrient levels except during upwelling periods). Although coastal coral reefs can flourish at relatively high levels of particulate matter and siltation (van Woesik *et al.* 1999; Fabricius *et al.* 2005; DeVantier *et al.* 2006), they tend to be restricted to the upper 4 m to 10 m depth of well-flushed wave-

sheltered locations in turbid water, while extending to >40 m in clear oceanic waters (Yentsch *et al.* 2002).

In coastal ecosystems, natural and anthropogenic disturbances are often difficult to separate. Nutrient exposure, water clarity and sedimentation vary both spatially and temporally by 1-2 orders of magnitude, due to sediment resuspension, floods, coastal morphology and hydrodynamics. Anthropogenically increased nutrient and sediment levels from run-off and new pesticide discharges are stressors, although the system is dynamic and characterised by steep gradients. Disturbances caused by changing climate and the resulting change in weather patterns further complicate the picture. Detecting the effects of both individual disturbances and the simultaneous influences of natural and anthropogenic disturbances is therefore exceedingly complex.

To assess the effects of terrestrial runoff at local and regional scales, Fabricius (2005) reviewed the available information on the direct effects of water quality on: (1) calcification, tissue growth, zooxanthellae populations and photosynthesis in adult hard corals, (2) the six main stages of coral reproduction and recruitment, and (3) five groups of other reef organisms that affect hard coral abundances. The latter includes those organisms that affect coral larval settlement, bioeroding filter feeders that weaken the structural integrity of reefs, macroalgae, octocorals and filter feeders competing for space with corals, disease pathogens, and coral predators. Responses of each of these groups are assessed separately against exposure to the four main water quality parameters in marine systems: (1) dissolved inorganic nutrients, (2) suspended particulate matter, (3) light reduction from turbidity and (4) sedimentation.

The review focuses on the effects of inorganic nutrients and sediments enriched with particulate organic matter, which though they are not considered ‘classical’ pollutants, are the most important contaminants at national and regional levels (GESAMP 2001). The review concluded that a number of fundamentally different processes have to be distinguished when assessing the effects of terrestrial runoff on coral reefs:

1. ***Dissolved inorganic nutrients*** can reduce coral calcification and fertilisation rates, increase macroalgal abundances, and curb organic enrichment of benthos, sediments and suspended particulate organic matter (POM).
2. Enrichment with POM enhances feeding rates and growth in some corals, providing a growth advantage that can partly or fully compensate for light reduction, especially in high-flow environments. Some corals can benefit from POM, but heterotrophic filter feeders will benefit even more so than corals, hence the competitive advantage shifts from corals that can grow at extremely low food concentrations to simpler, more heterotrophic communities. A promotion of the growth and survival of filter feeding larvae of *Acanthaster planci* also has profound negative consequences for coral populations.
3. ***Turbidity-related light limitation*** reduces photosynthesis. Light limitation increases with depth and under macroalgae, but will not occur in shallow water, even in very turbid environments. The effects of light limitation are more severe for phototrophic than mixotrophic species, while heterotrophic species such as filter feeders may be promoted. Light limitation also greatly reduces coral recruitment.
4. ***Sedimentation*** represents a severe disturbance for coral reefs. It reduces growth and survival in a wide range of coral species, although responses differ substantially between species and also between different sediment types. Smothering by sedimentation or sediment-trapping macroalgae is the main factor affecting recruitment and the survival of early life stages in corals: settlement rates are near-zero on sediment-covered surfaces and sedimentation tolerance in coral recruits is at least one order of magnitude lower than for adult corals. Some of the bioeroding and space-competing groups of organisms

are also sensitive to sedimentation by fine silt, as are crustose coralline algae, with negative consequences for coral recruitment.

5. ***Contamination by pesticides, heavy metals, hydrocarbons or other human-made pollutants*** can also significantly affect the health of exposed reefs at local scales (e.g. Guzman and Holst 1993). It has been shown that herbicides, such as diuron and atrazine cause rapid, but reversible, photophysiological stress in corals after short-term exposure at environmentally relevant concentrations of <1 $\mu g\ L^{-1}$ (Owen *et al.* 2003; Jones and Kerswell 2003; Jones *et al.* 2003; Negri *et al.* 2005). The effects of chronic low-level exposures to these contaminants are still largely unknown. Heavy metals such as copper and zinc and some hydrocarbons have also been linked to reduced fertilisation, fecundity and growth in adult corals (Brown 1987; Loya and Rinkevich 1987; Heyward 1988; GESAMP 2001). Other studies, too numerous to be listed here, document the uptake of a variety of pollutants by adult corals; some of these pollutants are known to have toxic effects above certain concentrations. The effects of these substances on coral reefs are diverse and still poorly understood.

The type and severity of response to terrestrial runoff at any particular location depends on whether changes occurred predominantly in sedimentation, turbidity, POM or dissolved inorganic nutrients and also depend on the physical, hydrodynamic, spatial and biological properties of a location. In most places reduced recruitment success in corals, together with the promotion of macroalgae and *A. planci*, arguably represent the most significant direct effect of terrestrial runoff on coral reefs. In severe conditions, the overall outcome is reduced reef calcification, shallower photosynthetic compensation points, changed coral community structure, and greatly reduced species richness. Hence reef ecosystems increasingly simplify with increasing exposure to terrestrial runoff, compromising their ability to maintain essential ecosystem functions at the presently increasing frequency of human-induced disturbances. The review also shows that there are significant gaps in the existing scientific knowledge of the effects of terrestrial runoff on coral reefs. There are also significant gaps in our understanding of the geographic and biological conditions that influence retention and exposure levels to pollutants, and of the factors that enhance the resistance and resilience of reefs to degradation.

1.2 Bioindicators for changing water quality

Impact-specific biomarkers and bioindicators are being increasingly used to monitor biotic responses to environmental change. Often, the term ‘biomarker’ is used to refer to measures at sub-organism to organism level. Such biomarkers are employed to detect biologically relevant changes at an early stage, before organisms start dying and population measures change. In contrast, the term ‘bioindicator’ is often used to refer to measures at higher population to community-levels. In reality, the distinction between biomarkers and bioindicators is rarely practical as it depends on the system under investigation (e.g. microbial communities are measured using molecular markers). For this reason, we refer to all measures tested in this study, from molecular to ecosystem level, with the general term ‘bioindicator’: we define an ecological indicator as a metric that is designed to inform about spatial and temporal changes in the condition of relevant ecosystem properties.

The use of biological indicators provides a number of significant advantages over direct measurements of pollutant concentrations in the environment. Direct measures are commonly restricted to a few sampling periods, a few typical pollutants, and lethal effects (e.g. changes in abundance or disappearance of certain taxa). Such sampling is bound to miss important processes and responses if the system under consideration is large and diverse, and when impacts are episodic (e.g. high temporal variability in terrestrial runoff). In most cases, concentration-dependent and synergistic effects are not understood, and other biologically relevant information is missing. The ability to detect a contaminant does not

ensure that its effect on the ecosystem can be predicted. The effect that a contaminant has upon a receiving system is dependant upon the physical and chemical parameters of the receiving waters. Chemical measurements are unable to integrate all the factors that are known to modify the effects of contaminants in aquatic systems. These problems can be overcome by applying bioindicators, as they can be used to detect sublethal effects, can integrate exposure over time periods of days to years, and, in an ideal case, allow the monitoring program to relate biologically relevant changes in ecosystem conditions to exposure even when pollutants cannot be continuously measured. For these reasons, a combination of specific measures is needed that allows the detection of both the exposure, and/or the effects of exposure in key biota to changing water quality.

A number of studies exist from around the world that aimed at developing and applying bioindicators to monitor ecological changes in coral reefs in response to changing environmental conditions, especially water quality. In particular, monitoring is required by federal and state agencies of the United States of America under their 'Clean Water Act'. The Act has led to the development of indices of biological integrity (IBIs), which combine several disparate matrices into a quantitative value of 'biological integrity' (community condition). An IBI framework has been developed for coral reef ecosystems under United States jurisdiction (Jameson *et al.* 2001). Jameson *et al.* (1998) have reviewed measures that have been previously proposed in the scientific literature as bioindicators for coral, fish, macrophyte and epibenthic communities, the protocol proposed, and specific information on relevant seasonal and spatial aspects (Appendix 1). These tables exemplify the existing enthusiasm for labeling, proposing or using a measure as 'indicator', often without inclusion of formal tests or developed protocols to ascertain their relationships to the purported perturbation. This is in stark contrast to existing freshwater biomonitoring programs with clearly established rigorous guidelines. The tables also clearly show the substantial gaps in the understanding of ecosystem processes in relation to changing water quality. This table was compiled 1998, but our own literature review of responses of corals to changing water quality (T. Cooper, in prep) shows that the problem has not been rectified since then.

1.3 About this study

This study aimed to better understand water, sediment and light characteristics around inshore reefs, and how these may be associated with changes in specific ecological measures of inshore reef communities. The study did not aim to ascertain whether the steepness of the water quality gradient is presently enhanced by the assumed 4-10 fold increased terrestrial runoff of nutrients and sediments compared with pre-European times (Furnas 2003; McCulloch *et al.* 2003). We investigated and compared the spatial and temporal patterns in a series of biotic parameters, to assess their consistency of change along water quality gradients and in experimental conditions. Our spatial gradients in the Whitsunday Islands (Chapters 2, 3, 5 and 8) and in the Wet Tropics and Princess Charlotte Bay (Chapters 4 and 7) were initially chosen based on the Long-term Chlorophyll Monitoring program (Brodie *et al.* in press). These data were complemented by our own water quality measurements conducted throughout the study. Levels of exposure in laboratory experiments were also chosen to resemble those found along water quality gradients in the field. The results of this study will form the basis to compare and prioritise measures for their suitability as future bioindicators for changing water quality (Marine and Tropical Sciences Research Facility Water Quality Project 3.7.1).

We chose to investigate biotic responses at several levels of organisation within the three groups, biofilms, corals and seagrasses, as they are likely to contrast and complement each other in their response and recovery times, and in their level of specificity. Indicators at low levels (molecular or physiological) are often quite specific, and respond at low levels of exposure. However, they often revert back to background levels within days to weeks after exposure discontinues. Thus, the advantage of specificity of low-level indicators has to be

weighed against the rapid disappearance of their signal. In contrast, many indicators at higher levels (community and ecosystem) are often less specific and start responding only at more severe levels of exposure. This disadvantage is partly compensated by the fact that they may remain in an altered state over prolonged periods of time: even after exposure has discontinued, the measure is likely to remain different from background level for one or several generation times. The challenge of using such higher-level indicators is to distinguish between different types of exposure as responses are often less specific, and to assess whether the exposure occurred in the past or recently. Within the community-based indicators, we investigated both highly sensitive and less sensitive groups of taxa. While robust groups may only show sublethal changes after severe exposure, more sensitive groups might show reduced abundances, and the most sensitive species groups may have disappeared entirely (which is difficult to interpret, as more sensitive species quite often respond to not just one but a number of environmental stress factors). Because of such contrasting response times and specificity, we are working on developing a composite system of indicators, to detect early warning signs of water quality related stress, trends in stress levels and long-term shifts in communities at individual sites in relation to changing exposure.

A priori, we identified a number of steps that are essential in the process of indicator development, namely:

a) Define the function and role of the proposed indicators;
b) Conduct field assessments of many potential indicators;
c) Prioritise by determination of temporal and spatial variability, specificity and ease of measurement through review of own and published data;
d) For priority indicator candidates, conduct laboratory tests and do field verification, develop dose-response relationships, and identify threshold concentrations; and
e) Develop rating system / index, and form indicator system.

In this Interim Report, we present our research that has so far covered the steps A, B and parts of C. We focused on biofilms, corals and seagrasses, and within these groups we measured the changes in genetic, physiological, population and community-based properties along water quality and depth gradients, and in experimental conditions. The remaining steps (C-E) will require laboratory and field research, assessing causal relationships and dose-response relationships in the priority indicator measures, in combination with an assessment of threshold concentrations, which will all be incorporated into a formal indicator system as a research project within the MTSRF Project 3.7.1. Monitoring programs that specifically include such indicators will be in a better position to assess changes in the status of those areas of the GBR that are most exposed to terrestrial runoff, and to monitor and assess the effectiveness of changing land management practices on the condition of inshore reefs, both in the GBR and elsewhere in the tropics.

Appendix 1.1

Review of previously used bioindicators to assess the status of coral reefs, and measures tested in the present study. Review by Jameson *et al.* 1998: Biological Criteria for Coral Reef Ecosystem Assessment, Appendix 1-5: http://www.epa.gov/owow/oceans/coral/biocrit (with small modifications; References are given to facilitate literature searches, but are not listed here).

a) Coral-based indicators

Bioindicator	Protocol	Location	References	Included here
Percentage Hard Coral Cover, Benthic cover diversity indices	"Traditional" reef monitoring parameters. Generally calculated using data from line intercept transects (LIT), but occasionally use belt transects, quadrats, and even manta tow.	Pacific, Caribbean, Indian Ocean	Dodge *et al.* 1982, DeVantier 1986, Gomez & Yap 1988, Aronson *et al.* 1994, English *et al.* 1994	Yes: video transects
Coral vitality / mortality indices	Various models, but all calculate an index based on ratios of live and dead hard coral colonies. Some use data from LIT's, others use "random" searches for coral colonies of particular species. No formal interpretive framework.	Pacific (Hawaii, Philippines), Caribbean (Florida Keys)	Grigg & Dollar 1990, Dustan 1994, Gomez *et al.* 1994, Ginsburg *et al.* 1996	Yes: partial mortality in *Porites*
Coral growth rate	Measurement of coral growth rates as an indication of water quality. Confused literature - some suggest growth rates decline with organic pollution, others suggest growth rates may increase. No formal interpretive framework.	Pacific, Caribbean, Indian Ocean	Hudson 1981, Brown & Howard 1985, Cortes & Risk 1985, Tomascik & Sander 1985, Brown 1988, Rogers 1990, Brown *et al.* 1990, Risk *et al.* 1995,	Yes: field and lab (*Porites* and *Acropora millepora*
Productivity and calcification profiles	Measurement of productivity and calcification profiles as an indication of water quality. No formal interpretive framework.	Pacific, Caribbean, Indian Ocean	Barnes 1983, Chalker *et al.* 1985, Brown 1988, McLanahan 1997	Yes: in *Porites* heads

Bioindicator	Protocol	Location	References	Included here
Coral fecundity and recruitment	Latest research from University of Guam looks at how different life-history stages of corals exhibit differential sensitivities to pollutants. Also, how different substances will differentially affect different stages in the reproduction/recruitment cycle. Formal interpretive framework under development.	Pacific, Caribbean, Indian Ocean (Guam)	Pearson 1981, Tomascik & Sander 1987b, Brown 1988, Richmond 1993, 1994a, 1994b, 1995, 1996, Peters *et al.* 1997	Yes, coral juvenile densities
Zooxanthellae loss	Quantifying the occurence and extent of coral bleaching as a general bioassay of environmental stress on corals. No formal interpretive framework.	Pacific, Caribbean, Indian Ocean	Brown 1988, Jones 1997	Yes: pigmentation, field and lab experiments on zooxanthellae densities, chlorophyl 'a' contents
RNA / DNA ratios			Meesters *et al.* 2002	Yes: tested in field and lab, and developed new laboratory analytical technique
Coral diseases and cyanobacterial blooms	Monitoring the frequency and severity of occurrences of coral diseases and cyanobacterial blooms. No formal interpretive framework.	Western Atlantic (Florida)	Richardson 1997	No
Bioaccumulation of metals, phosphorus	Measurement of bioaccumulation of seawater contaminants in hard coral skeletons. No formal interpretive framework.	Pacific, Caribbean, Indian Ocean	Dodge *et al.* 1984, LeTissier & Brown 1988, Hanna & Muir 1990	No
Physical damage	Measurement of physical damage to corals via transects or quadrates as an indicator of over use. The exact cause of physical damage is never totally certain.	Red Sea, Caribbean	Dixon *et al.* 1993, Chadwick-Furman 1996, Hawkins & Roberts 1996, Jameson *et al.* 1997	Yes: partial mortality in *Porites*

b) Macrophyte-based indicators

Bioindicator	Protocol	Location	References	Included here
Macrophytes as metal bioaccumulators	Analysis of macrophytic algal tissues for bioaccumulation of heavy metal seawater contaminants. Utilizes atomic absorption spectrophotometry. Inconclusive results from coral reef study, shown effective in temperate marine systems. No formal interpretive framework.	Pacific, Caribbean, Indian Ocean	Bryan & Hummerstone 1973, Phillips 1974, Brown & Holly 1982	No
Macrophyte communities	Several volunteer reef surveys (Aquanaut and Reef Check) suggest recording macrophytic algal blooms as an indication of high nutrient inputs on coral reefs (or overfishing of fish and invertebrate grazers). No formal interpretive framework.	Pacific, Caribbean, Indian Ocean	McManus *et al.* 1997, Hodgson 1997, Fabricius *et al.*, 2005	Yes

c) Indicators based on coral reef epifauna

Bioindicator	Protocol	Location	References	Included here
Foraminifers	Community response to gradually increasing nutrient flux, whether natural or anthropogenic, favours phytoplankton, benthic algae, and heterotrophic taxa lacking algal symbionts, rather than taxa that use algal symbionts for enhanced growth and calcification. Benthic succession along a nutrification gradient is a predictable response that has been commonly observed in foraminiferal assemblages.	Pacific, Caribbean, Indian Ocean	Cickey *et al.* 1996, Hallock-Muller 1996, Hodgson 1997	Yes
Diatom biofilms				Yes
Bacterial biofilms				Yes
Sessile reef community	Uses data from line intercept transects of sponge, gorgonian assemblages. Calculation of two well-known diversity indices, H' and J', and comparison of their relative values allows a classification of environmental conditions (favourability and predictability) on a reef.	Caribbean	Alcolado *et al.* 1994	Yes, octocoral communities

Bioindicator	Protocol	Location	References	Included here
Heterotrophic macroinvertebrates	Largely undeveloped, based upon the well-substantiated observation that many pollution-stressed reefs undergo an "ecosystem shift" from those dominated by coral-algal symbionts towards those dominated by heterotrophic macroinvertebrates, especially scavengers, filter feeders, and internal bioeroders. Abundance measures of many of these groups are included in several current monitoring schemes, but no formal interpretive framework is in place at this time.	Pacific, Caribbean, Indian Ocean	Dahl 1981, Dustan & Halas 1987, Tomascik & Sander 1987a, Kinsey 1988, Risk *et al.* 1994, Tomascik *et al.* 1994, Hodgson 1997, McManus *et al.* 1997	Yes, internal bioeroders in *Porites,* heterotrophic octocorals
Internal bioeroders	Studies in both the Caribbean and Pacific have shown conclusively that the proportion of rubble (or live coral colonies) invaded by bioeroding sponges and bivalves, as well as the number of invasions per rubble sample increase with increasing eutrophication. Not formally proposed as bioindicator, but obvious potential.	Pacific, Caribbean, Indian Ocean	Rose & Risk 1985, Sammarco & Risk 1990, Risk *et al.* 1995, Holmes 1997	Yes, internal bioeroders in *Porites*
Coelobites (reef cavity-dwellers)	Shown that coelobites such as foraminifers, bryozoans, tunicates, molluscs and serpulid worms decrease in abundance with proximity to an offshore oil drilling well-head. Developed numerical index with points assigned for presence/absence and abundance of various coelobites in each rubble piece, with resulting index used to classify reef health.	Pacific (Philippines)	Choi 1982	No
Stomatopod crustaceans	Bioassay still under development. Studies from both the Caribbean and Pacific show conclusively that stomatopod abundance, diversity, and recruitment are strongly negatively correlated with various pollution measures. No formal interpretive framework.	Pacific, Caribbean, Indian Ocean	Steger & Caldwell 1993, Erdmann 1997b, Erdmann & Caldwell 1997, Erdmann & Sisovann (in press)	No
Foraminifers	Community response to gradually increasing nutrient flux, whether natural or anthropogenic, favours phytoplankton, benthic algae, and heterotrophic taxa lacking algal symbionts, rather than taxa that use algal symbionts for enhanced growth and calcification. Benthic succession along a nutrification gradient is a predictable response that has been commonly observed in foraminiferal assemblages.	Pacific, Caribbean, Indian Ocean	Cickey *et al.* 1996, Hallock-Muller 1996, Hodgson 1997	Yes

Bioindicator	Protocol	Location	References	Included here
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Bacterial biofilms				Yes
Sessile reef community	Uses data from line intercept transects of sponge, gorgonian assemblages. Calculation of two well-known diversity indices, H' and J', and comparison of their relative values allows a classification of environmental conditions (favourability and predictability) on a reef.	Caribbean	Alcolado *et al.* 1994	Yes, octocoral communities
Heterotrophic macroinvertebrates	Largely undeveloped, based upon the well-substantiated observation that many pollution-stressed reefs undergo an "ecosystem shift" from those dominated by coral-algal symbionts towards those dominated by heterotrophic macroinvertebrates, especially scavengers, filter feeders, and internal bioeroders. Abundance measures of many of these groups are included in several current monitoring schemes, but no formal interpretive framework is in place at this time.	Pacific, Caribbean, Indian Ocean	Dahl 1981, Dustan & Halas 1987, Tomascik & Sander 1987a, Kinsey 1988, Risk *et al.* 1994, Tomascik *et al.* 1994, Hodgson 1997, McManus *et al.* 1997	Yes, internal bioeroders in *Porites,* heterotrophic octocorals
Internal bioeroders	Studies in both the Caribbean and Pacific have shown conclusively that the proportion of rubble (or live coral colonies) invaded by bioeroding sponges and bivalves, as well as the number of invasions per rubble sample increase with increasing eutrophication. Not formally proposed as bioindicator, but obvious potential.	Pacific, Caribbean, Indian Ocean	Rose & Risk 1985, Sammarco & Risk 1990, Risk *et al.* 1995, Holmes 1997	Yes, internal bioeroders in *Porites*
Coelobites (reef cavity-dwellers)	Shown that coelobites such as foraminifers, bryozoans, tunicates, molluscs and serpulid worms decrease in abundance with proximity to an offshore oil drilling well-head. Developed numerical index with points assigned for presence/absence and abundance of various coelobites in each rubble piece, with resulting index used to classify reef health.	Pacific (Philippines)	Choi 1982	No
Stomatopod crustaceans	Bioassay still under development. Studies from both the Caribbean and Pacific show conclusively that stomatopod abundance, diversity, and recruitment are strongly negatively correlated with various pollution measures. No formal interpretive framework.	Pacific, Caribbean, Indian Ocean	Steger & Caldwell 1993, Erdmann 1997b, Erdmann & Caldwell 1997, Erdmann & Sisovann (in press)	No

Bioindicator	Protocol	Location	References	Included here
Amphipods	In addition to acute and chronic sensitivities to pollutants and toxicants, amphipods exhibit a number of altered behavioral responses to sublethal levels of a variety of compounds that can cause reduction or elimination of the population. Amphipods are more sensitive than other species of invertebrates (decapods, polychaetes, molluscs, and asteroids) to a variety of contaminants. Amphipods also show responses to dredging, shoreline alteration, fishing practices, salinity, and dissolved oxygen.	Pacific, Caribbean, Indian Ocean	Barnard 1958, 1961, McCluskey 1967, 1970, Baker 1971, Widdowson 1971, Sandberg *et al.* 1972, Vobis 1973 Ahsanullah 1976, Percy 1976, Linden 1976a, 1976b, Lee *et al.* 1977, Oakden *et al.* 1984, Swartz *et al.* 1985, Swartz 1987, Thomas 1993,	No
Gastropod imposex	Well-developed bioassay. Gastropod imposex (imposition of male sexual characters on females) is extremely sensitive indicator of exposure to tributyl tin. Occurrence and severity of imposex in a particular population is quantified using both frequency of imposex in females and relative penis size index - mean ratio of penis weight to body weight for all females divided by same ratio for males.	Pacific, Caribbean, Indian Ocean	Ellis & Pattisina 1990, Foale 1993, Gibbs & Brya 1994, Evans *et al.* 1995	No
Corallivores	Records abundance of corallivores such as crown-of-thorns starfish (*Acanthaster planci*) and *Drupella gastropods*. No formal interpretive framework.	Pacific	Gajbhiye *et al.* 1987, Herrnkind *et al.* 1988, Garrity & Levings 1990 Erdmann 1997b,	Ongoing research on COTS.

d) 'Other' indicators

Bioindicator	Protocol	Location	References	Included here
Nitrogen isotope ratios	Stable isotope ratios of $^{15}N/^{14}N$ (denoted d ^{15}N) in reef organism tissues have been shown to be an excellent indicator of human faecal waste inputs on coral reefs. Calibration of d ^{15}N is necessary for each specific organism and region, but very powerful and accurate means of assessing this form of organic enrichment. Uses mass spectrophotometer to measure d ^{15}N.	Pacific, Caribbean, Indian Ocean	Risk *et al.* 1994, Dunn 1995, Risk & Erdmann (in press)	No
Soft-bottom benthic community structure	Used extensively in temperate marine ecosystems, but not yet applied to coral reefs. Large body of work shows consistent, predictable responses in soft bottom community structure to increasing pollution, including decrease in species richness, increase in total number of individuals, reduction in the mean size of the average species or individual, changes in shape of log-normal distribution of individuals among species, and increased variability in species diversity indices. Needs further research to apply to coral reefs.	Various	Pearson & Rosenberg 1978, Gray & Mirza 1979, Pearson *et al.* 1983, Gray, 1981, 1989, Warwick 1986, Bilyard 1987, Brown 1988, Weston 1990, Clarke 1993, Warwick & Clarke 1993	Yes, biofilms

Bioindicator	Protocol	Location	References	Included here
Map-based indicators of potential threats to coral reefs	While still experimental, the "Reefs at Risk" indicators flag problem areas around the world where – in the absence of good management – coral reef degradation might be expected, or predicted to occur shortly, given ongoing levels of human activity. Results are based on a series of distance relationships correlating mapped locations of human activity, such as ports and towns, oil wells, coastal mining activities and shipping lanes (component indicators) with predicted risk zones of likely environmental degradation. Detailed sub-national statistics on population density, size of urban areas, and land cover type were also incorporated into the analysis. Data on rainfall and topography are used to estimate potential runoff within watersheds, from inland deforestation and agriculture. To make these indicators approach reality, a time factor must be incorporated into them, otherwise there is no feeling of urgency to the threats. Some of the map-based indicator assumptions need work as they are confounded by other factors or simply invalid.	Global	Berke *et al.* 1998	Previously done by GBRMPA, formed basis of our assessments
Rapid Assessment of Management Parameters ("RAMP indicators") for assessing the human impacts (social, cultural and economic) on coral reefs	Indicators are organized according to proximity to the designated reef (e.g. national, regional and local), context (political, socioeconomic and cultural), reef uses (fishing, mining, tourism/recreational, etc.), and governance (institutional frameworks, knowledge bases, plans, implementation, monitoring and evaluation). A guide for information acquisition and subsequent coding for inclusion in ReefBase was also developed. Relating RAMP indicators to coral reef ecosystem integrity will require the development of special indices and calibration.	Pacific Caribbean	Pollnac 1997	No

1.4 References

Bourke L, Selig E, Spalding M. 2002. Reefs at risk in Southeast Asia. World Resources Institute, Cambridge

Brodie J, Fabricius K, De'ath G, Okaji K. 2005. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. Marine Pollution Bulletin 51: 266-278

Brown BE. 1987. Heavy metals pollution on coral reefs. In: Salvat B (ed) Impacts des activites humaines sur les recifs coralliens: connaissances et recommandations, pp 119-134

Bryant DG, Burke L, McManus J, Spalding M. 1998. Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, Washington DC

DeVantier L, De'ath G, Done T, Turak E, Fabricius K. 2006. Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. Coral Reefs 25: 329–340

Fabricius K, De'ath G, McCook L, Turak E, Williams DM. 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef.Marine Pollution Bulletin 51: 384-398

Fabricius KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50: 125-146

Fabricius KE. 2006. Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: Implications for coral bleaching? Limnology and Oceanography 51: 30-37

Fabricius KE, De'ath G. 2004. Identifying ecological change and its causes: A case study on coral reefs. Ecological Applications 14: 1448-1465

Furnas MJ. 2003. Catchments and Corals: Terrestrial Runoff to the Great Barrier Reef. Australian Institute of Marine Science, CRC Reef. Townsville, Australia.

GESAMP. 2001. Protecting the oceans from land-based activities. Land-based sources and activities affecting the quality and uses of the marine, coastal and associated freshwater environment. United Nations Environment Program, 71, Nairobi

Guzman HM, Holst I. 1993. Effects of chronic oil-sediment pollution on the reproduction of the Caribbean reef coral *Siderastrea siderea*. Marine Pollution Bulletin 26: 276-282

Harrington L, Fabricius K, Eaglesham G, Negri A. 2005. Synergistic effects of diuron and sedimentation on photosynthetic yields and survival of crustose coralline algae. Marine Pollution Bulletin 51: 415-427

Heyward AJ. 1988. Inhibitory effects of copper and zinc sulphates on fertilization in corals. In: Choat JH, Barnes D, Borowitzka MA, Coll JC, Davies PJ, Flood P, Hatcher GB, Hopley D (eds) Proceedings of the Sixth International Coral Reef Symposium, Townsville. pp 299-303.

Hoegh-Guldberg O, Hoegh-Guldberg H. 2004. The Implications of Climate Change for Australia's Great Barrier Reef. WWF-Australia, Sydney

Jameson SC, Erdmann MV, Gibson GR, Jr., Potts KW. 1998. Development of biological criteria for coral reef ecosystem assessment. Atoll Research Bulletin 450: 1-108

Jameson SC, Erdmann MV, Karr JR, Potts KW. 2001. Charting a course toward diagnostic monitoring: A continuing review of coral reef attributes and a research strategy for creating coral reef indexes of biotic integrity. Bulletin of Marine Science 69: 701-744

Jones RJ, Kerswell AP. 2003. Phytotoxicity of Photosystem II (PSII) herbicides to coral. Marine Ecology Progress Series 261: 149-159

Jones RJ, Muller J, Haynes D, Schreiber U. 2003. Effects of herbicides diuron and atrazine on corals of the Great Barrier Reef, Australia. Marine Ecology Progress Series 251: 153-167

Loya Y, Rinkevich B. 1987. Effects of petroleum hydrocarbons on corals. In: Salvat B (ed) Impacts des activites humaines sur les recifs coralliens: connaissances et recommandations, pp 91-102

Matson PA, Parton WJ, Power AG, Swift MJ. 1997. Agricultural intensification and ecosystem properties. Science 277: 504-509

McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D. 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421: 727-730

Negri A, Vollhardt C, Humphrey C, Heyward A, Jones R, Eaglesham G, Fabricius K. 2005. Effects of the herbicide diuron on the early life history stages of coral. Marine Pollution Bulletin 51: 370-383

Owen R, Knap A, Ostrander N, Carbery K. 2003. Comparative acute toxicity of herbicides to photosynthesis of coral zooxanthellae. Bulletin of Environmental Contamination and Toxicology 70: 541-548

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

Smith SV, and 10 other authors 2003. Humans, hydrology and the distribution of inorganic nutrient loading to the ocean. BioScience 53: 235-245

Spalding MD, Ravilious C, Green EP. 2001. World Atlas of Coral Reefs. University of California Press, Berkeley

Tilman D, and 9 other authors 2001. Forecasting agriculturally driven global environmental change. Science 292: 281-284

van Woesik R, Tomascik T, Blake S. 1999. Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. Marine and Freshwater Research 50: 427-440

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7: 737-750

Weber M, Lott C, Fabricius K. 2006. Different levels of sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, geochemical and organic properties. Journal of Experimental Marine Biology and Ecology 336: 18–32

Wolanski E, Fabricius K, Spagnol S, Brinkman R. 2005. Fine sediment budget on an inner-shelf coral-fringed island, Great Barrier Reef of Australia. Estuarine and Coastal Shelf Science: 65:153–158

Yentsch CS, Yentsch CM, Cullen JJ, Lapointe B, Phinney DA, Yentsch SW. 2002. Sunlight and water transparency: cornerstones in coral research. Journal of Experimental Marine Biology and Ecology 268: 171-183

Chapter 2: Gradients in water column nutrients, sediments, irradiance and coral reef development in the Whitsunday region, central Great Barrier Reef

Timothy F Cooper, Sven Uthicke, Craig A Humphrey and Katharina E Fabricius

Abstract

Spatial variation of water column characteristics, sediment and irradiance on coral reefs was examined in the Whitsunday region of the Great Barrier Reef during five sampling events between 2004 and 2006 (Fig. 2.1). Sampling locations were selected along a transect from outer reefs distant from terrestrial inputs, to coastal reefs near the Australian mainland. Most of the water column variables (especially chlorophyll *a*, total suspended solids, particulate organic carbon and particulate nutrients) and irradiance variables (Secchi and optical depth) changed significantly along the transect. For example, concentrations of chlorophyll *a* and total suspended solids increased two- and three-fold, respectively, from outer to coastal locations, while sediment inorganic carbon decreased and sediment colour became darker. Similarly, Secchi and optical depth, two measures of water transparency, decreased approximately three-fold towards the coast. Most of these gradients were persistent over the five sampling events, but for several parameters, the magnitude and steepness of the gradient changed. The maximum depth of zooxanthellate corals increased five-fold along the gradient and was related significantly to a water quality index derived for the Whitsunday Islands. Our data of the maximal depth limit for reef development at locations where suitable settlement substrata were available suggest that the absolute minimum of light required for a reef to persist is in the range of 6-8% of surface irradiance in the Whitsunday Islands.

2.1 Introduction

Catchments adjacent to the Great Barrier Reef (GBR) have undergone extensive modification over the past 150 years (Furnas 2003). This has led to the receiving waters of the GBR experiencing a four-fold increase in the input of nutrients (Moss *et al.* 1992; Neil *et al.* 2002), a five to ten-fold increase in the amount of sediment (McCulloch *et al.* 2003) and an increase in the zone of influence of nutrient enrichment by a factor of approximately 10 to 20 times (Wooldridge *et al.* 2006). Most of the terrestrial runoff affecting these reefs occurs during episodic flood events, predominately during the monsoonal wet season between December and May (Devlin and Brodie 2005). Concentrations of nutrients, sediments and contaminants are greatly enhanced in these plumes inundating nearshore reefs for periods of several days (Haynes and Michalek-Wagner 2000; Devlin *et al.* 2001). Consequently, reefs adjacent to catchments with high rainfall and altered land-use, such as the Wet Tropics and Whitsunday Islands, are considered to be at significant risk from changes in water quality (Devlin *et al.* 2001).

A growing body of evidence suggests that cross-shelf gradients in water quality are more persistent in regions with high agricultural runoff than in more remote areas of the GBR with greatest concentrations occurring nearest the coast (Brodie *et al.* 1997; Furnas *et al.* 1997; Fabricius and De'ath 2004; Brodie *et al.* 2007). Changes in water quality are known to influence the physiology, trophic structure and ecology of benthic coral reef assemblages (van Woesik *et al.* 1999; Fabricius 2005; Fabricius *et al.* 2005). Sedimentation also affects a wide range of physiological and ecological responses in benthic coral reef assemblages (Rogers 1990; Gilmour 2002; Philipp and Fabricius 2003). Sediment quality varies naturally with distance from the coast along the GBR, but variations may be enhanced through increased terrestrial discharges from agricultural lands. In general, the proportion of organic

carbon, nitrogen and chlorophyll *a* in sediments decreases with distance from the coast whereas the amount of inorganic carbon decreases (van Woesik *et al.* 1999; Hamilton 2001; Brunskill *et al.* 2002; Schaffelke *et al.* 2004; Schaffelke *et al.* 2005; Uthicke 2006). Recent studies have shown that different types of sediment have contrasting effects on coral photophysiology. Exposure of corals to sedimentation by nutrient-rich silt resulted in greater photophysiological stress (i.e. lower photosynthetic yields, F_v/F_m) than sedimentation by nutrient-poor sand, silt or carbonate sediments (Weber *et al.* 2006). Thus, investigations of sediment quality are necessary to understand the environmental controls on coral reefs.

The energetic requirements of corals are partially covered by autotrophy due to the presence of photosynthetic endosymbionts (zooxanthellae) within their tissue. Light is therefore amongst the most significant factors influencing the distribution of corals and coral reefs (Falkowski *et al.* 1984; Muscatine 1990). The light regime on coral reefs varies spatially and temporally by up to three orders of magnitude with depth, reef topography, cloud cover, tidal movement and turbidity (Larcombe *et al.* 1995; Anthony and Hoegh-Guldberg 2003; Anthony *et al.* 2004). For example, in Cleveland Bay (Central GBR), Anthony *et al.* (2004) found that temporal variation in irradiance on a nearshore reef was dominated by variations in turbidity (accounting for 74–79% of the variance), followed by cloud cover (14–17%) and tidal flow (7–10%). Light limitation due to turbidity or suspended solids for corals is weather-dependent (Larcombe *et al.* 1995; Orpin *et al.* 2004; Wolanski *et al.* 2005) and extended periods of rough weather can result in increased light attenuation for periods of up to several days (Cooper and Ridd, unpub. data). Few studies, however, have examined spatial patterns of variation in light regimes to assess the effects of variations in irradiance on coral reefs.

The depth where light intensity attains a level where oxygen production of the symbionts equals consumption in corals is known as compensation depth. Some species of corals can alter the proportion of their nutrition obtained from autotrophy and heterotrophy (Porter 1976; Anthony and Fabricius 2000), a strategy that can help to maintain some growth below their compensation depth. Since light attenuation is influenced by water quality, the lowest depth limit of autotrophic reef development is likely to approximate the compensation depth in corals (Titlyanov and Latypov 1991). Indeed, van Woesik *et al.* (1999) showed that the maximum depth of corals was related positively with distance away from the discharge of two rivers, and negatively with a range of water column and sediment variables.

To investigate the effects of changes in water column conditions on inshore coral reef systems, reliable physico-chemical and irradiance measures are needed as environmental variables against which to assess ecological changes in coral reef communities. The aim of this study was to estimate the spatio-temporal variation of a range of key resources required by corals. The variables characterised included nutrients, sediment and irradiance at twelve different locations in the Whitsunday Islands on five separate occasions. The measured changes in water quality were then related to the depth of coral reef development on reefs along the gradient. The locations were distributed along an inshore-offshore transect, tracing a water quality gradient that is confirmed by a long-term chlorophyll program that has been monitoring chlorophyll monthly over a 12 year period (Brodie *et al.* 2007). Episodic flood events are an important influence on the water quality in the Whitsunday Islands, as a of a flood event on 28 January 2005. The image highlights the complex nature of flood plumesin the region, , including retention through eddy formation, natural resuspension events, and areas of elevated suspended particles near the mouths of the two rivers changing to a plume of increased phytoplankton abundance (indicative of nutrient enrichment) that extends throughout the inner islands.

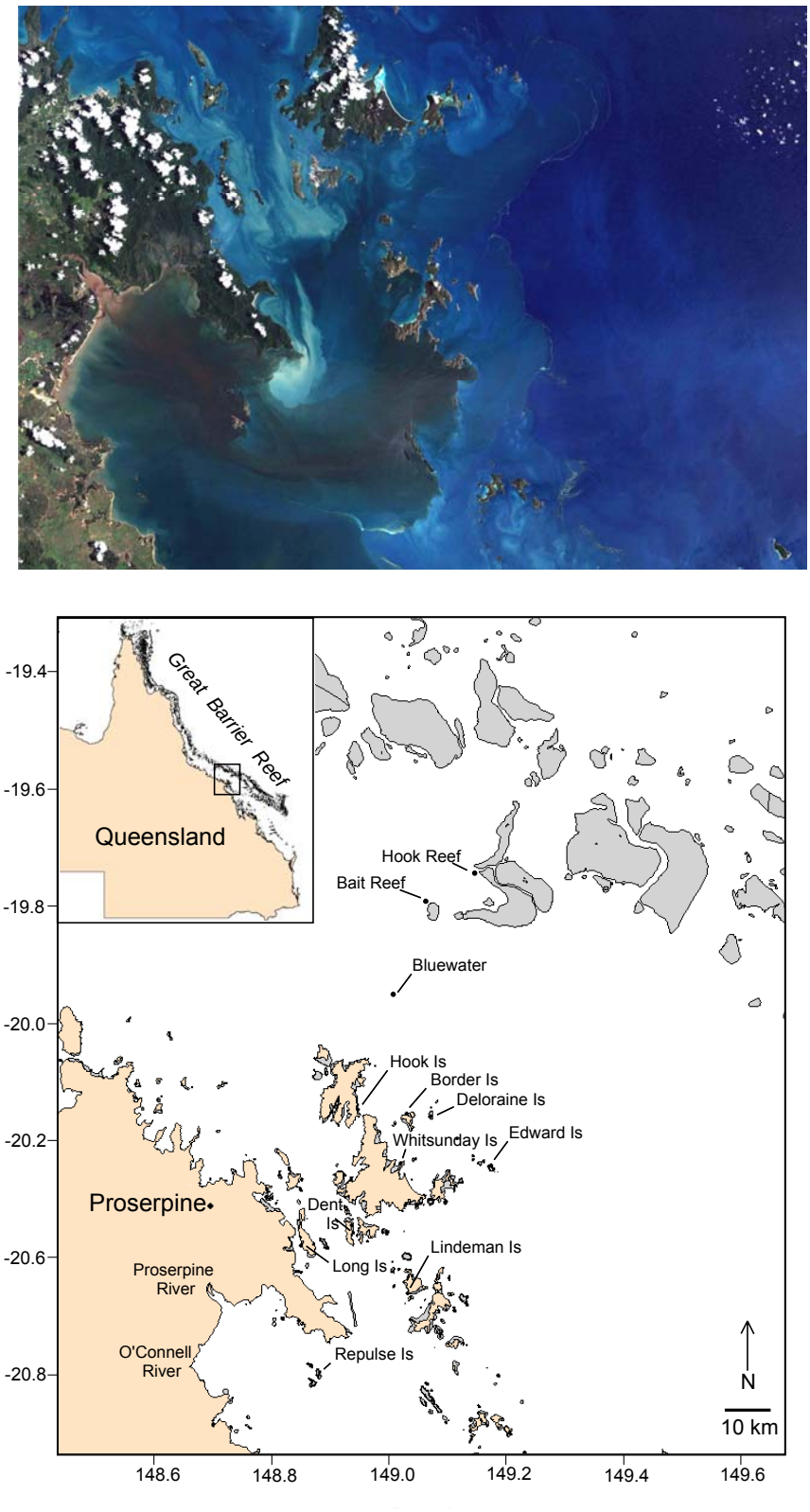

Figure 2.1. (a) Satellite image (Landsat 5 TM) of the Whitsundays Islands showing a flood plume emerging from the Pioneer and O'Connell Rivers, 28 January 2005. Areas of elevated suspended solids are visible near the mouths of the rivers, with areas of increased phytoplankton indicative of nutrient enrichment extend through the islands; (b) Map of study locations in the Whitsunday Islands of the Great Barrier Reef, Australia.

2.2 Materials and methods

Study area

The Whitsunday Islands are located in the central section of the GBR between latitude 20°00'-20°30'S and longitude 148°45'-149°15'E. Rainfall within the region occurs mostly during the Austral summer and varies inter-annually between 1200-2000 mm. Tides within the Whitsunday region are semidiurnal and the tidal range can exceed 4.0 m, which is slightly higher than most other areas on the GBR. The Proserpine and O'Connell Rivers flow into Repulse Bay (south-west of the Whitsunday Islands) and provide a point-source discharge of terrestrial runoff into the study area although water flow in the Proserpine River is regulated by the Peter Faust Dam built in 1991 (van Woesik *et al.* 1999). The catchment area of the two river systems combined is ~4900 km^2 and land use is dominated by agriculture such as grazing and cropping (mainly sugarcane), and minor urbanisation (Furnas 2003).

This study focused on twelve locations in the Whitsunday Islands b). This included reefs fringing Repulse, Lindeman, Long, Dent, Whitsunday, Hook, Deloraine, Edward and Border Islands; and further offshore two mid-shelf reefs (Bait and Hook) and a Bluewater location midway between the outer Whitsunday Islands and the mid-shelf reefs. Although distributed along a gradient, the locations naturally separated into nearshore locations, (directly influenced by rivers, and within 20 km of the Australian mainland), outer islands (>20 km from the coast and sheltered from direct coastal influences but potentially indirectly exposed to resuspended and materials transported further offshore), and offshore locations away from all coastal influences. Sampling was carried out in August 2004, August 2005, January 2006, February 2006 and August 2006. Several locations were sampled on more than one occasion during each sampling event, hence some variables were unbalanced with respect to Time.

Water column

Surface water was sampled at each location measuring the following variables: chlorophyll a, particulate nitrogen (PN), phosphorus (PP), particulate organic carbon (POC), total suspended solids (TSS), dissolved inorganic nutrients (NH_4, NO_2, NO_3, PO_4, $Si(OH)_4$), total dissolved nutrients (TDN and TDP) and dissolved organic nutrients (DON and DOP). For each of chlorophyll *a*, particulate nitrogen (PN), phosphorus (PP) and particulate organic carbon (POC), duplicate water samples were filtered through pre-combusted glass-fibre filters (25 mm, nominal pore size 0.2 μm) and stored at –20° C. In the laboratory, concentrations of chlorophyll *a* and phaeophytin were determined using a 10AU fluorometer following acidification with 0.1M HCl and 24-h dark extraction in 90% acetone at 4°C (Parsons *et al.* 1984) and the equations of Jeffrey and Humphrey (1975). Particulate nitrogen was determined using an ANTEK 9000NS analyser and ethylenediaminetetraacetic acid (EDTA) as standard. Levels of particulate phosphorus were determined by digestion with phosphate persulphate following the methods described by Menzel and Corwin (1965) and subsequent colorimetric determination of the phosphorus released as orthophosphate following Parsons *et al.* (1984). Particulate organic carbon was analysed on a Shimadzu analyser (TOC 5000A) after dissolving inorganic carbon with 1 M HCl and using standard reference material (BCSS-1 and MESS-1, Institute for Environmental Chemistry, Canada). To determine concentrations of total suspended solids, duplicate water samples (1 L) were filtered through pre-weighed polycarbonate filters (0.45 μm). Each filter was dried in an oven at 60°C for 24 hours and reweighed. For analysis of dissolved inorganic and organic nutrients, duplicate water samples were collected with a syringe and filtered through sterile polycarbonate filters (0.45 μm). Concentrations of dissolved inorganic nutrients and total dissolved nutrients (TDN and TDP) were determined using a Bran and Luebbe AA3

segmented flow analyser using methods described by Ryle *et al.* (1981). Concentrations of dissolved organic nutrients (DON and DOP) were determined by subtraction of the respective dissolved inorganic components (following UV irradiation of the samples to oxidise organic matter) from the levels of total dissolved nutrients.

Sediments

Grain size distribution, sediment colour and inorganic carbon content, which were not expected to vary in short time periods, were measured only in August 2004. Samples for sediment chemistry were collected in August 2004 and 2005, and February 2006. In August 2004, two sites were selected randomly on back (sheltered) and front (exposed) of ten of the study reefs. During all other times, two sites were selected on the back of each reef only. The sediment samples were taken in triplicates from each site using mini-corers (cut-off 60 ml syringes), and only the top 1 cm of sediment was used. This sediment was taken at the foot of the reef around 7 to 9 m depth, where the reef-slope usually intercepts the sandy bottom. On reefs more distant from the coast, the sampling depth was slightly deeper (foot of the reef ~12 m depth).

Sediment grain size was determined by sieving dried sediments (ca. 20-30 g) over a graded set of sieves (63, 125, 250, 500, 1000 and 2000 µm) and measuring the weight of each fraction, including the <63 µm fraction. The geometric mean for each sample was determined using Gradistat 4.0 (Blott and Pye 2001). Sediment grain size was analysed in two sub-samples from each location visited in August 2004.

The colour of each wet sediment sample in August 2004 was characterised in the laboratory using a set of Munsell colour charts (Hamilton 2001). In those charts, colours are defined by a hue, a value on a scale from 0 (black) to 10 (white) and a chroma between 0 (neutrally grey) and 20 using standardized colour fields. Subsequent to colour determination samples were frozen (-20°C) for further analyses. Concentrations of sediment chlorophyll *a* were determined following Sartory and Grobbelaar (1984) with adaptation to a Synergy HT (Bio-Tek) plate reader as described in Uthicke (2006). Approximately 1.5 g (wet-weight) of frozen sediment was heated for 5 min in 95% ethanol (78°C), followed by a 24 h extraction period in the dark at ca. 20°C. Of this extract, 320 µL was used in duplicate measurements on the plate reader before and after acidification with 18 µL of 0.1 M HCl. Measurements were conducted at 665 nm and values at 750 nm subtracted as a turbidity control. After extraction the dry weight of the sediment was determined and the chlorophyll *a* content calculated as in Sartory and Grobbelaar (1984).

The remaining sediment of each sample was dried and ground for carbon and nitrogen analysis. Total carbon was analysed on a Shimadzu analyser (TOC 5000A) and organic carbon was analysed on the same instrument after dissolving inorganic carbon with 1 M HCl. Concentrations of total nitrogen were determined with an ANTEK 9000NS analyser. Blanks were run with all samples and both carbon and nitrogen values were calibrated against Acetanilide (Ajax Chemicals) and a standard sediment (Gould Island 1.2.C).
Organic carbon and nitrogen concentrations and sediment pigment concentrations were determined for sediments in August 2004, August 2005 and February 2006. Chlorophyll *a* and C and N data from August 2004 have been summarised previously (Uthicke 2006).

Irradiance

Water clarity was measured using a Secchi disk during full sunlight between 1000 and 1400 to minimise confounding effects due to surface reflectance (Kirk 1994). At the same time, irradiance at each location was characterised using 2π cosine-corrected light sensor (LI-192, LI-COR, USA), which measures photosynthetically active radiation (PAR) between 400 to 700 nm. The light sensor was lowered through the water column and downward irradiance

measured at subsurface, then at 1 m increments, to a maximal depth of 15 m. The exponential decrease in irradiance with depth for each location was described using Beer-Lambert's Law:

$$E_z = E_0 \times e^{-kd.z} \qquad (1)$$

where E_z is irradiance at a given depth, E_0 is irradiance beneath the surface, k_d (PAR) is the diffuse attenuation coefficient for downwards irradiance and z is depth in metres. By rearranging Equation (1), we estimated k_d (PAR) as:

$$k_d = \ln(E_z/E_0)/z \qquad (2)$$

Optical depth can be used as a measure of transparency of the water column as it describes the proportion of light that is absorbed by the medium through which it passes. Curve fitting for estimation of k_d (PAR) and optical depth omitted values shallower than 5 m because k_d (PAR) does not remain constant in the upper depths of the water column (Kirk 1994). Estimates of the optical depth (τ) were determined using the inverse of k_d (PAR) determined from Equation (2). Large values for optical depth (small k_d PAR) indicate clear water, and conversely, small values for optical depth indicate turbid water.

To further characterise the light climate on selected nearshore (high turbidity) and outer (low turbidity) reefs, Odyssey data loggers (with a cosine corrected photosynthetic irradiance sensor 400-700 nm) were deployed at two depths (tide corrected; 3 m below lowest astronomical tide [LAT]; 6 m below LAT) on the leeward sides of Lindeman, Long and b) for 4 diurnal cycles each in January and February 2006. The Odyssey light loggers were calibrated against the LI-192 light sensor.

Maximum depth coral reef development

The lowest depth limit of coral reef development was estimated by two observers using Scuba on one or two sites per reef. We recorded the lowest limit of reef development, which coincided with the zone of transition from zooxanthellate hard corals to azooxanthellate octocorals wherever hard substratum was available. Using mean k_d (PAR) values measured at each location from three field surveys, combined with the depth distribution data, we estimated the percent of surface irradiance that would limit the depth distribution of coral reef development in the Whitsunday Islands.

Statistical analysis

A water quality index was calculated using the sum of a z-score transformation ($x = 0$, $\sigma = 1$) for water column variables (chlorophyll *a*, phaeophytin, total suspended solids, particulate organic carbon, particulate nitrogen and phosphorus, dissolved inorganic/organic nutrients, silicate, Secchi depth and optical depth) measured at each of the locations in the Whitsunday Islands averaged over all sampling times following Fabricius *et al.* (2005). A negative z-score indicates water clearer with fewer nutrients than the sample average, whereas a positive z-score indicates turbid and nutrient-rich conditions. Linear models were used to test for relationships of the response variables (water column, sediment and irradiance; $\log_2$ transformed) with distance from the coast and among time of sampling. Distance and Time were considered as random factors in the analyses but the number of levels for Time varied for some variables (as they were not measured on all sampling events), hence the different degrees of freedom in some of the statistical tests. Pooling procedures involving elimination of terms from the mean square estimates were done if a term was non-significant at $P>0.25$. Principal Components Analysis (PCA) was used to examine the relationships between the study locations and the environmental variables with separate analyses done for the water

column and sediment variables. The two environmental variables, distance from the coast and water quality index, were superimposed onto the biplot. Pearson correlations were used to examine the relationship between the maximal depth of coral reef development and the environmental variables averaged over the five times of sampling. All analyses were done using the statistical software R (R Development Core Team 2006).

2.3 Results

Water column

The relationships between water column characteristics and distance from the coast of each location in the Whitsunday Islands and the outer locations are presented in Figure 2.2. Mean concentrations of chlorophyll *a*, suspended solids and particulate phosphorus were generally greater at the nearshore compared with the outer islands for all times of sampling. For example, mean concentrations of chlorophyll *a* were up to 1.9 times greater at Repulse Island (RI) (0.59 μg L^{-1} ± 0.12 SE, N=6) compared with the outer Edward Island (EI) (0.31 μg L^{-1} ± 0.06 SE, N=4) when averaged over all times of sampling. Similarly, mean concentrations of total suspended solids were approximately 2.9 times greater at Repulse Island (3.97 mg L^{-1} ± 0.49 SE, N=6) compared with Edward Island (1.36 mg L^{-1} ± 0.12 SE, N=5). Particulate phosphorus (RI: 0.11 μmol L^{-1} ± 0.01 SE, N=6; EI: 0.06 μmol L^{-1} ± 0.01 SE, N=5) and particulate organic carbon (RI: 20.35 μmol L^{-1} ± 2.78 SE, N=5; EI: 12.95 μmol L^{-1} ± 1.24 SE, N=5) were approximately 1.5 to 2.0 times greater at Repulse Island compared with Edward Island. In contrast, there were few spatial differences for levels of dissolved (inorganic and organic) nutrients with increasing distance from the coast.

The patterns of variation for chlorophyll *a*, particulate nitrogen, particulate phosphorus, particulate organic carbon, dissolved inorganic phosphorus and dissolved organic nitrogen were dominated by differences among times of sampling (Table 2.1, Figure 2.2). In addition to these differences in magnitude between sampling events, levels of chlorophyll *a*, particulate organic carbon and dissolved organic phosphorus varied significantly with distance from the coast. Generally, levels of these nutrients were greater at nearshore locations and decreased with increasing distance from the coast (Figure 2.2), demonstrating the persistence of an environmental gradient for some water column parameters in the Whitsunday Islands. Dissolved organic phosphorus was the only variable with a significant distance effect, but no difference between the sampling times.

Some of the variables varied inconsistently with distance from the coast and among times of sampling (Distance x Time interaction, Table 2.1). For example, slopes of total suspended solids were distinctly steeper in August 2004, 2005 and 2006 compared with the other times of sampling, which were not different from each other (Figure 2.2). Interestingly, there were positive relationships for the ratio of particulate nitrogen and organic carbon to total suspended solids in August 2005 and January 2006 indicating that suspended particles were becoming enriched with nitrogen and organic carbon with increasing distance from the coast (Figure 2.2).

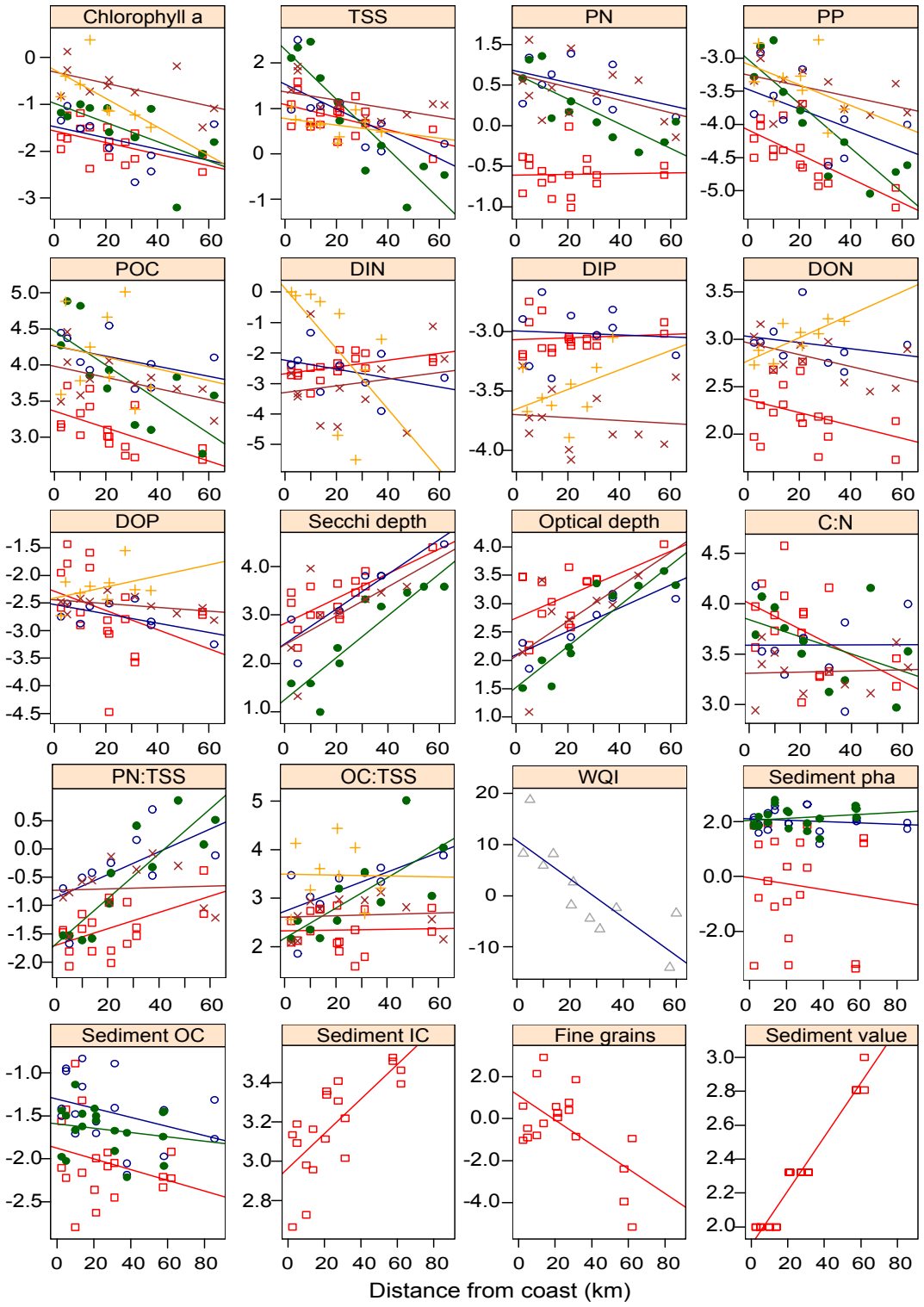

Figure 2.2. Summary of the relationships between each of the water column, sediment and irradiance variables and nearest distance from the coast. Samples collected from five sampling events between August 2004 and August 2006. Response variables are log_2 transformed, except for the Water Quality Index. Abbreviations: TSS = total suspended solids, PN = particulate nitrogen, PP= particulate phosphorus, POC = particulate organic carbon, DIN = dissolved inorganic nitrogen, DIP = dissolved inorganic phosphorus, DON = dissolved organic nitrogen, DOP = dissolved organic phosphorus. Water Quality Index (WQI) refers to the sum of z-scores calculated from z transformation of each of the water column and irradiance variables. Symbols represent each time of sampling: □ August 2004; ○ August 2005; + January 2006; × February 2006; ● August 2006.

Table 2.1. Summary of analyses comparing water column, sediment and irradiance parameters with distance from the coast and among times of sampling. Data are log_2 transformed, * denotes terms that were eliminated at *P*>0.25.

	Distance			Time			Distance x Time		
Variate	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Chlorophyll *a* (□g L^{-1})	1,46	19.78	0.0001	4,46	18.05	<0.0001	4,46	0.62	0.6514*
Total suspended solids (mg L^{-1})	1,4	6.34	0.0022	4,4	0.43	0.1365	4,49	7.79	0.0001
Particulate N (□mol L^{-1})	1,3	1.53	0.1506	3,3	22.11	0.0042	3,42	2.40	0.0809
Particulate P (□mol L^{-1})	1,4	14.17	0.0038	4,4	7.38	0.0073	4,49	2.56	0.0503
Particulate Organic C (□mol L^{-1})	1,47	15.49	0.0003	4,47	15.01	<0.0001	4,47	1.22	0.3162*
Dissolved inorganic N (□mol L^{-1})	1,3	0.19	0.4569	3,3	0.62	0.2509	3,40	3.81	0.0170
Dissolved inorganic P (□mol L^{-1})	1,40	0.12	0.7281	3,40	32.16	<0.0001	3,40	0.65	0.5869*
Dissolved organic N (□mol L^{-1})	1,3	1.16	0.2151	3,3	15.33	0.0087	3,40	2.11	0.1142
Dissolved organic P (□mol L^{-1})	1,40	4.23	0.0463	3,40	1.78	0.1659	3,40	1.20	0.3205*
C:N	1,3	3.32	0.1170	3,3	1.74	0.2356	3,40	1.43	0.2469
PN:TSS	1,3	6.30	0.0097	3,3	2.03	0.0385	3,42	5.55	0.0027
POC:TSS	1,4	2.82	0.0459	4,4	3.37	0.0242	4,47	2.90	0.0316
Sediment chlorophyll *a* (µg gDW^{-1})	1,2	0.03	0.8288	2,2	0.09	0.8321	2,51	2.17	0.1242
Sediment phaeophytin (µg gDW^{-1})	1,51	0.00	0.9682	2,51	26.77	<0.0001	2,51	0.28	0.7564*
Sediment pigment (µg gDW^{-1})	1,51	0.15	0.6970	2,51	0.17	0.8456	2,51	1.24	0.2967*
Sediment organic C (%DW)	1,50	3.04	0.0873	2,50	11.53	0.0001	2,50	0.19	0.8285*
Sediment N (%DW)	1,50	0.24	0.6251	2,50	0.48	0.6245	2,50	0.12	0.8874*
Secchi depth (m)	1,33	44.96	<0.0001	3,33	11.92	<0.0001	3,33	0.86	0.4694*
Optical depth (m)	1,33	27.60	<0.0001	3,33	7.18	0.0008	3,33	0.94	0.4340*

A PCA further illustrated the relationships of the water column variables among each other and their distribution across the locations. The nearshore reefs Repulse, Lindeman, Long and Dent Islands were associated with elevated levels of most of the water column variables (especially particulate organic carbon, particulate phosphorus, chlorophyll *a*, total suspended solids), and lower Secchi and optical depth (Figure 2.3). These nearshore islands also associated strongly with high values of the water quality index. In contrast, the outer islands and midshelf reefs (Whitsunday, Border, Deloraine, Edward, Bait Reef and Hook Reef) were related negatively to the water quality index and associated with distance from the coast (Figure 2.3). Only the dissolved inorganic nutrient forms DIP and DIN showed no clear correlation with distance from the coast in the PCA.

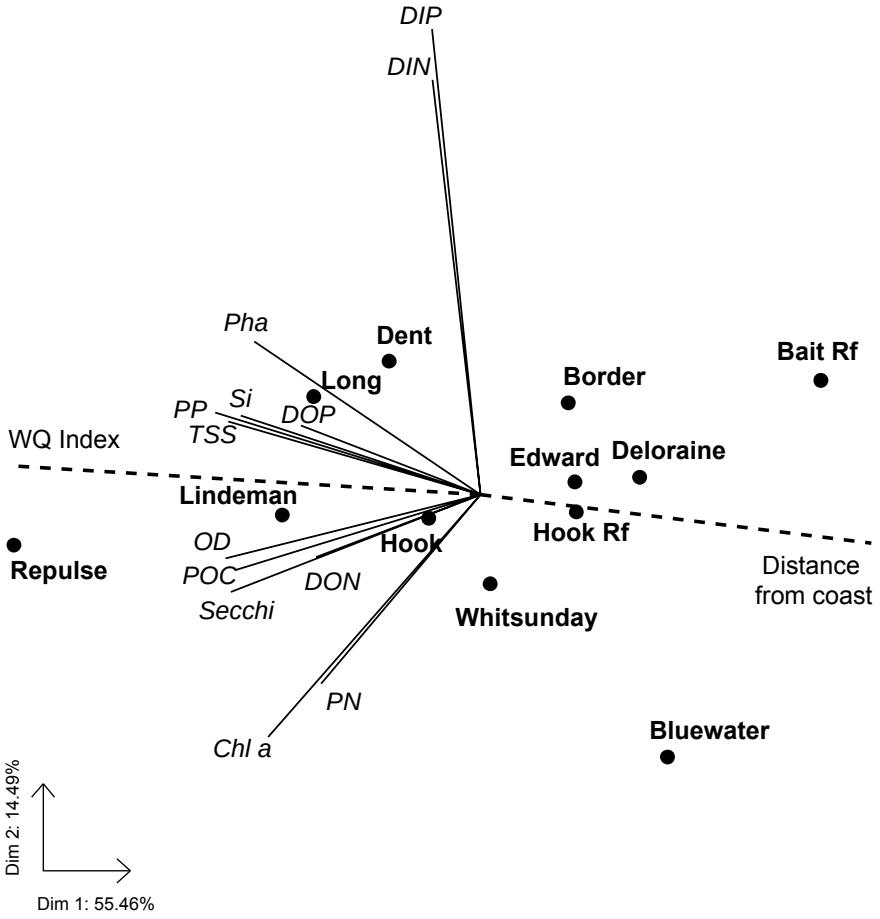

Figure 2.3. Principal components analysis of water column and irradiance variables sampled at the Whitsunday Islands for all sampling events. *Chl a* = chlorophyll *a*, *TSS* = total suspended solids, *PN* = particulate nitrogen, *PP* = particulate phosphorus, *POC* = particulate organic carbon, *DIN* = dissolved inorganic nitrogen, *DIP* = dissolved inorganic phosphorus, *DON* = dissolved organic nitrogen, *DOP* = dissolved organic phosphorus, *Si* = silicate, *Secchi* = Secchi depth, *OD* = optical depth. WQ Index refers to the index calculated for the water quality variables. Distance to coast is determined as nearest distance to the Australian mainland. The latter two parameters, indicated by dashed lines, are superimposed on the biplot.

Sediments

Average grain size varied widely among reefs and linear models did not detect a relationship with distance from the coast ($F_{(1, 17)} = 0.42$, $P = 0.5249$, $r^2 = 0.03$). In contrast, the percentage of fine sediments (<63µm) decreased significantly with distance from the coast ($F_{(1, 17)} = 10.28$, $P = 0.0051$, $r^2 = 0.34$, Figure 2.2).

The sediment colours (as defined by their hue, value and chroma) corresponded to colours found on Munsell charts 2.5Y and 5Y. The chroma exhibited little variation in August 2004. In contrast, the 'value' of the colour, expressing whether the sediment is dark or light, varied between very light colours (up to 8) and much darker values (4). Linear models demonstrated a highly significant relationship between the sediment colour value and the distance from the coast, with darker sediments found inshore than outer locations ($F_{(1, 17)} = 10.28$, $P < 0.0001$, $r^2 = 0.95$, Figure 2.2).

Mean concentrations of chlorophyll *a* and phaeophytin in surface sediments were 2.39 µg g DW^{-1} (± 0.16 SE, N=57) and 3.36 µg g DW^{-1} (± 0.24 SE, N=57), respectively, averaged over the three sampling periods. Linear models revealed no significant relationship with distance from the coast (Table 2.1), but phaeophytin levels were different between the sampling times (Table 2.1), with somewhat lower values in August 2004 (Figure 2.2).

Similarly, inorganic carbon concentrations showed a highly significant relationship with distance from the coast (presented in (Uthicke 2006), with values increasing with distance from the coast. However, even inshore reef sediments were dominated by inorganic carbon with values >50%, whereas outer shelf reef sediments reached values of over 90%.

Linear models of organic carbon as a function of the distance from the coast showed no significant deviation of the common slope from zero for all sampling dates (Table 2.1). However, the intercepts for the three sampling times were different as illustrated by a significant Time effect in the linear model. Indeed, average organic carbon content in the sediment was distinctly lower during the first collection period in August 2004 (0.257 %DW ± 0.021 SE, N=19), when compared with August 2005 (0.376 %DW ± 0.024 SE, N=18) and February 2006 (0.322 %DW ± 0.014 SE, N=19). In addition, there was a trend for concentrations of organic carbon to decrease with increasing distance from the coast (Table 2.1, Figure 2.2).

Sediment nitrogen concentrations varied considerably among reefs and locations (Figure 2.2). Although a general trend of greater values on reefs closer to the coast was observed, variability was high, and linear models did not detect a significant relationship between sediments nitrogen concentrations and distance from the coast (Table 2.1).

The relationships among the sediment variables and the reefs were illustrated in a PCA (Figure 2.4). This analysis also superimposed distance from coast and the water quality index for each reef (see above). The four nearshore reefs were located in close proximity, whereas all other reefs were more variable. High sediment organic carbon and phaeophytin content were associated strongly with the water quality index and the four nearshore reefs. In contrast, inorganic carbon content and sediment colour values were related negatively to the water quality index and associated with distance from the coast.

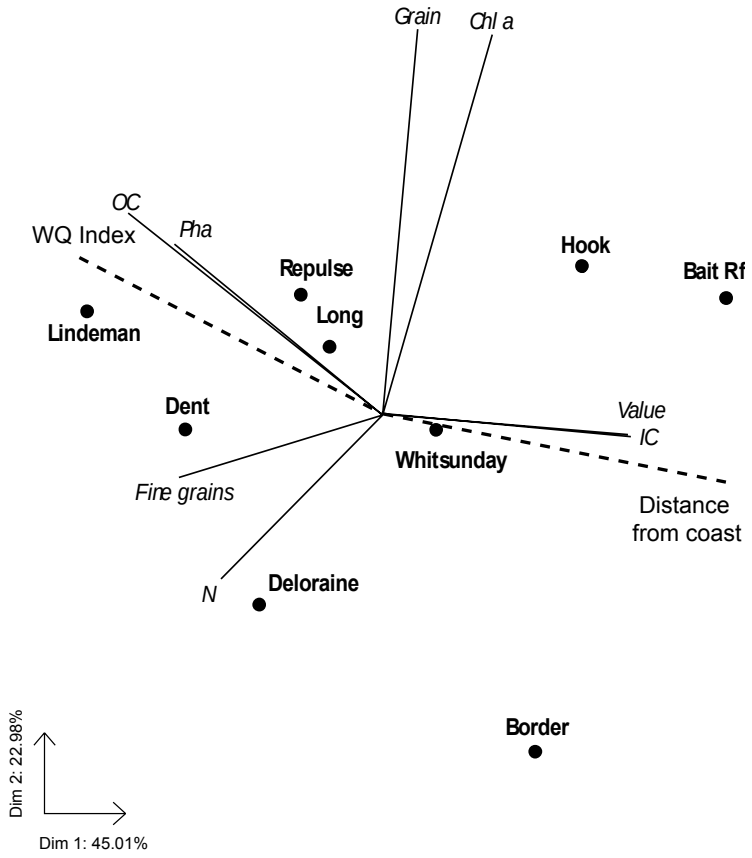

Figure 2.4. Principal components analysis of sediment variables at the Whitsunday Islands. *Chl a* = chlorophyll *a*, *Pha* = phaeophytin, *N* = nitrogen, *IC* = inorganic carbon, OC = organic carbon, *Value* = Munsell colour value of the sediment, *Grain* = average grain size, *fine grains* = sediments < 63 µm. WQ Index refers to the index calculated for the water quality variables. Distance from coast is determined as nearest distance from the Australian mainland. The latter two parameters are indicated by dashed lines.

Irradiance

Secchi depth differed among times of sampling and with distance from the coast in the Whitsunday Islands (Table 2.1). Mean Secchi depth increased from 4.0 m (± 0.8 SE, N=5) at Repulse Island to 12.3 m (± 1.0 SE, N=4) at Edward Island, and 15.3 m (± 3.3 SE, N=3) at the mid-shelf reefs (Figure 2.2). Similarly, the optical depth of the water column differed among times of sampling and with distance from the coast (Table 2.1) with the mean optical depth increasing from 3.77 m (± 0.60 SE, N=4) at Repulse Island to 8.92 m (± 0.49 SE, N=4) at Edward Island, and was 11.97 m (± 2.62 SE, N=3) at the mid-shelf reefs (Figure 2.2). The slopes in Secchi and optical depth with distance to the coast was similar on each sampling occasion, suggesting the existence of a light gradient as well as a water quality gradient in the Whitsunday Islands. Finally, the water quality index calculated from water column and irradiance variables decreased significantly with increasing distance from the coast (linear model, $F_{(1, 9)} = 17.85$, P=0.0022, $r^2 = 0.66$ Figure 2.2).

Total daily quanta received by the benthic community of three of the islands are summarised in Table 2.2. At any given depth, total daily quanta were about 1.5 - 2 times greater at the outer Deloraine Island compared with the nearshore Long and Lindeman Islands. Averaged over both deployments, total daily quanta at 6 m depth at Deloraine Island was similar to that at shallow depths of Long and Lindeman Islands (means: 23.2 ± 1.3 E m^{-2}, versus 24.1 ± 2.2 and 25.3 ± 3.0 E m^{-2}, respectively; Table 2).

Table 2.2. Total daily quanta (E m^{-2}) calculated from Odyssey PAR loggers deployed at 3 m and 6 m depth at three locations (Lindeman, Long and Deloraine Islands) on two occasions in the Whitsunday Islands. Data for Hardy Reef are for surface irradiance, supplied from the AIMS weather station (http://www.aims.gov.au/pages/facilities/weather-stations/weather-index.html). Numbers in brackets are % of surface irradiance at Hardy Reef.

	Hardy Reef	**Lindeman Is.**		**Long Is.**		**Deloraine Is**	
Date	Surface	3 m	6 m	3 m	6 m	3 m	6 m
18/01/2006	62.6	27.5 (44%)	15.8 (25%)	39.3 (63%)	16.8 (27%)	54.8 (87%)	27.1 (43%)
19/01/2006	63.9	25.0 (39%)	15.1 (24%)	31.2 (49%)	15.1 (24%)	49.3 (77%)	25.6 (40%)
20/01/2006	63.2	16.5 (26%)	10.4 (16%)	28.7 (45%)	17.3 (27%)	38.6 (61%)	24.6 (39%)
19/02/2006	61.0	31.5 (52%)	19.4 (32%)	20.2 (33%)	8.3 (14%)	39.3 (64%)	23.5 (39%)
20/02/2006	51.6	16.5 (32%)	10.4 (20%)	19.5 (38%)	8.8 (17%)	33.5 (65%)	21.2 (41%)
21/02/2006	60.2	28.5 (47%)	17.6 (29%)	20.2 (34%)	7.9 (13%)	37.9 (63%)	23.6 (39%)
22/02/2006	62.8	26.0 (41%)	14.4 (23%)	17.9 (29%)	7.3 (12%)	23.3 (37%)	16.7 (27%)
Mean January 06 (±SE)	**63.2 (0.4)**	**23.0 (3.3)**	**13.8 (1.7)**	**33.1 (3.2)**	**16.4 (0.7)**	**47.6 (4.7)**	**25.8 (0.7)**
Mean February 06 (±SE)	**58.9 (2.5)**	**25.7 (3.2)**	**15.4 (2.0)**	**19.5 (0.5)**	**8.1 (0.3)**	**33.5 (3.6)**	**21.3 (1.6)**
Overall mean (±SE)	**60.8 (1.6)**	**24.1 (2.2)**	**14.7 (1.3)**	**25.3 (3.0)**	**11.7 (1.7)**	**39.5 (3.9)**	**23.2 (1.3)**

Maximum depth coral reef development

The maximal depth of coral reef development increased almost five-fold from the nearshore to the outer islands. At Repulse Island, the depth limit of reef development was approximately 5 m (below LAT) increasing to approximately 24 m at the outer Edward Island, and 25 m at Hook Reef. The maximal depth of coral reef development showed significant negative correlations with a range of the water column variables including concentrations of water chlorophyll *a*, particulate phosphorus, particulate organic carbon and total suspended solids, and positive correlations with Secchi and optical depth (Table 2.3). The lower limit of reef development increased significantly with decreasing water quality index, i.e. from turbid to clear water conditions (linear model, $F_{(1, 9)} = 26.86$, P=0.0006, Figure 2.5).

Incorporating the estimates of the lower depth limits of corals into Equation 1 allowed determination of downward irradiance at the maximal depth of reef development (E_z). At Repulse, Whitsunday, Deloraine and Edward Islands, there was 6-8% of surface irradiance at the maximal depth limit of corals (Table 2.4). In contrast, at Lindeman, Long, Dent and Hook Islands, this limit was at 20-30% of surface irradiance (Table 2.4). At Hook Reef, there was approximately 4% of surface irradiance at the maximal depth limit of coral reef development (Table 2.4).

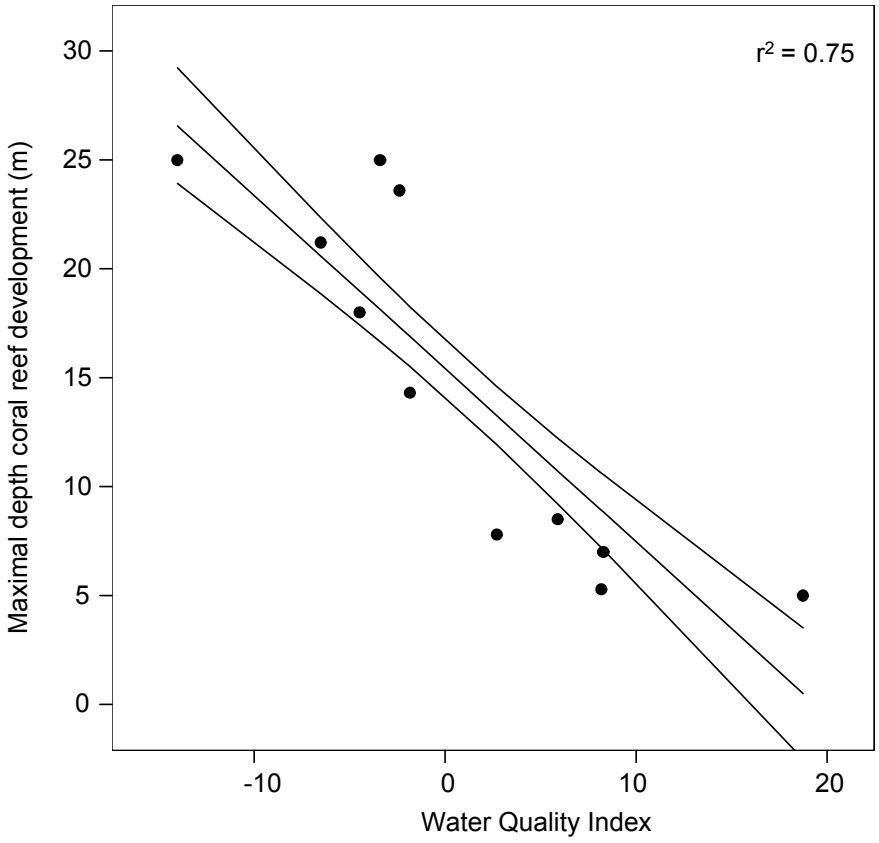

Figure 2.5. Relationship between maximal depth of coral reef development and the water quality index for the Whitsunday Islands.

Table 2.3. Pearson correlations between maximal depth coral reef development and environmental variables averaged for each time of sampling in the Whitsunday Islands. Abbreviations: Max depth = maximum depth of reef development; Chl *a* = chlorophyll *a*, PN = particulate nitrogen, PP= particulate phosphorus, POC = particulate organic carbon, TSS = total suspended solids, DIN = dissolved inorganic nitrogen, DIP = dissolved inorganic phosphorus, DON = dissolved organic nitrogen, DOP = dissolved organic phosphorus, OD = optical depth, Munsell = Munsell colour value, Sed org C = sediment organic carbon, Sed pha = sediment phaeophytin, Sed inorg C = sediment inorganic carbon, Fine grains = %grains <63 μm.

	Max depth	**Chl *a***	**PN**	**PP**	**POC**	**TSS**	**DIN**	**DIP**	**DON**	**DOP**	**Secchi**	**OD**	**Mun.**	**Sed org C**	**Sed pha**	**Sed inorg C**	**Fine grains**
Max depth	1.00																
Chl *a*	**-0.86**	1.00															
PN	**-0.78**	**0.80**	1.00														
PP	**-0.87**	**0.75**	**0.77**	1.00													
POC	**-0.79**	**0.69**	0.65	**0.97**	1.00												
TSS	**-0.68**	**0.73**	**0.77**	**0.91**	**0.90**	1.00											
DIN	-0.28	0.08	0.11	0.07	-0.06	-0.04	1.00										
DIP	0.12	-0.21	0.09	-0.03	-0.06	0.11	0.54	1.00									
DON	**-0.75**	0.65	**0.70**	0.53	0.50	0.32	0.00	-0.22	1.00								
DOP	-0.42	0.43	0.10	0.58	0.65	0.59	-0.23	-0.24	-0.04	1.00							
Secchi	**0.94**	**-0.89**	**-0.79**	**-0.86**	**-0.82**	**-0.71**	0.05	0.31	**-0.81**	-0.49	1.00						
OD	**0.90**	**-0.88**	**-0.88**	**-0.84**	**-0.76**	**-0.73**	0.08	0.27	**-0.81**	-0.37	**0.97**	1.00					
Munsell	**0.85**	**-0.78**	-0.59	**-0.74**	**-0.78**	-0.62	-0.19	-0.02	**-0.73**	-0.47	**0.83**	**0.73**	1.00				
Sed org C	-0.66	**0.67**	0.45	0.40	0.33	0.36	0.60	0.18	0.34	0.13	-0.45	-0.43	-0.58	1.00			
Sed pha	-0.26	0.53	0.29	-0.11	-0.20	-0.05	0.22	-0.04	0.35	-0.08	-0.26	-0.29	-0.31	0.51	1.00		
Sed inorg C	0.61	**-0.69**	-0.44	-0.41	-0.45	-0.36	-0.36	-0.09	-0.60	-0.12	0.55	0.47	**0.85**	**-0.68**	-0.54	1.00	
Fine grains	-0.29	0.37	-0.09	-0.07	0.00	-0.18	-0.10	-0.42	0.42	0.19	-0.34	-0.23	-0.45	0.44	0.58	-0.52	1.00

Table 2.4. Estimates of light attenuation coefficients and percent of surface irradiance resulting in light limitation of zooxanthellate corals on reefs in the Whitsunday Islands. k_d (PAR) averaged over three times of sampling. Data are presented as means ± standard error (SE). Maximal depth of coral reef development is presented as depth below lowest astronomical tide. E_z derived from Equation 1.

	Repulse	Lindeman	Long	Dent	Whitsunday	Hook	Deloraine	Edward	Hook Rf
Mean k_d (PAR)	0.5155	0.2367	0.2323	0.1475	0.1824	0.2088	0.1206	0.1171	0.1317
	(0.1532)	(0.0567)	(0.0489)	(0.0511)	(0.0247)	(0.0170)	(0.0131)	(0.0050)	(0.0234)
Maximal depth coral reef development (m)	5.0	5.3	7.0	8.5	14.3	7.8	21.2	23.6	25
E_z at maximal depth coral reef development (µE m^{-2} s^{-1})	107	432	224	410	123	284	115	104	62
Percentage surface irradiance	8	29	20	29	7	20	8	6	4

2.4 Discussion

This study has documented the persistence of an environmental gradient in the Whitsunday Islands and that strong relationships are present between a range of water column characteristics and the maximal depth limit of coral reef development along this gradient. Water column characteristics changed strongly from nearshore reefs in the coastal zone to outer reefs more distant from the effects of terrestrial inputs. The water column variables chlorophyll *a*, total suspended solids, particulate organic carbon and particulate phosphorus, and the irradiance variables of Secchi and optical depth, changed significantly along this gradient. The data presented here incorporate three sampling events during the Austral dry season (August 2004-2006) and two sampling events in the wet season (January and February 2006).

Water column

The doubling of water column chlorophyll *a* along the gradient, and the greater levels observed during the wet compared with the dry season, is consistent with cross-shelf and seasonal patterns typically found in the central GBR. For example, analysis of a long-term chlorophyll *a* dataset for the GBR found mean chlorophyll *a* concentrations of 0.37 $\mu g\ L^{-1}$ at inner locations compared with 0.15 $\mu g\ L^{-1}$ at outer locations in the Whitsunday Islands (Brodie *et al.* 2007). In an earlier study, Brodie *et al.* (1997) reported mean chlorophyll *a* concentrations of 0.91 ± 0.11 $\mu g\ L^{-1}$ at inshore locations of the Whitsunday/Pompey Section of the GBR compared with 0.69 ± 0.04 $\mu g\ L^{-1}$ at the outer reefs. Our time-averaged results are in agreement with Brodie *et al.* (1997), but approximately two-fold greater than the long-term chlorophyll monitoring time series suggests (Brodie *et al.* 2007). Such variability among studies highlights the need for longer term studies to clearly elucidate patterns of temporal variation in chlorophyll *a* in the GBR (Brodie *et al.* 2007).

Wind driven resuspension events are important influences on water column characteristics in the coastal zone. Total suspended solids increased two- to three-fold along the gradient in the Whitsunday Islands. Previous studies have demonstrated that wind driven resuspension events can result in sudden increases in turbidity within hours of a weather change (Orpin *et al.* 2004), elevating suspended solids to over 20 mg L^{-1} for several days (Larcombe *et al.* 1995), and up to 80 mg L^{-1} during cyclonic conditions (Wolanski *et al.* 2005). With the exception of sampling done in February 2006, the wind regime was similar during all sampling events. During the February 2006 sampling event, however, the mean wind speed was 19.8 ± 1.5 knots (determined as the average of wind speed at 3 pm, www.bom.gov.au/weather/qld/mackay), which resulted in higher levels of total suspended solids among the locations compared with the other sampling events and a comparatively lower slope with increasing distance from the coast. Interestingly, the slope of the relationship between total suspended solids and distance from the coast was steepest in August 2006 (14.9 ± 1.5 knots), which had similar wind conditions to the other times of sampling, i.e. August 2004 (13.9 ± 1.4 knots), August 2005 (14.2 ± 2.1 knots) and January 2006 (15.3 ± 0.7 knots). This suggests that other factors, e.g. tides and currents, also have important influences on levels of total suspended solids in the Whitsunday Islands. However, the retention times, fate, frequency and duration of resuspension and speed of northward transport of new materials discharged from rivers during the wet season, and their short- and long-term influences on water column characteristics, remain to be investigated for the Whitsunday Islands. Similarly, the enrichment by particulate nitrogen and organic carbon of total suspended solids with increasing distance from the coast at some but not all of the sampling occasions is interesting and illustrates that the quality of suspended sediment can vary on small spatial and temporal scales. This may have been caused by enhanced colonisation of particles with micro-organisms as they are transported offshore, or

alternatively, by settlement of larger particles with a low nutrient content out of the water column faster than fine-grained particles, which can be transported over longer distances.

Sediments

The clearest trends in the sediment variables investigated here were the changes in sediment colour and inorganic carbon, two variables which were closely correlated with each other. Studies by Hamilton (2001) conducted in the Northern GBR also indicated a strong correlation between optical lightness of the sediment and inorganic carbon content. The reduced amount of inorganic carbon along the gradient towards the coast (Uthicke 2006) is typical for the GBR (Brunskill *et al.* 2002), representing the greater proportion of terrestrial sediments near the coast. The trend of a greater percentage of fine sediment near the mainland also warrants further study, reflecting differences in bottom shear stress and/or flood-derived sediments that have settled out from the water column.

Sediment chlorophyll *a* concentrations measured in this study are comparable to those from other studies in the GBR (Uthicke and Klumpp 1998; Schaffelke *et al.* 2004). Schaffelke *et al.* (2004) found clear differences in chlorophyll *a* and total pigment concentrations between three islands in the Palm Island region in a monthly sampling regime over 18 months leading them to suggest that sediment chlorophyll *a* values could serve as an indicator for differences in the nutrient status of reefs. No such differences were found in the present study along the gradient. Because of the high patchiness of sediment chlorophyll *a*, with a coefficient of variation (CV) of about 34% of sample means, it may be possible that a greater sampling intensity is required than employed in the present study to detect such differences. In addition, we observed that chlorophyll *a* distribution is much deeper in sediments on outer shelf reefs, and is restricted to the uppermost few millimetres in the sediments of inner reefs with a greater percentage of fine sediments (Uthicke, data not shown). Thus, averaging chlorophyll *a* values over the first centimetre may mask differences which may exist in the upper photic levels of the sediment.

Although only marginally significant, sediment organic carbon tended to decrease along the gradient away from the coast, In August 2004, organic carbon values on the four nearshore reefs were nearly 40% higher than the remaining reefs. In addition, carbon values were significantly greater (on average 23%) in February 2006 compared with August 2004. The result that carbon values varied among sample occasions separated by only a few years appears inconsistent with the conclusions of van Woesik *et al.* (1999) who suggested that greater organic carbon values inshore might be persistent for long time scales (i.e. decades). No significant relationship between the sediment nitrogen values and distance from coast was detected in this study. Elevated nitrogen values on the four reefs closest to the coast were noted in August 2004, which was similar to organic carbon concentrations (Uthicke 2006). However, nitrogen concentrations on these reefs were only about 10% higher than the average of the remaining reefs, and concentrations were also very variable. The differences in these findings and the suggestion that sediment chemistry may change on smaller temporal scales than previously assumed (van Woesik *et al.* 1999) warrants further investigation.

Irradiance

Corals on the nearshore reefs received lower total daily quanta compared with reefs on the outer islands in both survey periods. Total daily quanta decreased by 47% at Lindeman Island and 15% at Deloraine Island after a weather change when wind speeds reached 20-30 knots in February 2006, and clouds decreased surface irradiance at Hardy Reef by approximately 15% (Table 2.2). The data show that clouds explained most of the decreased irradiance on the outer island; however, on the nearshore reefs, resuspension of bottom sediments additionally contributed to their reduction in irradiance (*sensu* Anthony *et al.*

2004). These data illustrate that nearshore benthic communities must be adapted to higher variation in light availability than those on reefs more distant from the coast.

Maximum depth coral reef development

Knowledge of the amount of irradiance reaching the surface of a coral reef, due to the optical properties of the water column, can provide insight to the patterns of variation in the depth distribution of coral reefs. Water clarity increased around three-fold along our gradient, with lowest Secchi and optical depth in the coastal zone and greatest values at the outer reefs. van Woesik *et al.* (1999) reported a negative correlation between the maximal depth of corals and levels of suspended particulate matter and turbidity, suggesting that the lower edge of coral distribution in the Whitsunday region might be determined by light availability. Corals persist to a maximal depth of 5 m on the fringing reefs around Repulse Island, despite the availability of suitable substrata at deeper depths, compared with reef development at depths >20 m at Deloraine Island. At these lower depth limits, communities gradually shift to dominance by azooxanthellate octocorals. This indicates that coral reef development is limited by irradiance as suitable substratum was available at deeper depths for the growth of azooxanthellate corals. In contrast, at Lindeman, Long, Dent and Hook Islands, 20-30% of surface irradiance was measured at the deepest depth of reef development, and corals at these locations appeared to be limited by the availability of suitable substrata for settlement, as sand and rubble dominated the substratum and few azooxanthellate octocorals were found. Our data of the maximal depth limit for reef development at locations where suitable settlement substrata were available (e.g. Repulse, Whitsunday, Deloraine and Edward Islands) suggest that the absolute minimum of light required for a reef to persist is in the range of 6-8% of surface irradiance in the Whitsunday Islands. It is important to note that live coral cover and coral diversity decreases before this limit is reached, suggesting that although 6-8% of surface irradiance allows some coral settlement, it is insufficient to support active reef growth. Our result is in agreement with Titlyanov and Latypov (1991) who reported that the lower light limit of corals in the Gulf of Siam was in the range of 2-8% of surface irradiance. The positive relationship between water clarity and lower edge of reef development deserves further study. If changes in water clarity would indeed result in a change in the lower depth distribution in corals, the latter may be used as an indicator for changes in water column light properties, similar to the use of the lower distribution limits of seagrasses in assessments of estuarine ecosystem health (Abal and Dennison 1996; Dennison and Abal 1999).

Light availability has important implications for the energy budget of corals (Edmunds and Davies 1986; Edmunds and Davies 1989). In the outer Whitsunday Islands, corals are likely to perform with maximum photosynthetic efficiency and maintain energy reserves. Conversely, at turbid locations the corals are likely to be light-limited at all but very shallow depths. Under light-limiting conditions, corals will rely on heterotrophy to compensate for low photosynthetic carbon gain to meet their energetic requirements (Anthony 2000; Anthony and Fabricius 2000; Anthony 2006). A study on the photo-physiology of benthic biofilms on marine sediments along the Whitsundays gradient showed that biofilm communities photo-adapt to local light conditions (Uthicke 2006). Benthic microalgae in biofilms were thus more efficient in using low irradiance on reefs closer to the coast than on offshore reefs. Most distinctly, the minimum saturating irradiance (E_k) was lower inshore than on the outer islands and strongly correlated to incident light levels (Uthicke 2006). The differences observed in irradiance along the gradient, combined with the differences in photo-adaptation of biofilms, suggests that photo-adaptation is also likely to occur at higher trophic levels such as in the coral community.

In conclusion, levels of chlorophyll *a*, particulate phosphorus and particulate organic carbon were consistently greater in the nearshore reefs and decreased toward the outer islands and nearby mid-shelf reefs. The opposite pattern applied to the irradiance variables Secchi and

optical depth. These patterns were generally consistent among sampling times, suggesting the existence of a persistent environmental gradient in water column nutrients and irradiance in the Whitsunday Islands. Concentrations of total suspended solids, however, varied inconsistently among locations and times of sampling and this was most likely due to resuspension of bottom sediments during some of the sampling periods in the dry season. Water column chlorophyll *a*, sediment colour and the irradiance variables Secchi and optical depth all showed strong relationships with distance from the coast. This suite of relatively simple techniques could be used as 'surrogate indicators' to monitor changes in water column characteristics. These variables would not only provide valuable information on the nutrient status of a coral reef, but also provide ecologically relevant data on the light regime penetrating to the benthic assemblage. Further, if changes in water clarity (measured by Secchi or optical depth) result in a change in the lower depth distribution in corals, the latter may be used as a simple and cost-effective indicator of the effects of changes in water column characteristics on coral reefs.

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2.6 References

Abal EG, Dennison WC. 1996. Seagrass depth range and water quality in southern Moreton Bay, Queensland, Australia. Marine & Freshwater Research 47: 763-771

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

Anthony KRN. 2006. Enhanced energy status of corals on coastal, high-turbidity reefs. Marine Ecology Progress Series 319: 111-116

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

Anthony KRN, Hoegh-Guldberg O. 2003. Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys? Functional Ecology 17: 246-259

Anthony KRN, Ridd PV, Orpin AR, Larcombe P, Lough J. 2004. Temporal variation of light availability in coastal benthic habitats: Effects of clouds, turbidity and tides. Limnology and Oceanography 49: 2201-2211

Blott SJ, Pye K. 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surface Processes and Landforms 26: 1237-1248

Brodie J, De'ath G, Devlin MJ, Furnas MJ, Wright M. 2007. Spatial and temporal trends of near-surface chlorophyll *a* in the Great Barrier Reef lagoon. Marine and Freshwater Research 58: xx-xx doi10.1071/MF06236

Brodie JE, Furnas MJ, Steven ADL, Trott LA, Pantus F, Wright M. 1997. Monitoring chlorophyll in the Great Barrier Reef Lagoon: trends and variability. Proceedings of the 8th International Coral Reef Symposium, Panama. Pp 797-802.

Brunskill GJ, Zagorskis I, Pfitzner J. 2002. Carbon burial rates in sediments and a carbon mass balance for the Herbert River region of the Great Barrier Reef continental shelf, North Queensland, Australia. Estuarine, Coastal and Shelf Science 54: 677-700

Dennison WC, Abal EG. 1999. Moreton Bay Study - A scientific basis for the healthy waterways campaign. South East Queensland Regional Water Quality Management Strategy, Brisbane

Devlin MJ, Brodie J. 2005. Terrestrial discharge into the Great Barrier Reef Lagoon: nutrient behavior in coastal waters. Marine Pollution Bulletin 51: 9-22

Devlin MJ, Brodie J, Waterhouse J, Mitchell A, Audas D, Haynes D. 2001. Flood plumes in the Great Barrier Reef: spatial and temporal patterns in composition and distribution. Great Barrier Reef Marine Park Authority, Townsville.

Edmunds PJ, Davies PS. 1986. An energy budget for *Porites porites* (Scleractinia). Marine Biology 92: 339-347

Edmunds PJ, Davies PS. 1989. An energy budget for *Porites porites* (Scleractinia), growing in a stressed environment. Coral Reefs 8: 37-43

Fabricius KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50: 125-146

Fabricius KE, De'ath G. 2004. Identifying ecological change and its causes: a case study on coral reefs. Ecological Applications 14: 1448-1465

Fabricius KE, De'ath G, McCook L, Turak E, Williams DM. 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Marine Pollution Bulletin 51: 384-398

Falkowski PG, Dubinsky Z, Muscatine L, Porter JW. 1984. Light and the bioenergetics of a symbiotic coral. Bioscience 34: 705-709

Furnas M, Mitchell A, Skuza M. 1997. Shelf-scale nitrogen and phosphorus budgets for the Central Great Barrier Reef (16-19^{o}S) Proceedings of the 8th International Coral Reef Symposium, Panama. Pp 809-814.

Furnas MJ. 2003. Catchments and corals: terrestrial runoff to the Great Barrier Reef. Australian Institute of Marine Science, CRC Reef. Townsville, Australia.

Gilmour JP. 2002. Acute sedimentation causes size-specific mortality and asexual budding in the mushroom coral, *Fungia fungites*. Marine and Freshwater Research 53: 805-812

Hamilton LJ. 2001. Cross-shelf colour zonation in northern Great Barrier Reef lagoon surficial sediments. Australian Journal of Earth Sciences 48: 193-200

Haynes D, Michalek-Wagner K. 2000. Water quality in the Great Barrier Reef World Heritage Area: Past perspectives, current Issues and new research directions. Marine Pollution Bulletin 41: 428-434

Jeffrey SW, Humphrey GF. 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie der Pflanzen 167: 191-194

Kirk JTO. 1994. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, London

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

McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D. 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421: 727-730

Menzel DW, Corwin N. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnology and Oceanography 10: 280-282

Moss AJ, Rayment GE, Reilly N, Best EK. 1992. A preliminary assessment of sediment and nutrient exports from Queensland coastal catchments. Queensland Department of Environment & Heritage, Queensland Department of Primary Industries, Queensland

Muscatine L. 1990. The role of symbiotic algae in carbon and energy flux in coral reefs. In: Dubinsky Z (ed) Ecosystems of the World: Coral Reefs. Elsevier, Amsterdam, pp 75-87

Neil DT, Orpin AR, Ridd PV, Yu B. 2002. Sediment yield and impacts from river catchments to the Great Barrier Reef lagoon. Marine and Freshwater Research 53: 733-752

Orpin AR, Ridd PV, Thomas S, Anthony KRN, Marshall P, Oliver J. 2004. Natural turbidity variability and weather forecasts in risk management of anthropogenic sediment discharge near sensitive environments. Marine Pollution Bulletin 49: 602-612

Parsons TR, Maita Y, Lalli C. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press, London

Philipp E, Fabricius KE. 2003. Photophysiological stress in scleractinian corals in response to short-term sedimentation. Journal of Experimental Marine Biology and Ecology 287: 57-78

Porter JW. 1976. Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. American Naturalist 110: 731-742

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Ryle VD, Mueller HR, Gentien P. 1981. Automated analysis of nutrients in tropical seawaters, AIMS Oceanography Series Tech. Bulletin No.3, AIMS.OS.81.2

Sartory DP, Grobbelaar JU. 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia 114: 177-187

Schaffelke B, Mellors J, Duke NC. 2005. Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. Marine Pollution Bulletin 51: 279-296

Schaffelke B, Uthicke S, Klumpp DW. 2004. Water quality, sediment and biological parameters at four nearshore reef flats in the Herbert River Region, Central GBR. Research Publication No. 82. Great Barrier Reef Marine Park Authority, Townsville

Titlyanov EA, Latypov YY. 1991. Light-dependence in scleractinian distribution in the sublittoral zone of South China Sea Islands. Coral Reefs 10: 133-138

Uthicke S. 2006. Photosynthetic efficiency and rapid light curves of sediment-biofilms along a water quality gradient in the Great Barrier Reef, Australia. Marine Ecology Progress Series 322: 61-73

Uthicke S, Klumpp DW. 1998. Microphytobenthos community production at a near-shore coral reef: seasonal variation and response to ammonium recycled by holothurians. Marine Ecology Progress Series 169: 1-11

van Woesik R, Tomascik T, Blake S. 1999. Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. Marine and Freshwater Research 50: 427-440

Weber M, Lott C, Fabricius KE. 2006. Sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, organic and geochemical properties. Journal of Experimental Marine Biology and Ecology 336: 18-32

Wolanski E, Fabricius K, Spagnol S, Brinkman R. 2005. Fine sediment budget on an inner-shelf coral-fringed island, Great Barrier Reef of Australia. Estuarine, Coastal and Shelf Science 65: 153-158

Wooldridge S, Brodie J, Furnas MJ. 2006. Exposure of inner-shelf reefs to nutrient enriched runoff entering the Great Barrier Reef Lagoon: Post-European changes and the design of water quality targets. Marine Pollution Bulletin: 1467-1479

Chapter 3: Biofilms as bioindicators of changes in water quality in coastal and offshore marine systems: A preliminary report

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3.1 Introduction

General

Biofilms (or '*Aufwuchs*', periphyton if only referred to the autotrophic part of the community) cover most aquatic surfaces and are generally mixed communities of bacteria, micro algae, protist and small metazoan in a polymer matrix. These communities have important ecological functions in food webs and productivity, but are also often important as primary settlers of substrata, providing chemical settlement cues for other organisms.

The use of biofilms as indicators of water quality has been well established in freshwater systems. For example, diatoms have been established indicators of freshwater quality in streams since the 1950s (Patrick *et al.* 1954). More recently, bacterial communities and diatoms have also been used as indicators for water quality in estuaries and wetlands (e.g. Gaiser *et al.* 2005; Milbrandt 2005; Snyder *et al.* 2005). With the exception of the foraminifera (see details below), little work has been conducted on marine tropical biofilm communities as indicators of water quality.

I hypothesize, that similar to other aquatic environments, biofilms in the Great Barrier Reef (GBR) have a large potential to serve as indicators for a wide array of disturbances such as water quality changes resulting from increased runoff (sedimentation and light reduction) or changes in nutrient regimes. In the studies presented, I focused on three major groups of organisms in natural biofilms on sediments near GBR reefs: bacteria, benthic microalgae and foraminifera. Because of high reproduction and turnover rates (bacteria: hours to days, microalgae: days to weeks, foraminifera: weeks to months) it is expected that these organisms react more rapidly to changes in water quality than larger community members, such as coral or fish. Further advantages are that 1) the expected high species and functional diversity in each of these groups increases the chance of detecting indicators for specific conditions, 2) collection of large numbers of organisms can be conducted without major ethical concerns, 3) because of their the hard tests, some of these organisms (diatoms and foraminifera) are likely to leave fossil records, which would allow hindcasting from sediment cores from later studies. The major disadvantage in studying biofilms as indicators of water quality of the GBR is the general lack of knowledge of the species diversity, their distribution and ecology. Therefore, these studies have mainly focused on developing methods (genetic and traditional) to describe the biodiversity of these species. As a second step, I have used gradients in the GBR (e.g. the "Whitsunday Gradient", see Chapter 2, a comparison between Princess Charlotte Bay and Wet Tropics, Fabricius *et al.* 2005, or

simple inshore outer shelf comparisons) to investigate differences in community composition or function.

Bacteria

Marine bacterial communities are highly diverse, though only a low percentage of this diversity can be described with culture-based techniques (Amann *et al.* 1995). For this reason, research in the last decade has concentrated on culture-independent molecular techniques such as restriction fragment length polymorphism (RFLP), denaturing gradient gel electrophoresis (DGGE), clone libraries or a combination of these. In the marine environment, most research has focused on plankton communities (e.g. Cottrell and Kirchman 2000; Venter *et al.* 2004; Brown *et al.* 2005). Although some marine sediment communities have been investigated, most of these studies have been conducted on Arctic or Antarctic (Ravenschlag *et al.* 1999; Bowman *et al.* 2000; Bowman and McCuaig 2003), temperate (Wise *et al.* 1997; Cifuentes *et al.* 2000) or deep sea (Li *et al.* 1999; Yanagibayashi *et al.* 1999) sediments. Two tropical studies on sediment bacteria exist, but these have been conducted on fine mobile sediments (Todorov *et al.* 2000; Madrid *et al.* 2001). In tropical coral reef environments, some information exists on bacterial communities associated with the water column, corals and coral diseases (Frias-Lopez *et al.* 2002; Bourne and Munn 2005) and biofilm communities on artificial substrata (Webster *et al.* 2004). Bacteria in sediments of coral reefs on the GBR of Australia occur in densities between 10^8 and 10^9 x mL^{-1} (Uthicke 1994; Schaffelke *et al.* 2004). To our knowledge no molecular study using clone libraries exists that investigates the composition of the microbial communities in carbonate-dominated sediments of coral reefs.

As a first step towards finding bacterial indicators of water quality in GBR sediments, I investigated eight 16S rDNA clone libraries from coral reef sediments in the Wet Tropic area to 1) provide a first description of bacterial communities on calcareous reef sediments of the GBR and 2) to test if these communities harbour characteristic species or groups that could be used as indicators of Water Quality. A hierarchical sampling design allowed robust statistical comparison of sediment communities from two inshore reefs potentially influenced by anthropogenic impacts, with those from two reefs at the outer shelf that are less affected. Differences between clone libraries were investigated both on a community level (grouping clones sequenced into nine higher taxa) and on a molecular level using analysis of molecular variance to estimate genetic similarity between individual clone libraries, reefs and inshore and outer shelf regions.

Benthic Microalgae

Microphytobenthos communities potentially contribute 30-40% of the production on coral reefs (Sorokin 1993). However, the use of these communities as indicators of changing water quality on coral reefs has not been investigated, despite fulfilling several important pre-requisites as ideal indicators. 1) These communities are ubiquitous and easily accessible, because up to 40% of individual reefs can be sediment covered and is therefore suitable habitat (Uthicke and Klumpp 1998), 2) several studies have indicated that these communities are N limited and respond rapidly to increased nutrient levels with increases in biomass and production (Uthicke and Klumpp 1998; Uthicke 2001; Dizon and Yap 2003), 3) Microphytobenthos also rapidly responds to changes in light condition with adaptations in photo-physiology (Uthicke and Klumpp 1998).

In planktonic microalgae, the quantum efficiency of photosystem II (PSII) was suggested as a rapid indicator for nutrient limitation for both N and P (e.g. Geider *et al.* 1993; Beardall *et al.* 2001), but data on the photophysiology and nutrient dynamics of marine microphytobenthos are sparse. Development of Pulse-Amplitude-Modulated (PAM) fluorometers (Schreiber *et al.*

1986) facilitated *in situ* measurements. PAM fluorometry allows rapid assessments of maximum quantum efficiency and effective quantum efficiency of PSII.

Most data on quantum efficiency in marine microphytobenthos communities were derived from PAM measurements either on sediment cores, cultures, or from intertidal mud flats during low tide (Kromkamp *et al.* 1998; Hartig *et al.* 1998; Barranguet and Kromkamp 2000; Serôdio *et al.* 2001; Perkins *et al.* 2001, 2002; Glud *et al.* 2002; Serôdio 2003). Additionally, most of these data are from temperate to arctic regions, with only one study available from coral reef environments (Underwood 2002). A second advantage of PAM fluorometry is that light dependent electron transport as a proxy for productivity can be estimated using rapid light curves (RLCs). These allow estimation of light curve parameters similar to those used in "classical" Production-Irradiance (P-E) curves obtained with other methods.

Although studies on community productivity indicated N limitations for coral reef microphytobenthos (Uthicke and Klumpp 1998; Uthicke 2001; Dizon and Yap 2003), the diatom communities in coral reef sediments are poorly described. In tropical benthic diatoms, especially, knowledge about the taxa and community composition along ecological gradients is rare. To our knowledge, only one study from the Capricorn-Bunker group exists in the GBR region (Heil *et al.* 2004). In contrast extensive studies of benthic microalgae have been conducted in temperate systems (e.g. Hillebrand and Sommer 1997, 2000a, b; Hillebrand *et al.* 2000). These studies and experiments in temperate regions established clear responses of microalgal cell numbers to enhanced nutrients, but also showed that individual species respond differently to nutrient enhancement.

Here, the use of *in situ* and *in vitro* PAM fluorometry as an indicator for nutrient and light status of biofilm communities on coral reef sediments was investigated. The maximum quantum efficiency and RLCs were measured after dark adaptation *in situ* and on board a research vessel on 10 reefs along the Whitsunday gradient. Diatom species composition and number was determined for reefs in Princess Charlotte Bay, the Wet Tropics area and on outer shelf reefs, with the aim of detecting differences in total abundances and to identify indicator species for the three different areas with presumed differences in nutrient regimes. In addition, genetic methods to identify diatom species were tested as an initial step to identify and quantify indicator species from field samples.

Foraminifera

Foraminifera are single celled animals, or protists, abundant in benthic and pelagic marine environments. Their calcareous tests are deposited in deep sea sediments above the lysocline, and the species composition is a standard geological tool for biostratigraphy in sediment cores. Sedimented planktonic foraminifera can also serve as palaeo-indicators for water temperature and global change (e.g. Field *et al.* 2006). In shallow water habitats, some benthic foraminifera were found to be sensitive indicators for pollution, e.g. by heavy metals, chemicals, sewage or oil (reviewed in Alve 1995).

Many large (up to 2cm in diameter) benthic foraminifera in coral reefs harbour symbiotic algae, which benefit from inorganic nutrients excreted by foraminifera and in turn provide organic compounds to their host. In principal, this symbiosis is similar to the one between corals and dinoflagellates, however, foraminifera realise symbiotic relationships with a much higher diversity of primary producers. Depending on the family, foraminifera can host diatoms, chlorophytes, dinoflagellates, single celled red algae or even isolated chloroplasts retained from food organisms (Lee and Anderson 1991). Symbiont bearing foraminifera have high calcification rates and contribute around 30% of the carbonate across the shelf of the GBR (Scoffin and Tudhope 1985) and on coral cays (Yamano *et al.* 2000). Benthic foraminifera are established indicators of coral reef water quality conditions in Florida and the Caribbean Sea (Hallock 2000; Hallock *et al.* 2003). Hallock (1981) suggested that

foraminiferal-algal symbioses are advantageous in clean coral reef waters because dissolved inorganic nutrients (required by the symbiotic algae) and particulate food sources (required for heterotrophic feeding of the foraminifera) are scarce. Under decreased water quality conditions, when light becomes limiting and more inorganic and particulate nutrients are available, species which rely on heterotrophy for food acquisition are hypothesised to be dominant. The information on species composition from sediment samples was summarised into a simple index that can be used as a monitoring tool (FORAM index, Hallock *et al.* 2003).

The aim of the present study was to investigate benthic foraminifera community structure along a transect in the Whitsunday region of the GBR. Water quality along this transect was studied extensively (van Woesik *et al.* 1999; Uthicke 2006; see Chapter 2). In short, turbidity distinctly decreased and inorganic nutrient availability decreased with increasing distance from the mouths of two rivers.. Therefore, this was an ideal setting to test if communities change to more symbiont bearing taxa towards the outer reef and if the FORAM index as applied in Florida and the Caribbean provides a useful measure of reef-health and water quality of the GBR.

3.2 Material and methods

Bacteria

Sampling

Sediment samples were taken in the Wet Tropics area of the GBR. Sampling followed a hierarchical design on two inshore reefs (Fitzroy Island: 16˚ 55.4'S, 145˚59.8'E, High Island: 17˚ 9.5'S, 146˚ 0.3'E) potentially subjected to higher nutrient and sediment load because of their proximity to the mainland (5-7 km) and close location to river mouths. Two outer shelf reefs sampled (Hastings Reef: 16˚ 31.2'S, 146˚ 6.0'E; Flynn Reef: 16˚ 43.7'S, 146˚ 16.2'E; [Fig. 3.1(a), all GPS positions given in this chapter use WGS 84 as chart datum]) were located in more pristine water conditions between 38 and 45 km from the mainland. On each reef, sediment from one station on the front-reef and one at the back-reef (labelled as station 1 and 2 for each reef, respectively), with less exposure to water motion, were collected at a water depth of between 8-10 m. Sediments were cored on SCUBA using cut-off 10 mL syringes. Immediately upon return to the research vessel, the upper 1 cm sediment horizon was snap frozen in liquid nitrogen and upon return to the laboratory stored at -80°C.

DNA extraction, Clone library construction and sequencing

The DNA of 100 to 200 mg of the frozen sediment sample were extracted using the Soilmaster DNA kit (Epicentre), following the manufacturers instructions.

A fragment of the 16S rDNA gene was amplified using universal 16S rDNA primers 519f (5'-CAGCMGCCGCGGTAATAC-3') and 1492r (5'-TACGGYTACCTTGTTACGAC-3') (Reysenbach and Pace 1995; Suzuki and Giovanni 1996; Bowman and McCuaig 2003).

PCR amplification was conducted, using final concentrations of 1μM of each primer, 2.5 μM $MgCl_2$, 1 x PCR Buffer, 200 μM of each dNTP, 1 x Bovine Serum Albumin, 2.5 units HotStarTaq DNA polymerase (Qiagen). 5 μl of the DNA extracts were added to the PCR reactions. An initial 15 min cycle at 95ºC preceded the PCR reactions to activate the HotStarTaq. This was followed by 35 cycles of 60sec of denaturation at 95ºC, 60 sec of annealing at a temperature of 50°C, and 60sec extension at 72ºC. The 35 cycles were followed by a final extension of 10 min.

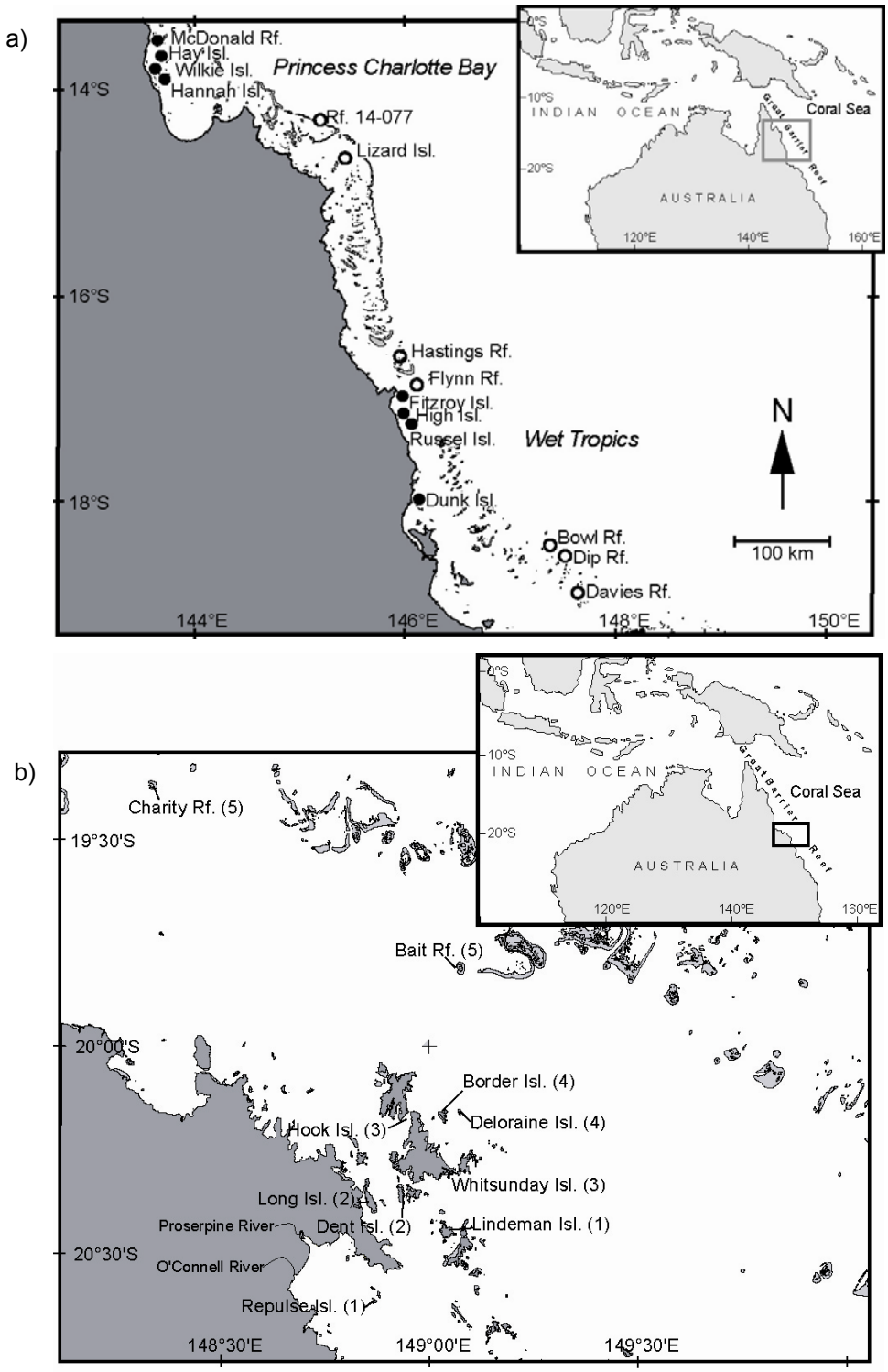

Figure 3.1. Sample locations for biofilm research described in this report: a) locations for Bacterial and Diatom collections, outer shelf reefs are marked by hollow circles; b) locations for foraminifera collections and PAM fluorometry work along the Whitsunday transect, "Zone"-designations as used for some statistical analyses are given in brackets behind location names.

Prior to cloning, PCR products were purified using QIAaquick PCR purification kit (Qiagen), and their concentrations measured on a GeneQuant spectrophotometer. 40 to 50 ng of the purified PCR product were cloned into pGEM-T Easy System II vector (Promega). Ligations followed the manufacturer's protocol, and subsequent transformations were conducted in 50% of the recommended reaction volume. 150 μL of each transformation were plated on LB/ampilicin/IPTG/X-Gal plates and colonies grown overnight at 37°C. White colonies were picked and dissolved in 50 μL Milli Q water. Five μL of this was used as template in the following PCR reaction, employing primers M13F (5'-GTAAAACGACGGCCAGT-3') and M13R (5'-GCGGATAACAATTTCACACAGG-3'). PCR reactions used the same concentrations as given above. The initial 15 min activation cycle at 95°C was followed by 30 cycles of 45 sec of denaturation at 95ºC, 45sec of annealing at 58°C, and 2 min extension at 72ºC, followed by a final extension period of 7 min.

For sequencing, PCR products were purified using a Montage PCR96 cleanup kit (Millipore). 20-50 ng μL^{-1} of each purified PCR product were used in subsequent sequencing reactions. Each PCR product was sequenced in both directions, using M13F and SP6 (5'-ATTTAGGTGACACTATAG-3') primers for the forward and reverse reactions, respectively. Big Dye TM Terminator Cycle Sequencing Kits and AmpliTaq (Applied Biosystems) were used for sequencing reactions. Sequencing reaction products were cleaned from unincorporated terminators with ethanol precipitation and sequenced on an ABI Prism 3730xl Analyzer. PCR and sequencing reactions were carried out on Peltier Thermal Cyclers (PTC-100 and PTC-225, MJ Research).

Phylogenetic and Statistical analysis

Forward and reverse sequences were aligned in Sequencher (Ver. 5, Gene Code Coperation, Ann Arbor, USA) and checked for chimera using Bellerophon (Huber *et al.* 2004), Check_Chimera (Ribosomal Database Project, Maidak *et al.* 1999) and Pintail (Ashelford *et al.* 2005). Sequences were imported into the ARB database (Ludwig *et al.* 2004) and aligned against existing bacterial 16S rDNA sequences. Neighbour joining trees were constructed from distance matrices (Jukes-Cantor corrected) and consensus trees constructed from 1000 bootstrap replicates. Bootstrapping, distance matrix calculations and tree construction were conducted with programs in the Phylip (Felsenstein 1993) package. All sequences were submitted to GenBank (Accession numbers: DQ256505-DQ256725).

Rarefaction curves were calculated with the free software aRarefact Win (Holland 1988) and coverage of the clone libraries was calculated as in Ravenschlag *et al.* (1999).

Community analysis

Community composition analysis of the 16S rDNA libraries were conducted in PRIMER (Clarke and Gorley 2001). To achieve this, bacterial sequences were grouped into nine higher taxa (divisions or families) based on their position in the total ARB database and as indicated in the phylogenetic trees presented. Distance matrices between the assemblages of single clone libraries were calculated using fourth root transformed and standardized data and the Bray-Curtis similarity index. Subsequently, the significance of assemblage differences between inshore and outer shelf clone libraries was tested using ANOSIM (Analysis of Similarity) based on permutation procedures. The contributions of each taxon to the total difference between inshore and outer shelf samples were analysed with the SIMPER (Similarity Percentage) routine.

Benthic microalgae

PAM fluorometry was tested on 10 reefs along the Whitsunday Gradient (See Fig. 3.1(b), also Chapter 2). On each reef, one sample location on the sheltered back-reef and one on

the more exposed front-reef was chosen and *in situ* measurements conducted during one dive at each station. Sampling was conducted during a ship-based field trip in August 2004.

Pulse-Amplitude Modulated (PAM) Fluorometry

All PAM fluorescent measurements were conducted with a WALZ Diving-PAM, using an 8 mm diameter fibre optic cable. A short transparent tube was fixed to the end of the measuring cable. The end of this tube rested on the sediment surface to standardise the distance between the sediment surface and the probe to 6 mm. All readings were performed using maximum measuring intensities and output gains.

To have reasonably similar light conditions between locations I avoided early morning, late afternoon and midday-period dives, thus all measurements were conducted between 0830 and 1000, and 1400 and 1600. I defined a sediment area between 6 and 8 m water depth as a standard location at each station. This depth was generally at the transition between reef slope and the surrounding sedimentary seafloor. However, at some locations a slightly greater depth was chosen because sediment did not occur at shallower depths.

At each of these locations, I conducted approximately 20 readings of the effective quantum efficiency of photosystem II (PSII) in a haphazard fashion on several sediment patches. In addition, three rapid light curves were conducted at each location. After initial tests on the first reef visited, all light curves were conducted using the same light intensities spanning from 0 - 750 µmol photon m^{-2} s^{-1}.

Dark-adapted readings were required to estimate the maximum quantum efficiency of PSII. *In situ* dark adapted readings were not practicable because diatoms leave the sediment surface upon darkening *in situ* (data not shown).

To obtain dark adapted *in vitro* readings, four sediment samples were collected from each location, using cut-off 60 mL syringes as micro-corers. On shipboard, the top 1 cm of each sample was transferred into a 50 mL Falcon tube and fresh seawater added. These tubes were dark adapted for 30 min at about ambient temperature before conducting five readings of maximum quantum efficiency of PSII. To test if *in situ* measured RLCs represent short-term adaptations in light curve parameters, RLC readings were also repeated under standardised laboratory conditions. Therefore, three RLC measurements were taken in each tube subsequent to the maximum quantum efficiency measurements and re-adaptation to low light (5 -10 µmol photon m^{-2} s^{-1}) for 10 min. The water was then decanted and tubes frozen for pigment, organic and inorganic carbon and nitrogen analysis.

Some confusion exists about the terminology of parameters used for quantum efficiency and rapid light curves. Here, I use definitions as given in Barranquet and Kromkamp (2000), Serôdio *et al.* (2001) and Ralph and Gademann (2005). Thus, the maximum quantum efficiency (F_v/F_m, also termed maximum energy conversion efficiency or quantum yield of photosystem II) of dark adapted samples is given as the ratio of the variable fluorescence [F_v, calculated as the difference between the maximum fluorescence (F_m) and the minimum fluorescence (F_0)] divided by F_m. The effective quantum efficiency of PSII (Φ_{PSII}) in light adapted samples is calculated from ΔF [difference between the maximum fluorescence under ambient light (F_m') and the minimum fluorescence under the same conditions (F)] divided by F_m'.

Average background fluorescence (termed $F_{0,sed}$ in Serôdio 2003) was measured for sediments from each location and subtracted from readings as described in Uthicke (2006).

Effective quantum efficiency measurements obtained during the rapid light curve can be used to calculate photosynthetic production expressed as electron transport rates. However, in the case of microphytobenthos the chlorophyll *a* specific absorbance coefficient is difficult

to determine (Underwood 2002) and cannot be assumed as a constant because of vertical migration into the sediment and associated changes in biomass involved in photosynthesis (Serôdio 2003). Therefore, it is more appropriate to report relative electron transport rates (rETR), calculated as:

$$rETR = \Phi_{PSII,\ corr} \times PAR$$

for each PAR (Photosynthetic Active Radiation) applied during the measurements.

Statistical analyses of PAM data

Quantum efficiency and RLC parameters were analysed with mixed model analyses of variance (ANOVA). The reefs investigated were regarded as pairs of reefs located in five zones (see Chapter 2) (Factor 'Zone', fixed) along the presumed water quality gradient. Individual 'Reefs' were regarded as random replicates nested in 'Zone'. The factor 'Method' compared on board measurements and *in situ* readings. Efficiency readings were averaged over each location and the average used for ANOVAs. Similarly, RLCs were constructed from average readings for each light intensity at each location.

Correlations between some parameters were described by Pearson's product moment correlation analysis. In addition, I tested the dependence of some parameters on the distance to the mainland, using regression analysis.

RLCs were fitted using the model of Platt *et al.* (1980) and light curve parameters calculated as in Kühl *et al.* (2001). The parameters presented here are the initial slope of the light curve (α), the maximal potential electron transport rate at light saturation ($rETR_{max}$), the irradiance at onset of light saturation (E_k) and the slope beyond the onset of (potential) photoinhibition (β). Curve fitting was conducted using Sigma-Plot (v.7, SPSS Inc. 2001), all other statistical analyses were conducted in Statistica (v.6, StatSoft, Inc., 2001).

Diatom Counts

Samples for diatom abundance and community composition were collected in three regions with different sediment types and presumed under contrasting water qualities. These were inshore reefs in Princess Charlotte Bay (PCB: Hannah, Hay, and Wilkie Islands, and McDonald Reef) and the Wet Tropics (WT: Dunk, Russell, High and Fitzroy Islands) and outer shelf reefs of the Central and Northern GBR (OS: Lizard Island and Reef 14-077 in the north, and Dip, Bowl and Davies Reefs in the Central Section of the GBR), all locations are shown in Fig. 3.1(a).

Sediment samples were taken in triplicate, at depth between 8 and 14 m. The upper 1 cm of the sediment was sampled using a cut off 10 mL plastic syringe and stored in 9 mL of 4% formalin in seawater. Samples were cleaned and separated from sediments following Sundbäck and Snoeijs (1991).

Diatoms on microscopic slides were taxonomically determined and enumerated along transects until a minimum of 300 valves was recorded with a microscope. The number of individuals of each diatom taxon per 1 mL sediment, representing 1 cm^2 of surface area, were calculated taking all dilution steps during preparation into consideration.

Statistical analysis of diatom community

Univariate Analysis of Variance (ANOVA) was used to test for differences in total diatom abundance of some numerically important species.

Diatom abundances in the back-reef samples of the eight inshore reefs of the WT and PCB, and the OS Reefs were pooled over each reef, and differences between the WT, PCB and

OS regions were tested by using a single-factor ANOVA (a more detailed analysis also comparing back reef to front reef samples is given in Gottschalk 2005).

Subsequent to univariate analyses, multivariate analyses were used to examine community structure. A redundancy analysis (RDA) was conducted to illustrate the relationships between the community structure at sampling regions and several environmental parameters, and the distance from the coastline in kilometres. Bray-Curtis similarity coefficient (unweighted group-average method) was used to construct a matrix between reefs. This matrix was subjected to the analysis of similarities (ANOSIM), testing statistical differences in taxa composition between these groups. Taxa primarily responsible for dissimilarities between them were identified using the SIMPER module. Before analyses, abundance data for each taxon were averaged over each reef and fourth root transformed, to balance the effects of rare and common species to the similarity measure between samples (Clarke and Gorley 2001). Multivariate analyses were conducted using the PRIMER v 5 software (package version 5.2.7) and the Biplot add-in for excel (Lipkovich and Smith 2002).

Indicator values for all taxa were determined following Dufrene and Legendre (1997) and their significance tested using permutation tests as implemented in the free software *IndVal* available at http://mrw.wallonie.be/dgrne/sibw/outils/indval/home.html. These indicator values can be calculated for any group within a hierarchical structure. I have chosen to test for indicator values for Inner and Outer Shelf reefs within the total dataset, and for the WT and PCB areas within the inshore reefs. Indicator values can assume values between 0 and 100, with 0 indicating that the respective taxon is evenly distributed within and across groups. A value of 100 indicates that the taxon occurs in all samples of the respective group, and in none of the alternative groups. For graphic representation, I have only shown indicator values when they are significant ($p < 0.05$), assume the maximum value in the respective hierarchic level and have a value of > 40.

Foraminifera

Sampling

I collected sediment samples for foraminifera community analysis from 10 reefs in August 2004. These reefs are located along a transect with increasing distance from the Proserpine and O'Connell rivers in the Whitsunday region. Distinct differences in water quality along this transect were shown in previous studies (Uthicke 2006, Chapter 2). In general, turbidity distinctly decreases with distance from the mainland and the two river mouths and therefore light availability increases. Similarly, chlorophyll and some other parameters show clearly decreasing trends with distance from the river mouths (see Chapter 2). The sampling locations (see Fig. 3.1(b)) were at Repulse and Lindeman Islands (Zone 1 in Uthicke 2006), Long and Dent Islands (Zone2), Whitsunday and Hook Islands (Zone 3), Border and Deloraine Islands (Zone 4) and Charity and Bait Reefs (Zone 5, midshelf reefs). On each reef, one sample location of the sheltered back-reef and one on the more exposed front-reef was chosen to collect foraminifera from a broad range of ecological settings within each reef. Two samples of > 50 g sediment from our standard collection depth of 7 - 9 m were carefully scraped from the top 0.5-1 cm of sediments per location. Samples were fixed in 100% ethanol and transported to the laboratory.

Enumeration

Sediments were washed with freshwater over a 63 μm sieve to remove small particles. Subsequently, a minimum of 30 specimens were collected from the sediment of each sample in Bogarov dishes. Samples were dried and species composition of foraminifera determined in microfossil slides under a dissection microscope. The two subsamples per location and the two locations per reef were pooled for comparison of the community, achieving sample sizes over 120 foraminifera per reef.

3.3 Results

Bacteria

In total, I analysed 221 bacterial sequences from the eight clone libraries. Genetic diversity in these libraries was high, both on the entire sequence level and expressed as nucleotide diversity (Table 3.1). Only very few sequences were identical within each clone library and the coverage of sampled diversity was between 3 - 15%. One Hundred and eighty-nine out of the 221sequences were unique and total coverage was 14.5%. High diversity was illustrated for most individual clone libraries in rarefaction curves (Fig. 3.2). Most libraries showed only very little saturation in these curves, suggesting that actual diversity in each library would at least be several folds higher than sample size. Also the rarefaction curves of the combined sample exhibited hardly any saturation. Thus, coverage data and rarefaction curves clearly suggested that only a small proportion of the total bacterial diversity was sampled, and it seems conservative to extrapolate that the actual diversity was clearly in excess of 1,000 phylotypes.

Table 3.1 Molecular characteristics of 16S rDNA bacterial clone libraries from sediments of two inshore and two outer shelf reefs of the GBR.

	Sample Size	No. different clones	Nucleotide diversity	No. variable bases	Mean No. differences (π)
Fitzroy Is. 1	27	26	0.217 (0.107)	698	240.60 (106.22)
Fitzroy Is. 2	25	23	0.204 (0.101)	909	273.11 (120.86)
High Is. 1	31	27	0.232 (0.113)	638	251.29 (110.45)
High Is. 2	28	17	0.232 (0.114)	573	245.70 (108.34)
Hastings Rf. 1	27	23	0.254 (0.125)	667	271.22 (119.70)
Hastings Rf. 2	25	22	0.236 (0.116)	631	252.47 (111.74)
Flynn Rf. 1	29	26	0.245 (0.120)	644	263.26 (115.94)
Flynn Rf. 2	29	28	0.206 (0.101)	590	213.86 (94.24)

Composition of the clone libraries

With the exception of three diatom plastid sequences and one archaebacteria all sequences clustered within the bacteria. None of the bacterial sequences had a 100% similarity to sequences published in various data banks. However, several sequences were closely associated with published sequences, and would fall within the same species if a 97% similarity criterion was applied to distinguish species, as is commonly done for 16S sequences of Bacteria. Examples of these are discussed below in the individual taxonomic groups.

The sequences clustered into the following nine main domains and subdivisions; the distribution among these divisions is shown in Table 3.2.

γ-proteobacteria

Sixty-five sequences from the eight 16S rDNA clone libraries (29.4% of the total) clustered in several families of the γ subdivision of the proteobacteria (Fig. 3.2A). Many of the sequences were closely aligned to a group of sulphur-oxidizing bacteria, and some were within 3% of published sequences of sulphur-oxidizing symbionts of marine invertebrates from shallow and deep sea habitats (e.g. Di Meo *et al.* 2000; Dubilier *et al.* 2001). Several clones from different libraries had less than 3% sequence difference from a species of *Pseudomonas* from deep sea sediments (Yanagibayashi *et al.* 1999). One ribotype had a 1.5% sequence distance from *Thalassomonas ganghwensis*, an alteromonadales described from an intertidal mudflat (Yi *et al.* 2004). Fig. 3.3 illustrates the diversity of this subdivision as an example for all subsequent divisions.

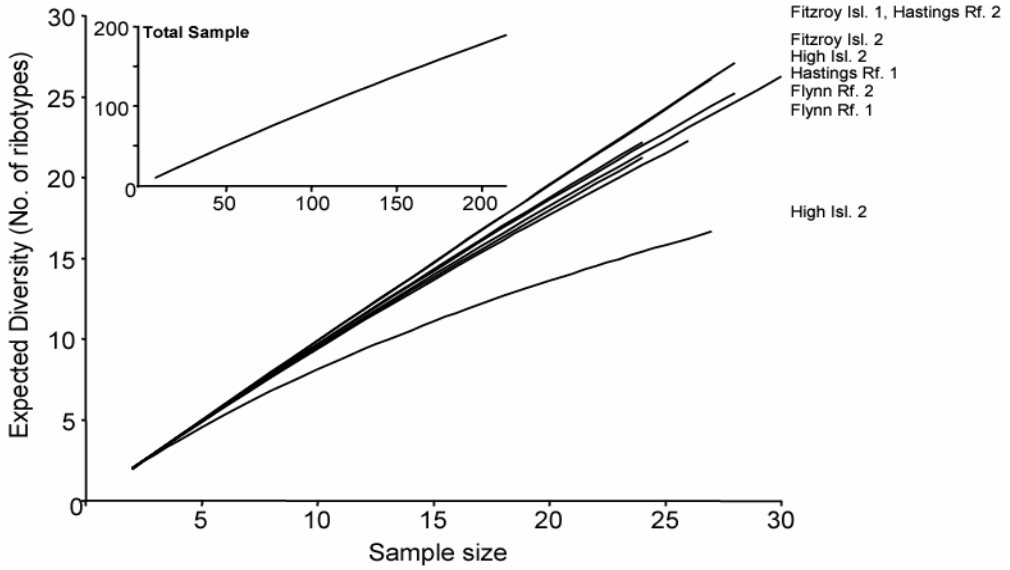

Figure 3.2. Rarefaction curves for eight 16S rDNA clone libraries from sediments of the GBR. The insert shows a rarefaction curve for all eight clone libraries combined.

Table 3.2. Percent contribution of each bacterial group to the total inshore and offshore samples calculated for all clones and repeated clones removed from each library, and results from SIMPER analysis.

	All Clones			Repeated sequences removed		
	% of assemblage		Contribution to difference	% of assemblage		Contribution to difference
	Inshore	Outer shelf		Inshore	Outer shelf	
Acidobacteriaceae	4.6	0.9	17.9	5.5	1.0	19.1
Cyanobacteriaceae	1.8	9.3	16.2	2.2	7.2	15.3
Planctomycetaceae	6.4	9.3	13.9	6.6	8.3	13.6
δ-proteobacteria	17.4	10.3	13.5	17.6	10.4	13.2
Verrucomicrobiaceae	11.8	2.8	10.9	8.8	3.1	10.6
α-proteobacteria	8.3	5.6	10.4	9.9	6.2	10.6
unknown	5.5	5.6	8.2	5.5	6.3	8.7
γ-proteobacteria	22.9	37.0	5.2	23.1	39.6	5.3
CBF group	22.0	19.4	3.8	20.8	17.7	3.5

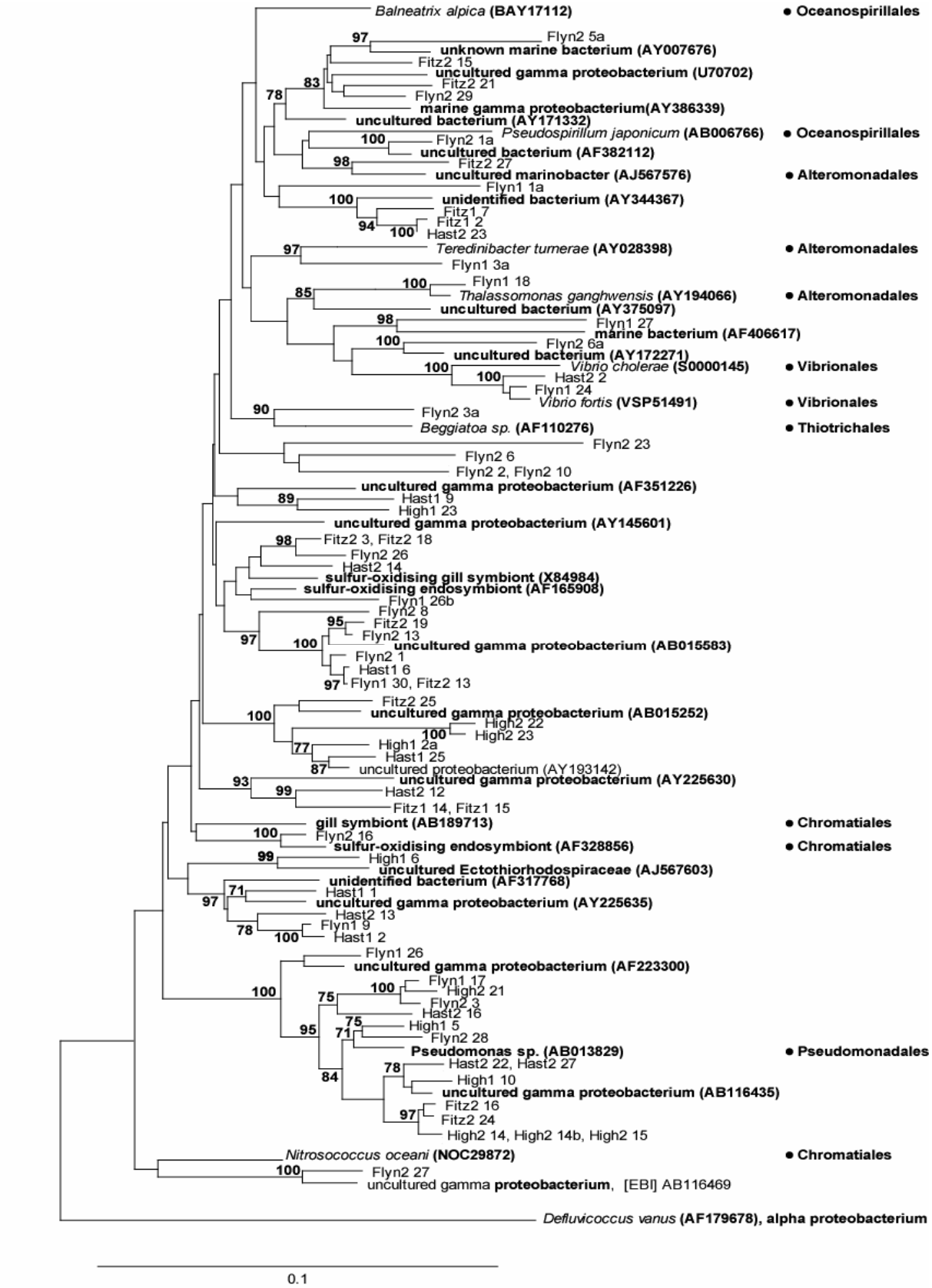

Figure 3.3. Neighbour-Joining trees representing γ-proteobacteria sequences from 8 clone libraries of the 16S rDNA gene of GBR sediments and close matches from public databases in bold (access numbers given in brackets). Trees were rooted to appropriate outgroup sequences from other domains. The percentage of bootstrap replicates (1000 replicates) resulting in the same clusters is given near the respective nodes for bootstrap values higher than 70%.

α-proteobacteria

Fifteen clones (6.8%) from seven of the clone libraries clustered in the α-proteobacteria. The nearest known bacterial species were from the families Rhodospirillales, Rickettsiales, Rhizobiales and Rhodobacterales. Only two of those were within 3% divergence of previously published sequences.

δ-proteobacteria

With 30 (13.6%) sequences clustering in this group, the δ-proteobacteria were well represented in our clone libraries. Most of these sequences were associated with the sulphur-reducing groups Desulfobacterales and Desulfovibrionales. Sulphate reduction in marine sediments may account for up top 50% of total organic carbon remineralisation (Jørgensen 1982).

Cytophaga-Flavobacteria-Bacteroidetes (CFB) group

The CFB group was the second largest group in our clone library, with 45 clones (20.4%) clustering into this group. Not many of the ribotypes retrieved were closely related to published sequences. Nearest matches include representatives of the Cytophagales, Flavobacteriales, and Sphingobacteriales.

Cyanobacteriaceae

Twelve sequences (5.4%) clustered in the Cyanobacteria family (Fig. 3.3D). Three ribotypes and six clone sequences were closely related (> 98.9% sequence identity) to *Oscillatoria rosea* and one showed affiliation to a *Trichodesmium* species.

Other bacterial taxa

Several sequences clustered near the Planctomycetaceae (7.7%), Verrucomicrobiaceae (6.8%), and Acidobacteriaceae (2.7%). Some sequences clustered near those taxa, but could not be unambiguously grouped with any of these (5.4%). Two clones had 98.6% sequence identity with a *Pirellula* species found in the plankton (Vergin *et al.* 1998). Several clones had > 97% identities to uncultured Verrucomicrobia.

Community analysis

For community analysis using *Primer* I grouped bacteria detected in the clone libraries into α- δ- and γ-proteobacteria, CBF group, Planctomycetaceae, Verrucomicrobiaceae, Acidobacteriaceae, unknown bacteria related to the latter three groups and Cyanobacteria. A cluster analysis on Bray-Curtis similarities indicated that the clone library from High Island 2 was quite different to other libraries, with reduced diversity compared with other sites. The other main differences to the other libraries were the absence of α-proteobacteria and δ-proteobacteria and a higher then average occurrence of the CFB group (35.7%) and Verrucomicrobiaceae (28.6%).

The remaining clone libraries only roughly clustered into inshore and offshore populations, and had similarities close to or higher than 80%. However, Analysis of Similarities (ANOSIM) indicated marginally significant differences in the assemblage of these two regions, both with the entire dataset (Global R = 0.250, p = 0.057) or after removal of repeated sequences from libraries (Global R = 0.208, p = 0.057). When High Island 2 was removed from this analysis, significance levels remained the same, but R-values (expressing the magnitude of difference) distinctly increased (entire dataset: R = 0.389, repeated sequences removed: R = 0.330), reflecting the higher within-region similarity when omitting that sample.

The largest contribution to the difference between inshore and outer shelf sediment bacterial communities was attributed to Acidobacteriaceae and Cyanobacteriaceae; the former being more abundant inshore and the latter being more abundant in outer shelf sediments (Simper

analysis, Table 3.2). Together, these two bacterial groups accounted for more that 30% of the difference (both for the dataset with all sequences retained, or that with repeated ribotypes removed) between the regions despite the fact that they were relatively low in abundance in either region. The least important groups for regional differentiation were the γ-proteobacteria and the CFB group, the most abundant taxa in the dataset. The reason for this was the large intra-regional variation in the γ-proteobacteria and the small differences in averages for the CBF group.

Benthic Microalgae

Physiology

Differences in average minimum fluorescence were statistically significant between *in situ* (F) and laboratory dark adapted (F_0) treatments and between the zones (Table 3.3, factors "Method" and "Zone"), but also the interaction term between these two main factors was significant. However, graphical inspection of this interaction term showed that trends were consistent over the different zones (Fig. 3.4). F readings for Zones 1-4 were on average 3.7 times higher than estimates of F_0. The interaction term was significant because the differences in Zone 5 were less pronounced. F estimates decreased towards Zone 4 and were higher again in Zone 5 (Fig. 3.4). Neither F_0 nor F readings were significantly correlated with chlorophyll *a* contents of the upper 1 cm of the sediments (F: r = -0.012, p = 0.962; n = 19; F_0 : r = 0.3032, p = 0.194, n = 20).

The effective quantum efficiency ($\Phi_{PSII,\ corr}$, overall average 0.59, SE = 0.02) was not significantly different (Table 3.3, ANOVA factor "Method") from the maximum quantum efficiency measured in the laboratory ($F_v/F_{m,\ corr}$, overall average 0.56, SE = 0.01). The quantum efficiency of PSII (averaged $\Phi_{PSII,\ corr}$ and $F_v/F_{m,\ corr}$) showed no significant differences between zones (Table 3.3, Fig. 3.4, ANOVA factor "Zone"). Similarly, there was no apparent decline in effective quantum efficiency with distance from the mainland (regression analysis, $R^2 = 0.01$, $F_{1,17} = 0.21$, p = 0.6500).

Table 3.3. Mixed model analysis of variance for minimum fluorescence (F_0 and F, corrected for $F_{0,\ sed}$) and quantum efficiency ($F_v/F_{m,\ corr}$ and $\Phi_{PSII,\ corr}$) in sediment biofilms of the Whitsunday area, GBR. F_0 and F data were square-root transformed and efficiency data were arcsine transformed for analyses.

	DF	F_0, F			$F_v/F_{m,\ corr}$, $\Phi_{PSII,\ corr}$		
		MS	F	p	MS	F	p
Zone	4	30.9067	6.87	**0.0293**	0.0238	3.60	**0.0961**
Method	1	263.7323	324.48	**<0.0001**	0.0085	1.30	0.3060
Reef(**Z**)	5	4.5276	1.91	0.1378	0.0066	0.79	0.5705
Z x **M**	4	5.3463	6.58	**0.0316**	0.0182	2.77	0.1470
M x **R**(**Z**)	5	0.8128	0.34	0.8808	0.0066	0.78	0.5729
Residual	20	2.3719			0.0084		

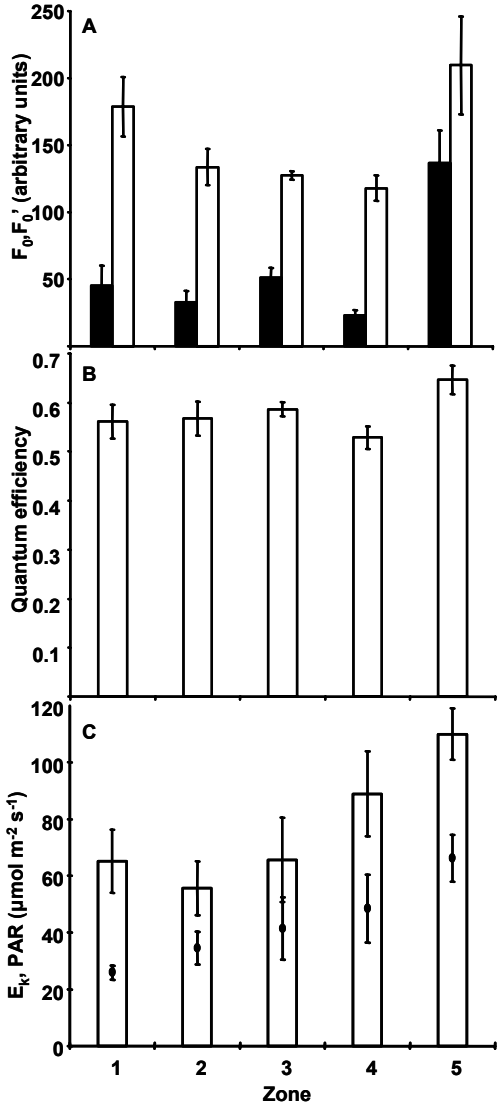

Figure 3.4. Minimum fluorescence (A; F_0: black bars; F : white bars), quantum efficiency (B, average of $F_v/F_{m,\ corr}$ and $\Phi_{PSII,\ corr}$) and light saturation point (E_k: white bars) and incident light (PAR, black dots) values in biofilm communities of five zones in the Whitsunday area of the GBR. Error bars represent one standard error, N = 4.

Rapid light curves

The model chosen gave a good fit to the rapid light curves (RLCs), with somewhat better fit for *in situ* measurements (overall average R^2 = 0.986, SE = 0.003, n = 20) than for measurements in the laboratory (R^2 = 0.859, SE = 0.021, n = 20). This was likely to be caused by the lower fluorescent signal in the latter samples (see above) resulting in lower signal to noise ratios.

The initial slope of the light curves (α) showed significant differences (Table 3.4, ANOVA factor "Method") between *in situ* measurements (average = 0.664, SE = 0.023) and on board readings (average = 0.418, SE = 0.032). Similarly, the maximal potential electron transport rate at light saturation ($rETR_{max}$) was significantly higher (ANOVA, Table 3.5, Factor "Method") during *in situ* readings (63.60, SE = 3.80) than in the laboratory (20.54, SE = 2.72). No differences between the zones were detected for α or $rETR_{max}$ (ANOVA, Table 3.4, factor "Zone").

Table 3.4 Mixed model analysis of variance for rapid light curve parameters (the initial slope α, the asymptotic maximum relative electron transport rate $rETR_{max}$ and the light compensation point E_k) in sediment-biofilms of the Whitsunday area, GBR. Data were square-root transformed for analyses.

	DF	α			$rETR_{max}$			E_k		
		MS	F	p	MS	F	p	MS	F	p
Zone	4	0.00205	1.54	0.3206	3.512	2.47	0.1735	13.5931	5.52	**0.0445**
Method	1	0.05991	18.99	**0.0073**	118.151	181.32	**<0.0001**	67.3622	14.54	**0.0125**
Reef(**Z**)	5	0.00133	1.12	0.3815	1.418	1.69	0.1830	2.4619	1.15	0.3674
Z x **M**	4	0.00102	0.32	0.8519	1.371	2.12	0.2178	5.4739	1.18	0.4197
M x **R**(**Z**)	5	0.00315	2.65	0.0540	0.652	0.78	0.5765	4.6329	2.17	0.0981
Residual	20	0.00119			0.837			2.1320		

The light intensity at onset of saturation (E_k) was significantly higher (ANOVA, factor "Method", Table 3.4) when measured *in situ* (average = 96.76, SE = 5.48) compared to values obtained in the laboratory under low light conditions (average = 57.41, SE = 8.95). Average E_k values were also significantly different between the Zones (ANOVA, factor "Zone", Table 3.4). The light compensation point clearly increased towards the outer shelf reef (Fig. 3.4C), and post hoc tests revealed that values from Zone 5 were significantly higher than in Zone 1,2 and 4 (Fishers LSD test, $p < 0.05$).

Figure 3.4C also depicts average PAR readings for each Zone *in situ* (measured at the depth and time of the PAM readings). These values nearly triple from the inner reefs (Zone 1) towards the midshelf reefs (Zone 5). Correlation analysis using averages from each location confirm that E_k values obtained from RLC measurements both *in situ* ($r = 0.62$, $p < 0.05$, $n = 17$) and in the laboratory ($r = 0.58$, $p < 0.05$, $n = 18$) were significantly correlated with ambient average PAR readings. Similarly, $rETR_{max}$ values were correlated with incident PAR values both for *in situ* measurements ($r = 0.49$, $p < 0.05$, $n = 17$) and laboratory readings ($r = 0.58$, $p < 0.05$, $n = 18$). No significant correlations existed between α and PAR (*in situ*: $r = -0.17$, $p > 0.05$, $n = 17$; laboratory: $r = -0.26$, $p > 0.05$, $n = 18$).

No formal statistical analysis was conducted on the beta values, because removal of that term from some of the light curves led to an unbalanced statistical design. However, values were relatively low, with very low values observed in Zone 1 (0.010, SE = 0.006, n = 5) and 5 (0.016, SE = 0.004, n = 8), and intermediate values in Zones 2 (0.036, SE = 0.018, n = 8), 3 (0.068, SE = 0.026, n = 8), and 4 (0.114, SE = 0.042, n = 6). Figure 3.5 illustrates the shape of the average rapid light curves for each individual Zone.

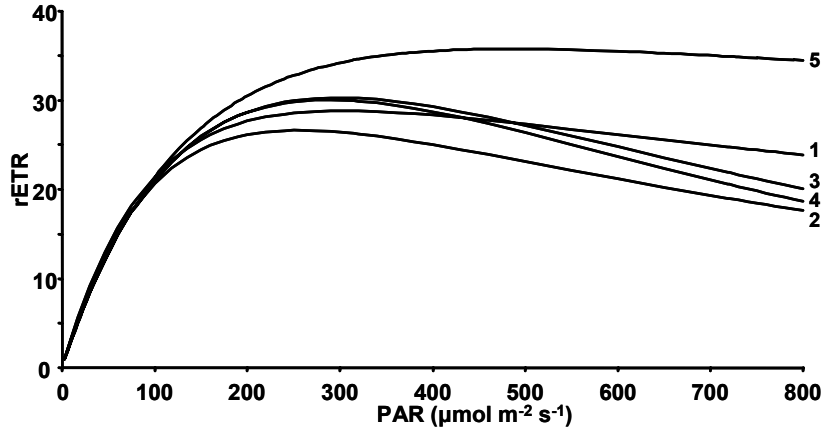

Figure 3.5. Rapid light curve modelled from average parameters (α, β, $rETR_{max}$, E_k) for each of the five zones along the water quality gradient in the Whitsunday Islands.

Diatom Communities

In the samples from Princess Charlotte Bay (PCB), Wet Tropics (WT) and the Outer Shelf Reefs (OS), 55 genera of Bacillariophyceae were observed, and 78 species could be identified; a total of 209 taxa were distinguished and used for multivariate analyses. The overall diatom abundance was high, with about 2.55 × 10^6 cells × mL^{-1} sediment. *Amphora delicatissima*, *Cocconeis placentula*, *Nitzschia* cf. *panduriformis*, *Amphora richardiana*, *Navicula* sp. sect. *Lyratae* and *Diploneis* sp. 2 and taxa belonging to the five size groups of raphid cells (*Navicula* sp.) and *Nitzschia* sp. were the most abundant taxa and had abundances higher than 3.5 × 10^4 cells mL^{-1}. These 16 taxa, together with the group of unidentifiable diatoms, represented more than 78.5 % of the total abundance.

Average diatom numbers in back-reef sediments were nearly twice as high on inshore reefs of the WT (3.7 x 10^6 cells mL^{-1}, SE = 3.7 x 10^5) and PCB (3.1 x 10^6 cells x mL^{-1}, SE = 2.7 x 10^5) compared with OS (1.9 x 10^6 cells mL^{-1}, SE = 5.3 × 10^5), with slightly higher values in WT than PCB. ANOVA indicated that differences between these averages were significant ($F_{(2, 9)}$= 5.074, p = 0.033), however, post hoc analysis revealed that this difference was only significant for the comparison of diatom abundances of OS and WT (Tukey HSD test, p = 0.032). Thus, diatom numbers roughly correspond to the nutrient availability assuming nutrient availability follows the pattern WT > PCB > Outer Shelf Reefs as shown in Fabricius and Death (2004).

The first two axes of the redundancy analysis (RDA) explained 60% of the variation in the species distribution (Fig. 3.6). This analysis clearly separated all Outer Shelf reefs from the inshore reefs. Furthermore, the RDA suggested that the inshore reefs distinctly cluster into the WT and PCB regions. As expected, vectors representing carbonate content of the sediments and the distance from the mainland corresponded to the outer shelf reefs. High organic carbon and nitrogen values in the sediments were roughly correlated with reefs in PCB, whilst most other environmental parameters measured exhibited no apparent correlation to the sample locations. Several diatom species appeared highly specific to individual regions (RDA, Fig. 3.6), this pattern was investigated in detail using indicator values (see below). The RDA also illustrated the higher diversity of diatoms in inshore reef than offshore reefs; because more species were associated with inshore locations. ANOSIM statistically confirmed differences between the three geographic regions, with differences between OS and PCB (p = 0.008), OS and WT (p = 0.008) and WT and PCB (p = 0.029) all being significant.

The average dissimilarity was 44.19 % between OS and PCB, 44.63 % between OS and WT and 28.87 % between PCB and WT (SIMPER analysis). This confirmed patterns observed in the RDA (Fig. 3.6) and ANOSIM, suggesting a higher dissimilarity in diatom distribution between PCB and OS regions, and the WT and OS regions compared with the distributions in PCB and WT sediments.

With the exception of *Nitzschia* cf. *panduriformis* the six most abundant species did not belong to the most important contributors to dissimilarity between the three groups (Table 3.5). When outer shelf reefs were compared with inshore reefs, many rarer species contributed much to the dissimilarity.

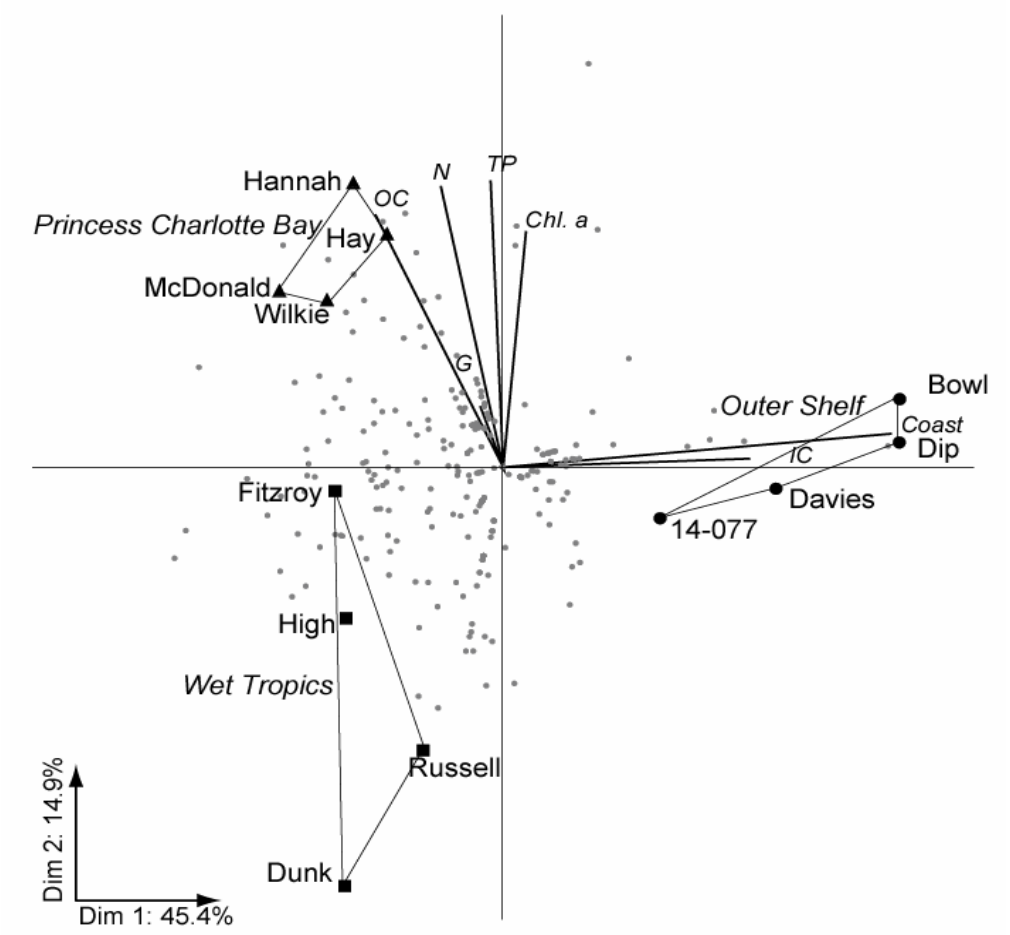

Figure 3.6. Biplot of a redundancy analysis (RDA) of diatom community composition data (the endpoint of each species vector is represented by a grey dot) in the Wet Tropics (black squares, Russell, Dunk, High and Fitzroy Islands), Princess Charlotte Bay (black triangles, Hannah, Hay and Wilkie Islands, and McDonald Rf.) and outer shelf reefs (black dots, Davies, Dip, and Bowl Rf., Rf. 14-077) of the Great Barrier Reef. Environmental sediment data (OC: organic carbon, IC: inorganic carbon, N: nitrogen, Chl. a: chlorophyll a, TP: total pigment, G: grain size) and the distance to the coastline (Coast) are represented by black lines.

Most abundant taxa (>3.5 x 10^4 cells mL^{-1}, see above) have highest indicator values, between 98.6 and 100, for the total dataset (Fig. 3.7). Thus, these species were characteristic for all reefs in all regions but were not good indicators for specific regions or water quality conditions.

Eleven taxa were characteristic indicators for inshore reefs, as indicated by their high (>40) and significant indicator values for that group (Fig. 3.7, Table 3.6). The highest values were obtained by *Paralia* sp., *Thalassionema nitzschoides* and *Cocconeis scutellum.* Only three of these potential indicator species occurred exclusively on inshore reefs, however, nearly all other nearshore indicator species were at least an order of magnitude more abundant on these reefs (Table 3.6a). Six taxa (e.g. *Amphora* sp. 4, *Raphoneis bilineata*, Unknown 8) were highly characteristic for OS samples when compared with Inner Shelf samples. The three Amphora species and one unidentified pennate diatom identified as indicators occurred exclusively on Outer Shelf reefs (Table 3.6a). One taxon (*Amphora veneta*) was identified as

a possible indicator species for the Wet Tropics area. The estimate of the average density in both regions indicated that it was more than twice as abundant in WT, although, this species was relatively abundant in both regions. Five taxa (*Gyrosigma* sp., Unknown 23, *Diploneis* sp. 1, *Amphora granulata*, *Pleurosigma* sp.) were identified as indicators for the Princess Charlotte Bay area (Fig. 3.7, Table 3.6b). These species were about 3 to 6 times more abundant in PCB. Some examples of diatoms with high indicator values are shown in Fig. 3.8.

Table 3.5. Abundances of 13 benthic diatom taxa averaged for the regions PCB, WT and OS and their contribution (%) to the dissimilarity between the regions PCB and OS, and WT and OS.

OS vs. PCB	Contribution dissimilarity (%)	OS abundance (cells mL^{-1})	PCB abundance (cells mL^{-1})
Amphora sp. 4	2.01	8.39×10^4	0
Nitzschia cf. *panduriformis*	1.63	7.94×10^4	6.79×10^5
Thalassionema nitzschoides	1.63	9.41×10^2	5.88×10^4
Paralia sp.	1.58	0	3.25×10^4
Diploneis sp. 1	1.54	0	3.25×10^4
Unknown 8	1.33	3.07×10^4	0
Diploneis crabro	1.30	1.57×10^2	2.16×10^4
Gyrosigma sp.	1.29	1.46×10^3	5.14×10^4
Raphoneis bilineata	1.24	2.91×10^4	6.72×10^2
sum	14.76		

OS vs. WT	Contribution dissimilarity (%)	OS abundance (cells mL^{-1})	PCB abundance (cells mL^{-1})
*Amphora s*p. 4	2.04	8.39×10^4	0
Paralia sp.	1.96	0	7.39×10^4
Thalassionema nitzschoides	1.85	9.41×10^2	9.83×10^4
Raphoneis bilineata	1.47	2.91×10^4	0
Suriella intermedia	1.45	0	2.11×10^4
Amphora sp. 2	1.36	6.75×10^4	9.41×10^3
Unknown 8	1.35	3.07×10^4	0
Amphora bigibba	1.28	1.05×10^3	2.20×10^4
Nitzschia sp. 8	1.18	1.25×10^3	1.90×10^4
Amphora veneta	1.18	1.47×10^4	7.68×10^4
sum	15.12		

PCB vs. WT	Contribution dissimilarity (%)	OS abundance (cells mL^{-1})	PCB abundance (cells mL^{-1})
Amphora sp. 2	1.65	4.06×10^4	9.41×10^3
Gomphonema sp.	1.44	8.69×10^3	0
Grammatophora oceanica	1.43	1.10×10^4	0
Centric Diatoms in chains	1.22	1.36×10^4	1.29×10^4
Amphora sp. 23	1.19	7.00×10^4	2.96×10^4
Caloneis sp. 7	1.11	8.40×10^3	9.41×10^2

PCB vs. WT	Contribution dissimilarity (%)	OS abundance (cells mL^{-1})	PCB abundance (cells mL^{-1})
Gyrosigma sp.	1.10	5.14×10^4	1.15×10^4
Unknown 23	1.10	2.13×10^4	3.29×10^3
Amphora sp. 26	1.08	1.19×10^4	3.32×10^4
Opephora sp.	1.07	1.86×10^4	3.47×10^3
sum	12.39		

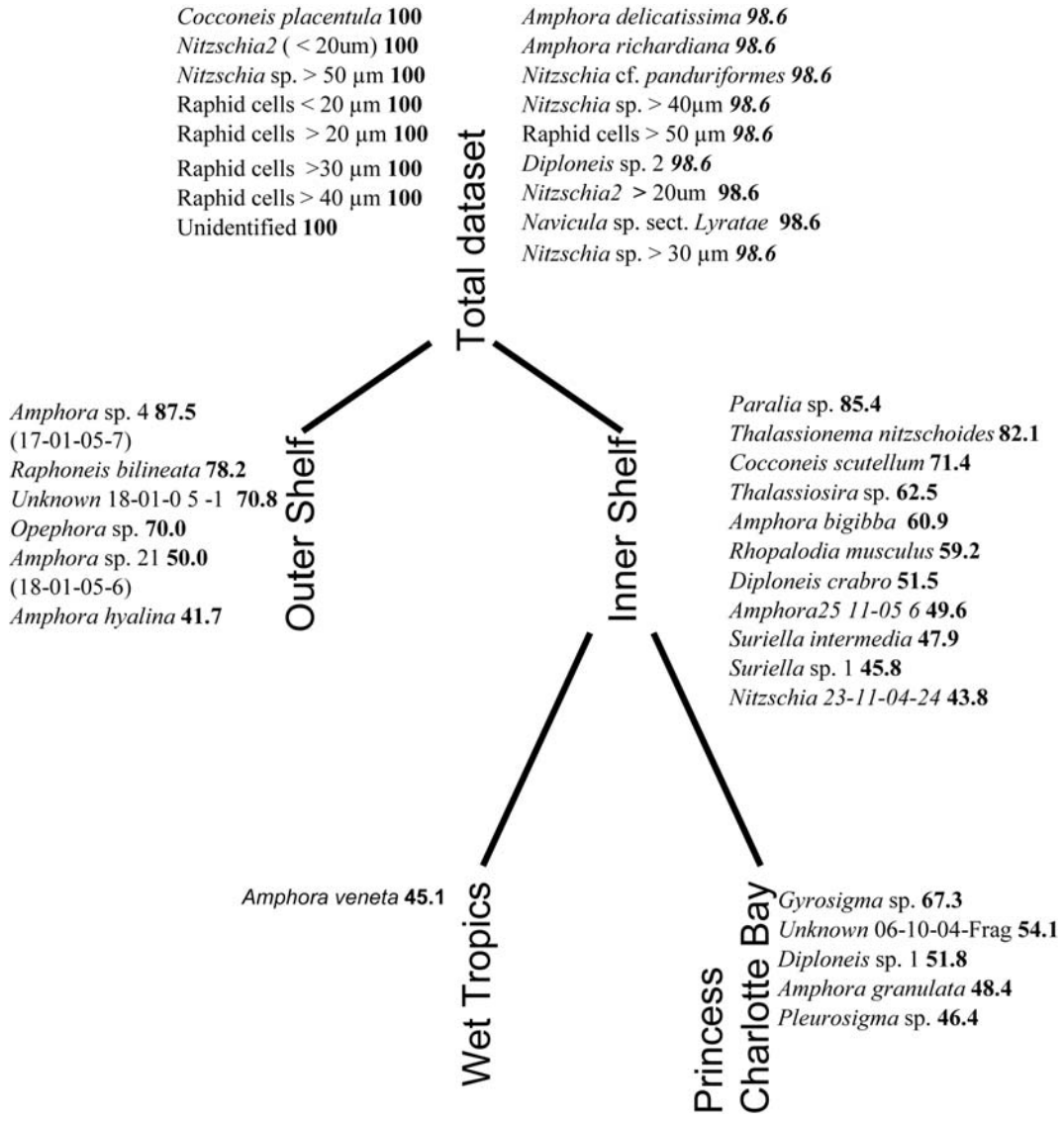

Figure 3.7. Dendrogram showing species with the highest indicator values for the whole dataset, inshore vs. offshore and WT vs. PCB.

Table 3.6. Benthic diatom taxa with highest indicator values for each region, and their average abundance in the respective regions. a) Comparison Inshore vs. offshore, b) comparison WT vs. PCB.

a) Region	Taxa	Inner Shelf	Outer Shelf
		cells mL^{-1}	cells mL^{-1}
Inner Shelf	*Amphora bigibba*	10366.5	653.4
	Amphora sp. 27	15381.2	1191.9
	Cocconeis scutellum	27469.4	2247.8
	Diploneis crabro	8721.6	98.0
	Nitzschia sp. 8	9253.5	806.5
	Paralia sp.	26461.9	0.0
	Rhopalodia musculus	17374.7	2189.0
	Suriella intermedia	7648.8	0.0
	Suriella sp. 1	5118.4	0.0
	Thalassionema nitzschoides	39388.9	588.1
	Thalassiosira sp.	9400.2	326.7
Outer Shelf	*Amphora* cf. *hyalina*	0.0	5593.4
	Amphora sp. 21	0.0	5488.8
	Amphora sp. 4	0.0	39839.6
	Opephora sp.	5476.5	22229.7
	Raphoneis bilineata	168.0	14264.4
	Unknown 8	0.0	12748.4
b) Region	**Taxa**	**PCB**	**WT**
		cells mL^{-1}	cells mL^{-1}
Wet Tropics	*Amphora veneta*	18766.5	40424.1
Princess Charlotte Bay	*Amphora granulata*	19122.3	4740.9
	Diploneis sp. 1	16237.0	3353.6
	Gyrosigma sp.	25689.4	6067.8
	Pleurosigma sp.	12994.6	3932.6
	Unknown 23	10656.4	1773.3

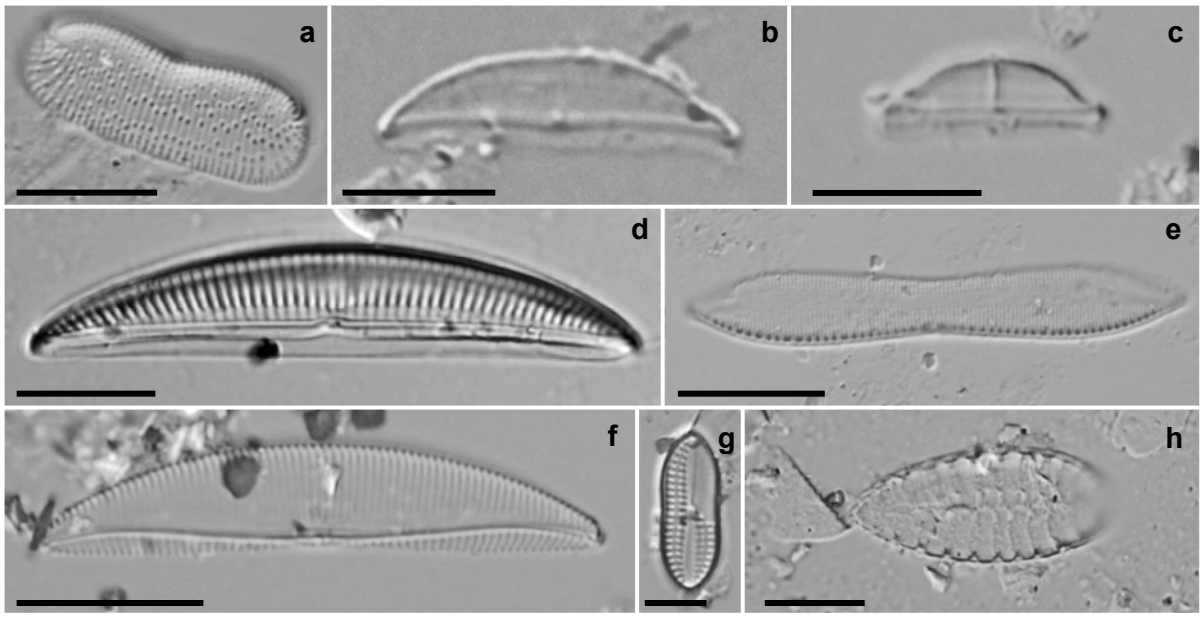

Figure 3.8. Examples of taxa not identified to species level, but showing high indicator values for one of the regions Inner Shelf, Outer Shelf, Wet Tropics or Princess Charlotte Bay. a. Unknown sp. 23, scale bar: 20 µm; b. Unknown sp. 8, scale bar: 10 µm; c. *Amphora* sp. 4, scale bar: 5 µm; d. *Amphora* sp. 27, scale bar: 20 µm; e. *Nitzschia* sp. 8, scale bar: 20 µm; f. *Amphora* sp. 21, scale bar: 20 µm; g. *Diploneis* sp.1, scale bar: 10 µm; h. *Surirella* sp. 1, scale bar: 20 µm.

Foraminifera

Foraminifera communities in the sediments of the Whitsunday region were highly diverse. Most of the large symbiont bearing (~ >200µm) foraminifera could be determined to species level (Table 3.7) using a dissection microscope. Most of the smaller taxa were determined to genus or family level. Further taxonomic resolution requires electron microscopy, which would be too time-consuming for processing large sample numbers required in an ecological context. Thus, foraminifera were sorted into 27 taxonomic groups (Table 3.7).

These taxa showed distinct differences in their distributional patterns along the water quality gradient in the Whitsundays region (Fig. 3.9). Some taxa, like *Quinqueloculina spp.*, exhibited no apparent trend with distance from the rivers along this gradient (Fig. 3.9A). Other taxa showed distinct preference for inner reef, and clearly decreased in importance with distance from the rivers. Amongst these, the clearest trend was observed in the small rotaliids (Fig. 3.9B) and *Elphidium spp*. (Fig. 3.9C). Most of the symbiotic taxa showed a clear preference for conditions further from the coast, and therefore lower turbidity and lower nutrient availability. *Amphistegina spp.* was reasonably common on inshore reefs, but contributed more than 4 times more to foraminifera communities further than 70 km from the river mouths (Fig. 3.9D). *Calcarina spp.* were usually absent from the inner reefs, however, one exception was observed (Fig. 3.8E). The abundance of this genus increased towards the outer reef.

The first two dimensions of a redundancy analysis of the foraminifera community data explained 44.4% of the variance. This analysis clearly separated heterotrophic species and symbiotic species with very little overlap between these groups (Fig. 3.10). The symbiotic foraminifera were correlated with higher distance from the coastline, higher secchi depth, brighter sediment colour and higher inorganic carbon. In contrast, the heterotrophic

communities were correlated to higher organic carbon and nitrogen contents of the sediments (Fig. 3.10). In Figure 3.10, the size of the location markers is proportional to the water column chlorophyll concentrations from the long term chlorophyll monitoring, illustrating that values increases towards inner reefs dominated by heterotrophic foraminifera.

Table 3.7. Foraminifera taxa which can be determined with relative ease under dissection microscope magnification. Functional group follows the classification used by Hallock *et al.* (2003) to calculate the FORAM index.

Functional group	Order	Family	Species	Symbiont type
Symbiont Bearing	Rotaliida	Calcarinidae	*Baculogypsina sphaerulata*	Diatom
			Calcarina hispida	Diatom
			Calcarina spengleri [1]	Diatom
			Calcarina mayorii	Diatom
			Neorotalia calcar	Diatom
		Amphisteginidae	*Amphistegina radiata*	Diatom
			Amphistegina spp.[2]	Diatom
		Numulitidae	*Heterostegina depressa*	Diatom
			Operculina ammonoides	Diatom
	Miliolida	Alveolinidae	*Alveolinella quoyi*	Diatom
		Peneroplidae	*Peneroplis planatus*	Red alga
			Peneroplis cf. arietinus	Red alga
		Soritidae	*Marginopera vertebralis*	Dinoflagellate
			Sorites orbiculus	Dinoflagellate
			Sorites orbiculus var. marginalis	Dinoflagellate
Opportunistic	Rotaliida	Rotaliidae	*Ammonia spp.* and *Parotilla spp.*	None
		Elphidiidae	*Elphidium spp.*[3]	Plastids
		Cymbaloporidae	*Cymbaloporreta sp.*	None
Other small taxa	Miliolida	Nubeculariidae	*Spiroloculina spp.*	None
		Hauerinidae	*Quinqueloculina spp.*	None
			Pyrgo spp.	None
			Sigmohauerina involuta	None
	Rotaliida	Planorbulinidae	*Several taxa*	None
		Alfredonidae	*Epistomaroides sp.*	None
		Eponididae	*Eponides sp.*	None
			Unknown small rotaliids	None
	Textulariida	Textulariidae	*Textularia spp.*	None

[1] May be a group with *C. gaudichaudi* and *C. defrancii*

[2] This group contains *A. lobifera* and *A. lessonii*

[3] Distinctly large forms of *E. craticulatum* occur inshore, however, also some other species are in this group.

I applied the formula of the Caribbean FORAM index to the foraminifera community data in the Whitsunday region (Fig. 3.11). The index showed a distinct increase with increasing distance from the river mouths. If Hallock *et al.*'s (2003) interpretation was literally applied to this dataset three of the inner reefs (Repulse, Long and Dent Islands) fall into the 'marginal conditions for reef development' category.

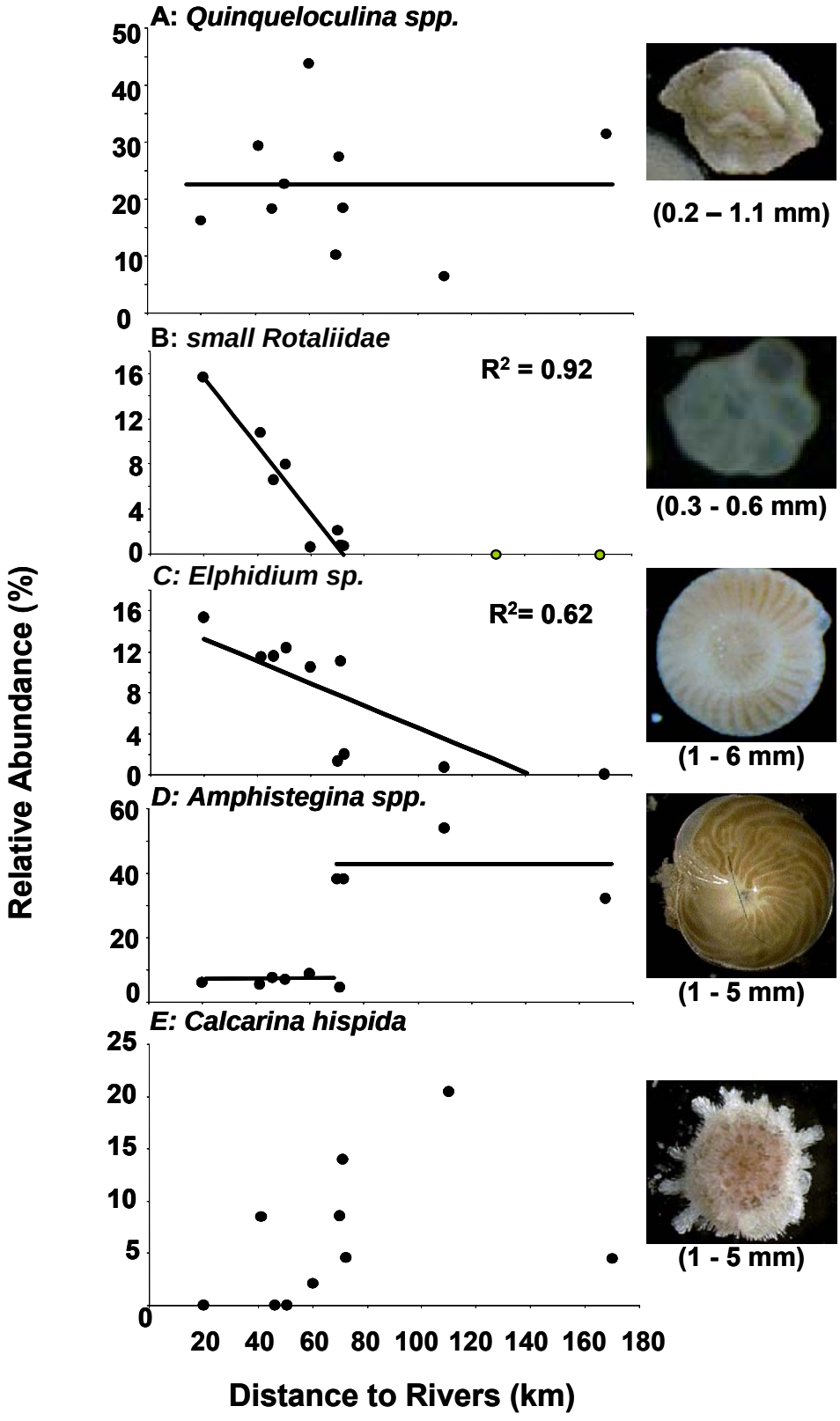

Figure 3.9. Relationships of abundances of selected foraminifera taxa with the distance to the river mouths.

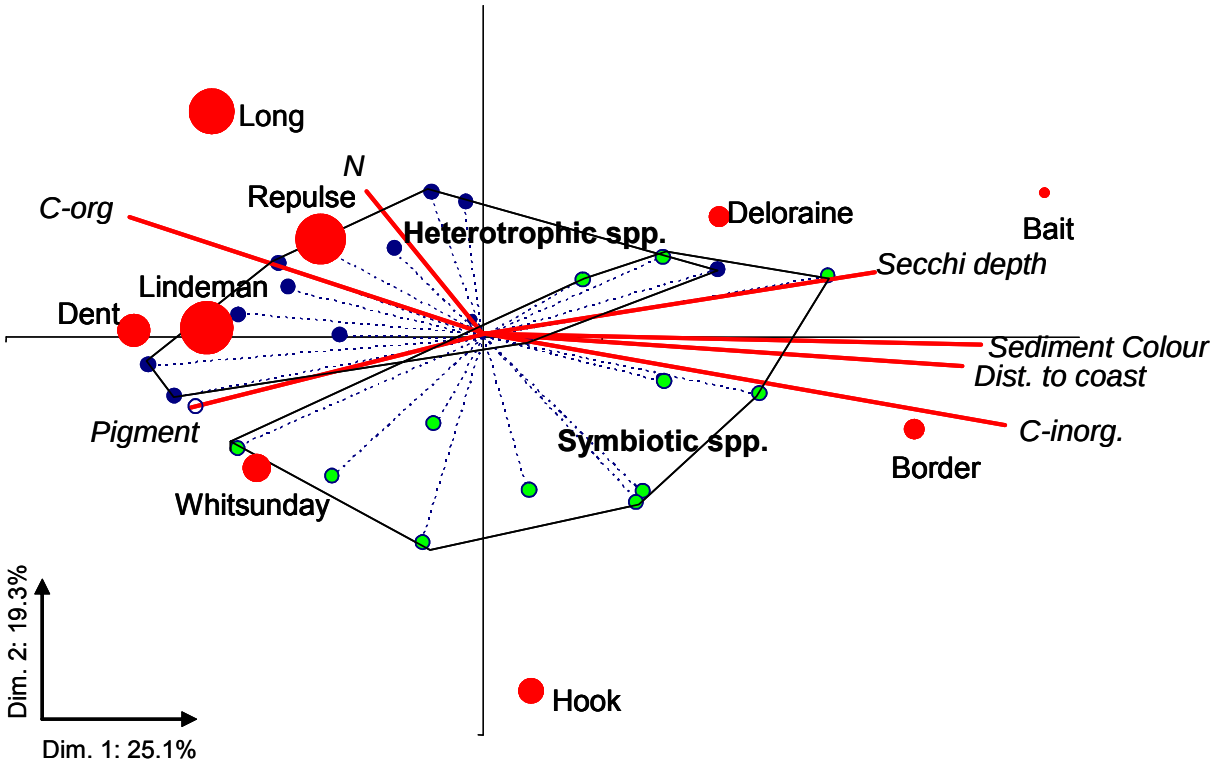

Figure 3.10. Biplot of a redundancy analysis (RDA) of foraminifera community composition data in the Whitsunday area. The diameter of the location markers is proportional to the water column chlorophyll data (see Chaper 2), red lines represent vectors of the environmental parameters, dotted lines represent species vectors (blue markers: heterotrophic species; green markers: symbiotic species).

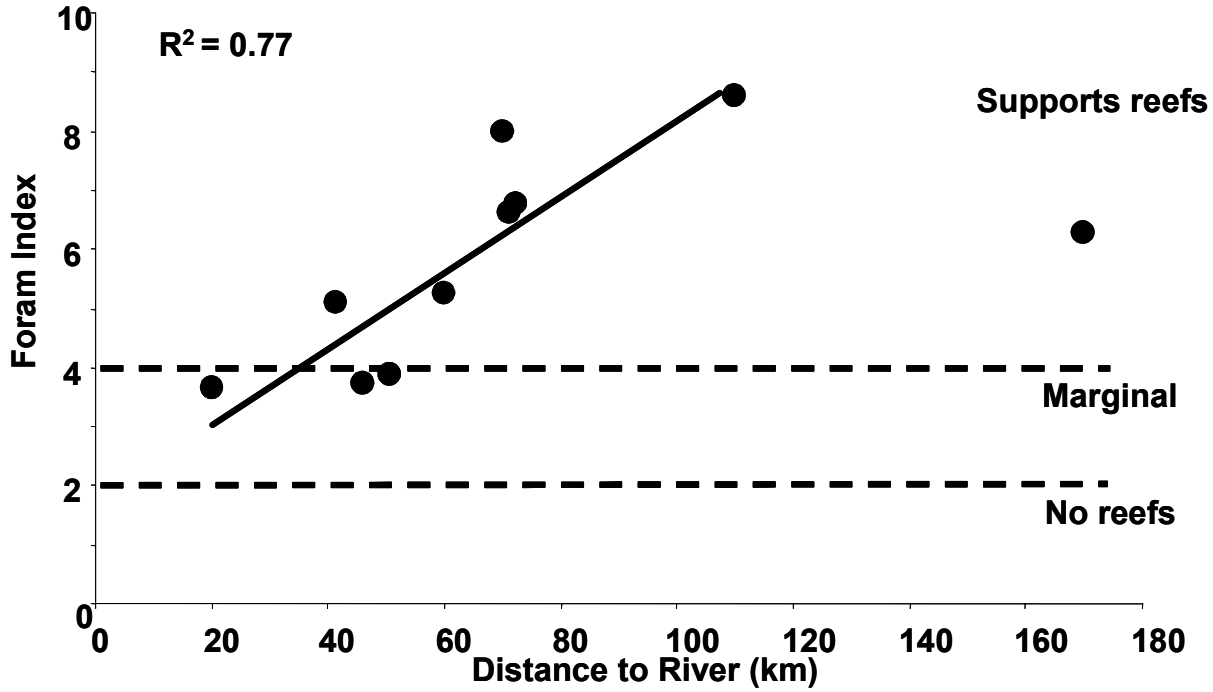

Figure 3.11. Application of the equation for the Caribbean FORAM index (Hallock *et al.* 2003) to data from the GBR.

3.4 Discussion and conclusions

The biofilm work presented here focussed on three biofilm groups, which, based on assessment of the literature, held large promise as indicators for water quality: 1) bacteria, 2) diatoms and 3) benthic foraminifera. The main obstacle for work on the first two groups in the tropics in general or specifically on the GBR is the lack of even basic knowledge on the biodiversity and taxonomy. To improve this and simultaneously investigate the potential as indicators I chose a similar approach for each of these groups. This approach consisted of a basic study of the biodiversity of the species, in conjunction with studies of distribution and abundance along environmental gradients. At the same time, I developed methods to genetically identify some of these groups and potential indicator taxa within these groups, and commenced experimental work to establish causality and identify main factors influencing the distribution of these species.

The sediment bacterial community investigated exhibited an astonishing diversity, with rarefaction curves indicating that the true diversity in this group is in the 1000 if not 10,000 species. Despite this diversity, I was able to get some leads on potential indicators by investigating the distribution of major groups within the bacteria. Bowman and McCuaig (2003) observed increased abundances of Acidobacteriaceae and δ-proteobacteria in deeper and anoxic sediment layers. Therefore, the higher abundance of these groups in inshore sediments may indicate that anoxic metabolic processes are more prevalent, or occur at shallower sediment layers, than on midshelf reefs. Inversely, increased numbers of cyanobaceria on the outer shelf may be explained by higher light availability for this autotrophic group. Although these trends are subtle and require further investigation, the enhanced knowledge of the biodiversity of these sediments and the suggested differences in some taxa can form the basis for more detailed searches for indicator species for changes in water quality. These may include larger sample sizes in clone libraries or more targeted searches in some bacterial groups using group specific primers or other techniques such as group specific visualisation using FISH (Amann *et al.* 1997). Also, further genetic approaches such as quantification of the activity of specific metabolic enzymes (e.g. nitrogenase in cyanobacteria) can now be developed.

Physiological studies using PAM fluorometry yielded no indication for nutrient limitation of the biofilm community *in situ*. This was somewhat surprising because a variety of experimental studies had indicated distinct productivity enhancement of tropical marine microphytobenthos under nutrient (especially N) addition. Uthicke and Klumpp (1997, 1998) and Uthicke (2001) demonstrated both *in situ* and in aquaria, that production increased within 12 h and increased after several days of ammonium enrichment of only 1 - 2 µM above background level. Similarly, several other studies (Dizon and Yap 2003; Heil *et al.* 2004; Gottschalk 2005) demonstrated rapid production enhancement or biomass increases of coral reef microphytobenthos upon N addition.

Induced by higher nutrient levels, differential vertical migration may alter the taxonomic composition on the top layer of the sediment towards higher productive species with higher nutrient demand. Thus, the actual community involved in photosynthesis under *a specific nutrient regime at a specific time* may not be nutrient limited, but additional N can enhance community productivity because more productive species become dominant on the sediment surface. Testing this hypothesis requires investigating the actual species distribution under different nutrient regimes, for example in thinly sliced sediment cores, or additional studies combining PAM fluorometry and respirometry. However, the PAM fluorometry conducted here has demonstrated a clear influence of the available light on the photophysiology of the microalgae.

The benthic diatoms were highly diverse with close to 300 species detected. The ecological and taxonomic studies on diatoms revealed a variety of potential indicator species. Several

of these appeared to be specific for outer shelf conditions, whereas other species preferred reefs closer to the shore. Also the total amount of diatoms appeared to increase towards the coastline. Future research can now focus on species with high indicator values. To improve our knowledge of the ecology of these species and also to develop specific genetic markers it is desirable to obtain some pure cultures. Similar to work on the bacteria, additional genetic work should also focus on the quantification of gene activity, for example testing if the expression of RUBISCO genes could serves as an index for autotrophy of the total algal community.

Compared with tropical benthic bacteria and diatoms, a reasonably good knowledge does exist of the benthic foraminifera in the Pacific region (e.g. Hohenegger 1994; Renema and Troelstra 2001; Renema 2003; Langer and Lipps 2003), with some studies available from the GBR (e.g. Lobegeier 2001, 2002). The main aim of the studies presented here was to test if a FORAM Index as applied in the Caribbean and Florida (Hallock *et al.* 2003) could be developed for the GBR. Several taxa studied here exhibited clear distributional patterns along the water quality gradient in the Whitsunday Region. These patterns clearly suggest that a variety of indicator species for either high turbidity/nutrient or low turbidity/nutrient regimes are available in the GBR. The specificity of indicators to these stressors, or other potential stressors such as pesticides, needs to be evaluated in experimental studies.

In general, foraminifera communities where distributed along the gradient as was hypothesised initially: larger-species that harbour microalgal symbionts dominated communities in high light/low nutrient conditions further from the coast, whereas smaller heterotrophic species were more common inshore. Also, a literal application of the formula for the Caribbean FORAM index showed a clear increasing trend with distance from the rivers. I conclude that it will be possible to apply the FORAM index to GBR reefs, but adaptations based on a better understanding of the forams physiology and ecology will distinctly improve the index' specificity to certain environmental factors.

3.5 Summary and outlook

In summary, our research on the three biofilm groups has provided important leads for further indicator development. Two groups of bacteria were more common on the inshore reef surveyed, while the Cyanobacteria were more abundant offshore. Microphytobenthos showed distinct differences in their photophysiology along an inshore-offshore gradient. Benthic diatoms provided a number of potential indicator species that appeared specific for different water quality environments. Similarly, benthic foraminifera exhibited distinct community differences along water quality gradients and several species were associated with either high nutrient/high turbidity or low nutrient/low turbidity conditions. To further develop these indicators and test their specificity, the following additional work is required, some of which has already commenced:

Bacteria:

- I investigated the use of DGGE gels and FISH to determine community composition in bacteria. Both methods worked for the sediment communities, and can now be applied to quantify bacterial groups that are potential indicators.
- A method to quantify cyanobacteria by measuring expression of the nitrogenase gene could be developed.
- I need to experimentally evaluate the mechanisms that drive differences in bacterial communities and the likely stressors.

Benthic microalgae:

- Pilot experiments on the effect of nutrient enhancement on algal biomass and species composition were conducted, further experiments are required.
- I started the development of genetic primers to identify diatoms to species level, and other microalgae to higher taxonomic levels. Putative indicator species will have to be cultivated as pure cultures to obtain uncontaminated DNA to develop genetic methods for their identification and quantification.
- The same pure cultures can be used for experimental work to establish cause-effect relationships and to test the effect of individual stressors.
- Initial tests to genetically quantify the activity of functional genes have been commenced. Further development will allow to test if, for example, the RUBISCO gene can be used as an indicator for heterotrophic vs. autotrophic metabolism in the benthic community.

Foraminifera:

- I commenced development of genetic primers to identify diatom symbionts in foraminifera.
- Initial experimental work on light physiology of algal-symbionts has been conducted. Further work is required to elucidate to what extent the algal-symbiont contributes to the host's metabolism, and what role symbionts have in influencing distribution of the hosts.
- Experimental work on growth and carbonate production of individual species under different light conditions has been conducted. This research needs to be extended to a larger number of species. In experimental manipulations of a variety of parameters I will investigate cause and effect relationships of single and combined stressors on foraminifera.

3.6 Acknowledgements

I would like to thank all volunteers during field and lab experiments for their great help in the field and laboratory during this project, especially Katharina McGuire, Danika Tager and Nadine Koch. The skippers and crews of the research vessels "Lady Basten" and "Cape Ferguson" were great company and support. Some of the work presented in the diatom and foraminifera chapters was part of two honours projects:

1) Diatoms: Gottschalk S .2005. Tropical benthic microalgal communities and the effect of regional and seasonal enhanced nutrient levels on their distribution in the Great Barrier Reef. Diplomarbeit (Honours Thesis), University of Rostock, 132pp. Co-supervised by Dr S. Uthicke (AIMS) and Dr K. Heimann (James Cook University)

2) Foraminifera: Nobes, K. 2006. Growth, distribution and ecology of benthic symbiontic foraminiferal assemblages along a turbidity gradient on the Central Great Barrier Reef. (Honours Thesis), James Cook University, Townsville, 105pp. Co-supervised by Dr S. Uthicke (AIMS) and Prof. B. Henderson (James Cook University)

3.7 References

Alve E. 1995. Benthic foraminiferal responses to estuarine pollution: a review. J Foram Res 25:190-203

Amann R, Ludwig W, Schleiffer K-H. 1995. Phylogenetic identification and *in situ* detection of individual microbial cells without cultivation. Microbiol Rev 59:143-169

Amann R, Glöckner FO, Neef A. 1997. Modern Methods in Subsurface Microbiology: *In situ* identification of microorganisms with nucleic acid probes. FEMS Micobiology Reviews 20:191-200

Ashelford K, Chuzhanova N, Fry J, Jones A, Weightman AJ. 2005. At least one in twenty 16S rRNA sequence records currently held in public repositories estimated to contain substantial anomalies. Applied and Environmental Microbiology 71:7724-7736

Barranguet C, Kromkamp J. 2000. Estimating primary production rates from photosynthetic electron transport in estuarine microphytobenthos. Marine Ecology Progress Series 204:39-52

Beardall J, Roberts S, Young E. 2001. Approaches for determining phytoplankton nutrient limitation. Aquat. Sci. 63:44-69

Bourne DG, Munn CB. 2005. Diversity of Bacteria associated with the coral *Pocillopora damicornis* from the Great Barrier Reef. Environmental Microbiology 7:1162-1174.

Bowman JP, McCuaig R. 2003. Biodiversity, community structural shifts, and biogeography of prokaryotes within Antarctic continental shelf sediment. Applied and Environmental Microbiology 69:2463-2483

Bowman JP, Rea SM, McCammon SA, McMeekin TA. 2000. Diversity and community structure within anoxic seiment form marine salinity meromictic lakes and a coastal meromictic marine basin, Vestford Hills, Eastern Antarctica. Environmental Microbiology 2:227-237

Brown MV, Schwalbach M, Hewson I, Fuhrman JA. 2005. Coupling 16S-ITS rDNA clone libraries and ARISA to show marine microbial diversity; development and application to a time series. Environmental Microbiology 7:1466-1479

Cifuentes A, Anton J, Benllock S, Donnelly A, Herbert RA, Rodriguez-Valera F. 2000. Prokaryoic diversity in *Zostera noltii*-colonized marine sediments. Applied and Environmental Microbiology 66:1715-1719

Clarke K, Gorley R. 2001. Primer v5: User manual/tutorial. Primer-E: Plymouth, 91pp.

Cottrell M, Kirchman D. 2000. Community Compostition of marine bacterioplankton determined by 16S rRNA gene clone libraries and fluorescence in situ hybridization. Applied and Environmental Microbiology 66:5116-5122

Dizon RM, Yap HT. 2003. Metabolic changes and compositional shifts in nutrient-enriched tropical reef sediment communities. Scientia Marina, Barcelona, 67:117-127

Dufrene M, Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monographs 67:345-366

Di Meo C, Wilbur A, Holben WE, Feldman RVR, Cary SC. 2000. Genetic variation among endosymbionts of widely distributed vestimentiferan tubeworms . Applied and Environmental Microbiology 66:651-658

Dubilier N, Mulders C, Ferdelman T, de Beer D, Pernthaler AKM, *et al.* 2001. Endosymbiotic sulphate-reducing and sulphide-oxidizing bacteria in an oligochaete worm. Nature 411: 298-302

Fabricius K, De'ath, G. 2004. Identifying ecological change and its causes: a case study on coral reefs. Ecological Applications 14, 1448-1465

Field D, Baumgartner T, Charles C, Ferreira-Bartrina V, Ohman M. 2006. Planktonic foraminifera of the California Current reflect 20th-century warming. Science 311:63-66

Frias-Lopez J, Zerkle A, Bonheyo G, Fouke B. 2002. Partitioning of bacterial communities between seawater and healthy, black band diseased and dead coral surfaces. Applied and Environmental Microbiology 68:2214-2228

Gaiser E, Wachnicka A, Ruiz P, Tobias F, Ross M. 2005. Diatom indicators of ecosystem change in subtropical coastal wetlands. In: Estuarine Indicators. S Bortone (ed) CRC Press, St. Lucie, FL, USA: 127-144

Geider R, Roche J, Greene R, Olaizola M. 1993. Response of the photosynthetic apparatus of *Phaeodactylum tricornutum* (Bacillariophyceae) to nitrate, phosphate, or iron starvation. J Phycol 29:755-766

Glud RN, Kühl M, Wenzhoefer F, Rysgaard, S. 2002. Benthic diatoms of a high Arctic Fjord (Young Sound, NE Greenland): Importance for ecosystem primary production. Marine Ecology Progress Series 238:15-29

Gottschalk S. 2005. Tropical benthic microalgal communities and the effect of regional and seasonal enhanced nutrient levels on their distribution in the Great Barrier Reef. Diplomarbeit (Honours Thesis), University of Rostock, 132pp

Hallock P. 1981. Algal Symbiosis: a mathematical analysis. Marine Biology 62:249-155

Hallock P. 2000. Larger Foraminifers as Indicators of Coral-Reef Vitality. In Martin, R. (ed.), Environmental Micropaleontology. Plenum Press Topics in Geobiology.121-150

Hallock P, Lidz BH, Cockey-Burkhard EM, Donnelly KB. 2003. Foraminifera as bioindicators in coral reef assessment and monitoring: the FORAM index. Environmental Monitoring and Assessment 81:221-238

Hartig P, Wolfstein K, Lippemeier S, Colijn F. 1998. Photosynthetic activity of natural microphyto-benthos populations measured by fluorescence (PAM) and ^{14}C-tracer methods: A comparison. Marine Ecology Progress Series 166:53-62

Heil CA, Chaston K, Jones A, Bird P, Longstaff B, Costanzo S, Dennison W. 2004. Benthic microalgae in coral reef sediments of the southern Great Barrier Reef. Coral Reefs 23:336-343

Hillebrand H, Sommer U. 2000. Diversity of benthic microalgae in response to colonization time and eutrophication. Aquatic Botany 67:221-236

Hillebrand H, Sommer U. 2000. Effect of continuous nutrient enrichment on microalgae colonizing hard substrates. Hydrobiologia 426:185-192

Hillebrand H, Sommer U. 1997. Response of epilithic microphytobenthos of the Western Baltic Sea to in situ experiments with nutrient enrichment. Marine Ecology Progress Series 160:35-46

Hohenegger J. 1994. Distribution of living larger *Foraminifera* NW of Sesoko- Jima, Okinawa, Japan. Marine Ecology 15:291-334

Holland SH. 1988. *A Rarefactwin Program*, Version 1.2. [URL Document]. http://www.uga.edu/strata/Software.html

Huber T, Faulkner G, Hugenholtz P. 2004. Bellerophon: a program to detect chimeric sequences in multiple sequence alignments. Bioinformatics 20:2317-2319

Jorgensen B. 1982. Mineralization of organic matter in the sea bed-the role of sulphate reduction. Nature 296:643-645

Kromkamp J, Barranguet C, Peene J. 1998. Determination of microphytobenthos PSII quantum efficiency and photosynthetic activity by means of variable chlorophyll fluorescence. Marine Ecology Progress Series 162:45-55

Kühl M, Glud RN, Borum J, Roberts R, Rysgaard S. 2001. Photosynthetic performance of surface-associated algae below sea ice as measured with a pulse-amplitude-modulated (PAM) fluorometer and O_2 microsensors. Marine Ecology Progress Series 223:1-14

Langer MR, Lipps JH. 2003. Foraminferal distribution and diversity, Madang Reef and Lagoon, Papua New Guinea. Coral Reefs 22:143-145

Lee JJ, Anderson OR. 1991. Symbiosis in foraminifera. In: Biology of foraminifera (Lee, JJ and Anderson, OR (eds). Academic press, London:157-220

Li L, Guenzennec J, Nichols P, Henry P, Yanagibayashi M, Kato C. 1999. Microbial diversity in Nankai Trough sediments at a depth of 3843 m. Journal of Oceanography 55:635-642

Lipkovich I, Smith EP. 2002. Biplot and singular value decomposition macros for Excel. Journal of Statistical Software 7:1-15.

Lobegeier MK. 2002. Benthic foraminifera of the family *Calcarinidae* from Green Island Reef, Great Barrier Reef Province. Journal of Foraminiferal Research 32:201-216

Lobegeier MK. 2001. Foraminiferal assemblages and their bulk contribution to carbonate sediment, Green Island reef, Great Barrier Reef Province. PhD thesis JCU. PhD Thesis, JCU

Ludwig W, Strunk O, Westram R, Richter L, Meier H, Yadhukumar, Buchner A, Lai T, Steppi S, Jobb G, Förster W, Brettske I, Gerber S, Ginhart AW, Gross O, Grumann S, Hermann S, Jost R, König A, Liss T, Lüßmann R, May M, Nonhoff B, Reichel B, Strehlow R, Stamatakis A, Stuckmann N, Vilbig A, Lenke M, Ludwig T, Bode A, Schleifer K-H. 2004. ARB: a software environment for sequence data. Nucleic Acids Research 32:1363-1371

Madrid VM, Aller JY, Aller RC, Chistoserdov AY. 2001. High prokaryote diversity and analysis of community structure in mobile mud deposits off French Guiana: identification of two new bacterial candidate divisions. FEMS Microbiology Ecology 37:197-209

Maidak B, Cole J, Parker CJ, Garrity G, Larsen N, Li B, Lilburn T, McCaughey M, Olsen G, Overbeek R, Pramanik S, Schmidt T, Tiedje J, Woese C. 1999. A new version of the RDP (Ribosomal Database Project). Nucleic Acid Res 27:171-173

Milbrandt E. 2005. Bacterial communities as indicators of estuarine and sediment conditions. Estuarine Indicators. In: S Bortone (ed) CRC Press, St. Lucie, FL, USA99-109

Patrick R, Hohn M, Wallace J. 1954. A new method for determining the pattern of the diatom flora. Notulae Naturae 259:1-12

Perkins RG, Oxborough K, Hanlon ARM, Underwood GJC, Baker NR. 2002. Can chlorophyll fluorescense be used to estimate the rate of photosynthetic electron transport within microphytobenthic biofilms? Marine Ecology Progress Series 228:47-56

Perkins RG, Underwood GJC, Brotas V, Snow GC, Jesus B, Ribeiro L. 2001. Response of microphytobenthos to light: primary production and carbohydrate allocation over an emersion period. Marine Ecology Progress Series 223:101-112

Platt T, Gallegos C, Harrison W. 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. J Mar Res 687-701

Polz MF, Cavanaugh CM 1998. Bias in template-to-product ratios in multitemplate PCR. Applied and Environmental Microbiology 64:3724-3730

Ralph P, Gademann R. 2005. Rapid light curves: A powerful tool to assess photosynthetic activity. Aquatic Botany 82:222-237

Ravenschlag K, Sahm K, Pernthaler J, Amann R. 1999. High Bacterial Diversity in Permanently Cold Marine Sediments. Applied and Environmental Microbiology 65:3982-3989

Renema W. 2003. Larger foraminifera on reefs around Bali (Indonesia). Zool Verh Leiden 345:337-366

Renema W, Troelstra SR. 2001. Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). Palaeogeography, Palaeoclimatology, Palaeoecology 175:125-146

Reysenbach A-L, Pace N. 1995. Reliable amplification of hyperthermophilic archaeal 16*S* rRNA genes by PCR. In: Robb FT, Place AR (eds) Thermophiles. Cold Spring Harbor Press, NewYork. Pp 101–106

Schaffelke B, Uthicke S, Klumpp DW. 2004. Water quality, sediment and biological parameters at four nearshore reef flats in the Herbert River Region, Central GBR. Great Barrier Reef Marine Park Authority, Research Publication No. 82, Townsville, Australia. Pp 64.

Schreiber U, Schliwa U, Bilger W. 1986. Continuous recording of photochemical and non-photochemical chlorophyll flourescence quenching with a new type of modulating fluorometer. Photosynth Res 10:51-62

Scoffin T, Tudhope A. 1985. Sedimentary environments of the central region of the Great Barrier Reef of Australia. Coral Reefs 4:81-93

Serodio J. 2003. A chlorophyll fluorescence index to estimate short-term rates of photosynthesis by intertidal microphytobenthos. J. Phycol. 39:33-46

Serodio J, Da Silva JM, Catarino F. 2001. Use of in vivo chlorophyll a fluorescence to quantify short-term variations in the productive biomass of intertidal microphytobenthos. Marine Ecology Progress Series 218:45-61

Snyder R, Lewis M, Nocker A, Lepo J. 2005. Microbial biofilms as integrative sensors of environmental quality. Estuarine Indicators. IN: S Bortone (ed) CRC Press, St. Lucie, FL, USA:111-126

Sorokin YI. 1993. Coral Reef Ecology. Ecological Studies: Springer, 465pp.

Sundbäck K, Snoeijs P. 1991. Effects of nutrient enrichment on microalgal community composition in a coastal shallow-water sediment system: an experimental study. Botanica Marina 34:341-358

Suzuki MT, Giovanni SJ. 1996. Bias caused by template annealing in the amplification mixtures of 16S rRNA genes by PCR. Applied and Environmental Microbiology 62:625-630

Todorov JR, Aller J, Chistoserdov AY, Aller R 2000. Molecular microbial diversity in physically disturbed coastal sediments of southeastern Papua New Guinea. FEMS Microbiology Ecology 33:147-155

Underwood G 2002. Adaptations of tropical marine microphytobenthic assemblages along a gradient of light and nutrient availability in Suva Lagoon, Fiji. Eur. J. Phycol. 37:449-462

Uthicke S 1994. Distribution patterns and growth of two reef flat holothurians, *Holothuria atra* and *Stichopus chloronotus*. In: David, B., Guille, A., Féral, J.P. and Roux, M. (eds). Echinoderms through time: Proc. 8th Int. Echinoderm Conference, Dijon, AA Balkema, Rotterdam. Pp 569-576

Uthicke S. 2001. Interactions between sediment-feeders and microalgae on coral reefs: Grazing losses versus production enhancement. Marine Ecology Progress Series 210:125-138

Uthicke S. 2006. Photosynthetic Efficiency and Rapid Light Curves of sediment-biofilms along a water quality gradient in the Great Barrier Reef, Australia. Marine Ecology Progress Series 322: 61-73

Uthicke S, Klumpp DW. 1997. Ammonium excretion by holothurians enhances production and turnover in benthic diatom communities. In: Lessios HA, Macintyre IG (eds). Proc. 8th Int. Coral Reef Symp., Panama, VI. Pp 873-876

Uthicke S, Klumpp DW. 1998. Microbenthos community production in sediments of a near shore coral reef: seasonal variation and response to ammonium recycled by holothurians. Marine Ecology Progress Series 169:1-11

van Woesik R, Tomascic T, Blake S. 1999. Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. Mar Freshwater Res 50:427-40

Venter J, Remington K, Heidelberg J, Halpern AL, Rusch D, Eisen JA, Wu D, Paulsen I, Nelson KE, Nelson W, Fouts DE, Levy S, Knap AH, Lomas MW, Nealson K, White O, Peterson J, Hoffman J, Parsons R, Baden-Tillson H, Pfannkoch C, Rogers Y-H, Smith HO. 2004. Environmental Genome Shotgun Sequencing of the Sargasso Sea . Science 304:66-74

Vergin KL, Urbach E, Stein J, DeLong E, Lanoil B, Giovannoni SJ. 1998. Screening of a fosmid library of marine environmental genomic DNA fragments reveals four clones related to members of the order *Planctomycetales*. Applied and Environmental Microbiology 64:3075-3078

Webster NS, Smith LD, Heyward AJ, Watts JEM, Webb RL, Blackall LL, Negri AP. 2004. Metamorphosis of a scleractinian coral in response to microbial biofilms. Applied and Environmental Microbiology 70:1213-1221

Wise MG, McArthur JV, Shimkets LJ. 1997. Bacterial diversity of a Carolina bay as determined by 16S rRNA gene analysis: confirmation of novel taxa. Applied and Environmental Microbiology 63:1505-1514

Yamano H, Miyajima T, Koike I. 2000. Importance of foraminifera for the formation and maintenance of a coral sand cay: Green Island, Australia. Coral Reefs 19:51-58

Yanagibayashi M, Nogi Y, Li L, Kato C. 1999. Changes in the microbial community in Japan Trench sediment from a depth of 6292 m during cultivation without decompression. FEMS Microbiol Lett 170:271–279

Yi H, Bae K, Chun J 2004. *Thalassomonas ganghwensis* sp. nov., isolated from tidal flat sediment. Int J Syst Evol Microbiol. 54:377-380

Chapter 4: Changes in the RNA:DNA ratio of corals as an indicator of coral health

Craig Humphrey

4.1 Introduction

The ratio of ribonucleic acid (RNA) to deoxyribonucleic acid (DNA) in animal and plant cells has been used extensively to determine the protein synthetic capabilities and thus growth rates in a wide variety of marine organisms; microbial communities (Dell'anno *et al.* 1998), phytoplankton (Berdalet and Dortch 1991), zooplankton (Wagner *et al.* 1998), cnidarians (Bak and Meesters 2000; Meesters *et al.* 2002, Buckley and Szmant 2004), cephalopods (Melzner *et al.* 2005) and larval fishes (Buckley 1984; Buckley *et al.* 1999; Weber *et al.* 2003). The utility of the RNA:DNA ratio as an indicator of metabolic activity is based on the premise that DNA within a cell is constant, while the amount of RNA is a function of protein synthesis (Buckley 1984). Therefore, during periods of active growth or differentiation it is predicted that the RNA:DNA ratio will increase. As such, this indicator has been used to study the effects of a number of environmental variables on growth, including nutritional status (Bulow *et al.* 1981; Wagner *et al.* 1998), pollution (Wu *et al.* 2003), temperature (Calderone *et al.* 2003) and reproduction (Bulow *et al.* 1981).

Coral growth is intrinsically linked to levels of photosynthetically available radiation (PAR) due to the presence of dinoflagellate algae (zooxanthellae) within the tissues of the host animal, which provide fixed carbon (Muscatine *et al.* 1984). Therefore it is predicted that RNA:DNA ratios in corals will be highest in areas where PAR is high enough to ensure adequate photosynthesis in the zooxanthellae and translocation of fixed carbon to the hosts, and lower in environments where light is limited. Depth is a large determinant of light in marine waters and as such it would be expected that the RNA:DNA ratio would be lower in deeper waters. This is in fact supported by two studies in which a significant relationship between RNA:DNA and water depth was found, with higher RNA:DNA ratios in shallower waters than in deeper waters (Meesters *et al.* 2002; Buckley and Szmant 2004). Water clarity is also an important factor, as shown by Meesters *et al.* (2002). These authors found RNA:DNA ratios in massive *Porites* (*P. lutea* or *P. lobata*) declining at similar rates along gradients of depth (or irradiance) at two sites with low to moderate turbidity (light extinction rate k' = 0.26 and 0.42). However, contrary to expectations, intercepts were higher at the more turbid site than the clearer-water site, suggesting enhanced metabolic activity in turbid conditions. At a third, extremely turbid site (k' = 0.78), ratios were similar in value to the other sites but unrelated to depth/irradiance, apparently due to the short depth range at this reef (3 m), and extreme variability in irradiance and sedimentation rates. The authors suggested that these apparent anomalies of greater metabolic activity at higher turbidity may have been because of photoadaptation, higher rates of heterotrophy at high turbidity, or different strains of zooxanthellae with differential photosynthetic efficiency; the pooling of at least two species of massive *Porites* may have further complicated the patterns. The study by Buckley and Szmant (2004) demonstrated that significant interspecific variation in the RNA:DNA ratio exists between the Caribbean coral species *Porites astreoides*, *Montastraea annularis*, *M. cavernosa* and *M. faveolata*, and showed that the ratio in natural populations varied in a complex manner with depth, turbidity, and seasons. These two studies suggest that the measurement of RNA:DNA ratios in corals might provide a sensitive measure of coral response to changes in water quality, but that more research is needed to better understand the environmental conditions and natural variation that determine this measure.

In this study a number of experiments were conducted to help clarify changes in the RNA:DNA ratio in Indo-Pacific corals, in response to a number of different factors:

1. To investigate the effect of depth, and the rate of change on RNA:DNA ratios, fragments of two coral species (*Pocillopora damicornis* and *Acropora millepora*) were transplanted from 3 m to 7 m and 12 m, and sampled after five and nine days.
2. To investigate the effect of differences in water quality on the RNA:DNA ratios, fragments of two species of coral (*P. damicornis* and *A. millepora*) were collected from two inshore and two offshore reefs at constant depth (~5 m).
3. To investigate the effect of handling on RNA:DNA ratio, small branchlets from five different colonies of *A. millepora* were collected and treated by three different handling methods.
4. To investigate inter- and intracolonial variation, 10 branches were collected from five colonies each of *P. damicornis* and *A. millepora*.
5. To further investigate the effects of light and suspended solids on the RNA:DNA ratio in massive *Porites,* a controlled laboratory exposure study was conducted.

4.2 Materials and methods

Transplant experiment

A pilot experiment was conducted to test for the effect of changing depth on RNA:DNA ratios. Two large colonies each of *Pocillopora damicornis* and *Acropora millepora* (Photo plate 1) were collected at 3 m from the front reef of High Island (17° 09' S, 146° 00' E). These colonies were broken into three pieces each and one piece of each colony was transplanted to each of three depths; 3m, 7m and 12 m. Each section of coral was securely anchored to a large brick by means of cable ties. Three samples were collected from each fragment of coral at the time of transplant, then after five days and again after nine days.

Inshore/offshore reef comparison

An experiment was conducted to test for differences in RNA:DNA ratios between corals from inshore and offshore reefs. Corals were collected from the back reef of two inshore reefs; High (17° 09' S, 146° 00' E) and Bedarra Islands (17° 59' S, 146° 08 E) and two offshore reefs; Wardle (17° 26' S, 146° 31' E) and Gilbey (17° 34' S, 146° 34' E) Reefs. Three branches from five colonies each of *P. damicornis* and *A. millepora* were collected from ~5 m depth from each of the reefs. *A. millepora* was not found on the back reef of Bedarra Island.

Handling methods

To study the effects of handling on RNA:DNA ratios in corals an experiment was conducted in which the freshly collected corals were handled in three different ways before preservation. First, branches were held in a specially designed holder while the dive continued, which allowed complete water flow around the branches to minimise stress. Second, another set of branches were immediately taken to the surface where they were snap frozen in liquid nitrogen (LN_2). Third, another set of branches were placed in small, sealed plastic bags and carried around for the duration of the dive, approximately 70 min. The samples in the holder and in plastic bags were snap frozen in LN_2 on return to the research vessel. Nine branches were collected from five colonies of *A. millepora* and divided between the three treatments.

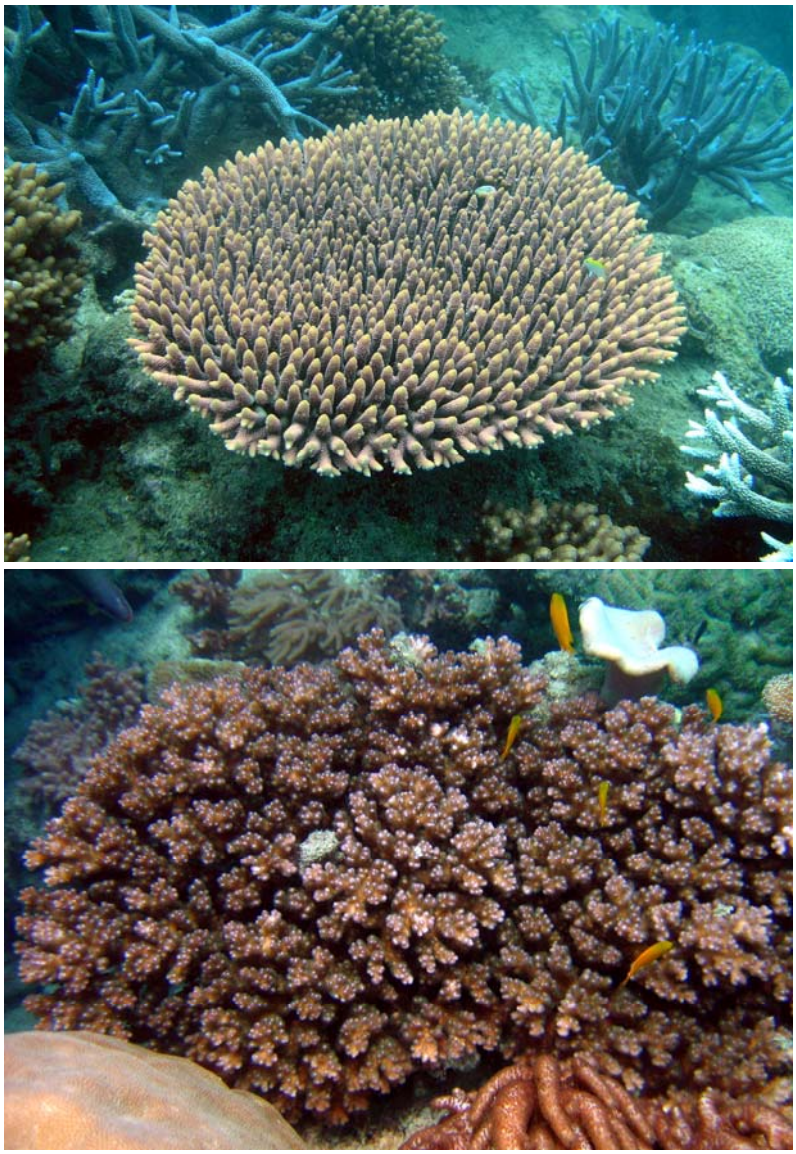

Photo plate. Colony of the study species *Acropora millepora* (top) and *Pocillopora damicornis* (bottom).

Inter- and intracolonial variation

To investigate the level of variability within an individual colony, ten branches were sampled from different locations within an individual colony. This was repeated in five different colonies, sampled to provide a range of different colony sizes. Samples were taken from five colonies of *P. damicornis* and five colonies of *A. millepora*. This sampling also enabled interspecific variation in the two species to be investigated.

Laboratory experiment

A laboratory experiment was carried out to investigate the effects of 3-4 weeks of exposure to contrasting light and suspended sediment on cores of massive *Porites* sp. Ten to twelve nubbins were analysed for each of the four treatments; filtered seawater no shading, filtered seawater with 70% shading, suspended solids (~20 mg L^{-1}) no shading, and suspended solids with shading. For details on the experimental design refer to Methods and Materials of the Coral Physiology chapter.

In all experiments once the coral fragments were collected they were immediately snap frozen in LN_2 and then stored at -80°C until required for analysis.

Tissue extraction

Samples were stored at -80°C and not allowed to thaw at any time. Pieces of coral (~5 cm for *A. millepora* and *P. damicornis*; ~2.5 cm diameter core for *Porites*) were crushed in liquid nitrogen (LN_2) to a fine powder. Care was taken to ensure that the samples were frozen through-out the procedure with the addition of further LN_2. The resulting powder was then placed into 2 mL nuclease-free vials, frozen again in LN_2 and stored at -80°C for later analysis.

Vials of samples were removed from the freezer and added to 10 mL of extraction buffer (Tris-EDTA (TE) buffer [10 mM Tris-HCl, 1 mM EDTA, pH 7.5] with 1% sarcosyl). A blank control was added at this stage that contained only the extraction buffer and was treated in the same manner as the samples. The samples and blanks were then sonicated in an ice bath for 60 s. After removal from the sonicator the samples and blanks were centrifuged for 3 min at 1200 × *g* to remove the skeletal material. 150 µL of the supernatant was taken and placed in a deep well plate along with 1350 µL of TE buffer in the format shown below (Fig. 4.1), and shaken thoroughly.

	1	2	3	4	5	6	7	8	9	10	11	12
A	RNA 0 µg/ml	DNA 0 µg/ml	sample 1	sample 1	sample 9	sample 9	sample 17	sample 17	sample 25	sample 25	sample 33	sample 33
B	RNA 0.25 µg/ml	DNA 0.25 µg/ml	sample 2	sample 2	sample 10	sample 10	sample 18	sample 18	sample 26	sample 26	sample 34	sample 34
C	RNA 0.5 µg/ml	DNA 0.5 µg/ml	sample 3	sample 3	sample 11	sample 11	sample 19	sample 19	sample 27	sample 27	sample 35	sample 35
D	RNA 0.75 µg/ml	DNA 0.75 µg/ml	sample 4	sample 4	sample 12	sample 12	sample 20	sample 20	sample 28	sample 28	sample 36	sample 36
E	RNA 1.0 µg/ml	DNA 1.0 µg/ml	sample 5	sample 5	sample 13	sample 13	sample 21	sample 21	sample 29	sample 29	sample 37	sample 37
F	RNA 1.5 µg/ml	DNA 1.5 µg/ml	sample 6	sample 6	sample 14	sample 14	sample 22	sample 22	sample 30	sample 30	sample 38	sample 38
G	Blank 0.1 % STEB	Blank 0.1 % STEB	sample 7	sample 7	sample 15	sample 15	sample 23	sample 23	sample 31	sample 31	sample 39	sample 39
H	+ve control	+ve control	sample 8	sample 8	sample 16	sample 16	sample 24	sample 24	sample 32	sample 32	sample 40	sample 40

Figure 4.1. 96-well microplate layout showing location of RNA and DNA standards, blanks, standards and samples.

RNA and DNA determination

Methods for the determination of RNA and DNA are modified from those of Kyle *et al.* (2003) and are represented schematically in Figure 4.2. Briefly three identical black 96-well microplates were created by adding 75 µL of nucleic acid standards (0-1.5 µg mL^{-1} for DNA and RNA), control homogenates or sample to each plate as outlined in Figure 4.1. Plate 1 had 15 µL of TE buffer and 75 µL of RiboGreen® solution added. Plate 2 had 7.5 µL of TE buffer and 7.5 µL of RNase, which was allowed to incubate at room temperature for 40 min before the addition of 75 µL of RiboGreen®. Plate 3 had 7.5 µL of RNase and 7.5 µL of

DNase added and allowed to incubate at room temperature for 90 min before the addition of 75 µL of RiboGreen®. Once each microplate was loaded it was placed into a BioTek Synergy HT microplate reader at 25°C and gently shaken before being read at 485 nm Ex and 528 nm Em. Fluorescence due to RNA was calculated by subtracting the fluorescence of Plate 2 from that of Plate 1 and fluorescence due to DNA was calculated by subtracting the fluorescence of Plate 3 from that of Plate 2 (Fig. 4.2). Concentrations of RNA and DNA were then calculated based on the standard curves from each plate.

Statistical analysis

Data from replicate samples per colony (N = 5 or 10) were pooled in all experiments, except for the comparison of inter- and intra-colony variation. The effect of transplanting corals from 3 m to 7 m and 12 m on RNA:DNA ratios of *Acropora millepora* and *Pocillopora damicornis* were analysed by means of separate one-way ANOVAs at the two different time periods. Post-hoc analysis (Tukey's HSD-test) identified the depths that differed (alpha = 0.05). Nested-ANOVAs were used to test for the effects of water quality on RNA:DNA ratios between inshore and offshore reefs (reefs nested within region). A two way-ANOVA was used to test for the effects of differential handling of branches from four different colonies, and a one way-ANOVA was used to test for the effects of inter- and intracolonial variation. If in each of these experiments a significant difference was found, post-hoc analyses (Tukey's HSD-test) were conducted to determine which of the samples differed at $p < 0.05$. Regression analysis was used to test for the effect of colony size on RNA:DNA ratios and their variation. All analyses were carried out with Statistica 6.0, StatSoft Inc., Tulsa USA.

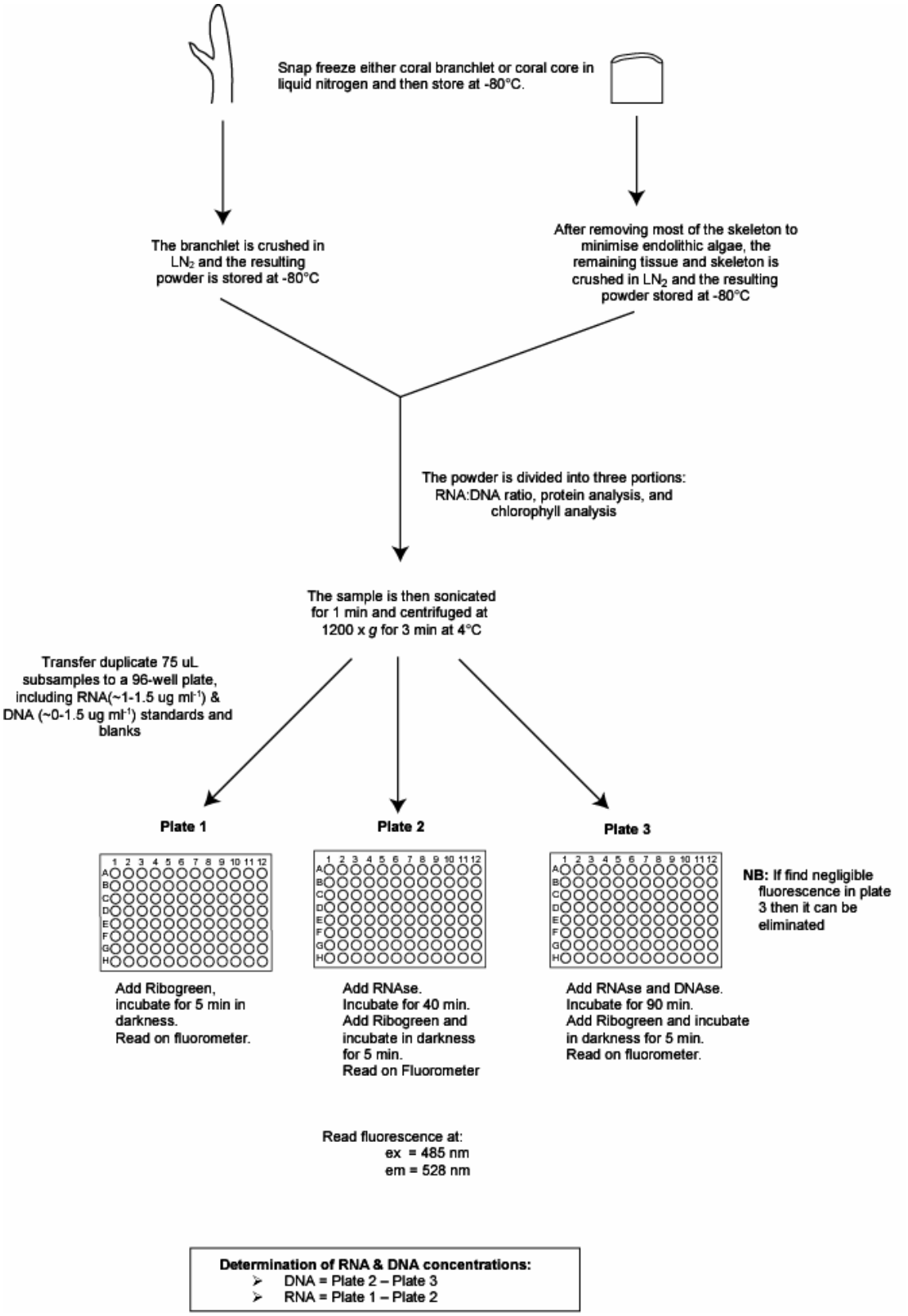

Figure 4.2. A schematic flow diagram of the nucleic acid extraction and analysis. See text for details.

4.3 Results

Transplant experiment

The results for the RNA:DNA ratio of corals transplanted to different depths are presented in Figure 4.3. They indicate that changing depth had a significant effect on RNA:DNA ratios, and that this effect was relatively rapid, occurring within five days for all of the corals. For *A. millepora* there was no change in the RNA:DNA ratio for corals that were left at 3 m. After five days, the RNA:DNA ratio of those transplanted to 7 and 12 m were elevated, though this was significant only for corals transplanted to 12 m (Table 4.1). After nine days the pattern had changed slightly with *A. millepora* at 7 m having a significantly higher RNA:DNA ratio than the corals at 3 m. The RNA:DNA ratio of those at 12 m was not significantly different to the corals at 3 m after nine days. The patterns exhibited by *Pocillopora damicornis* were different to those of *A. millepora*. For the corals left at 3 m there was no change over the nine days of the experiment. After five days the RNA:DNA ratios of the *P. damicornis* transplanted to 7 m and 12 m had dropped, though only at 7 m was this significant (Table 4.1). After nine days there was no significant difference in *P. damicornis* transplanted to both 7 n and 12 m compared with the corals left at 3 m.

Table 4.1. Effect of transplanting corals from 3 m to 7 m and 12 m on RNA:DNA ratio in *A. millepora* and *P. damicornis* after 5 days and after 9 days.

		df	MS	F	*p*	Tukey HSD
(a) Effects of transplanting *A. millepora* from 3 m to 7 and 12 m						
After 5 days	Depth	2	1.372	13.09	0.0330	3 = 7 < 12
After 9 days	Depth	2	0.7646	12.21	0.0362	3 = 12 < 7
(b) Effects of transplanting *P. damicornis* from 3 m to 7 and 12 m						
After 5 days	Depth	2	0.0894	36.47	0.0079	3 = 12 > 7
After 9 days	Depth	2	0.0982	5.122	0.1078	3 = 7 = 12

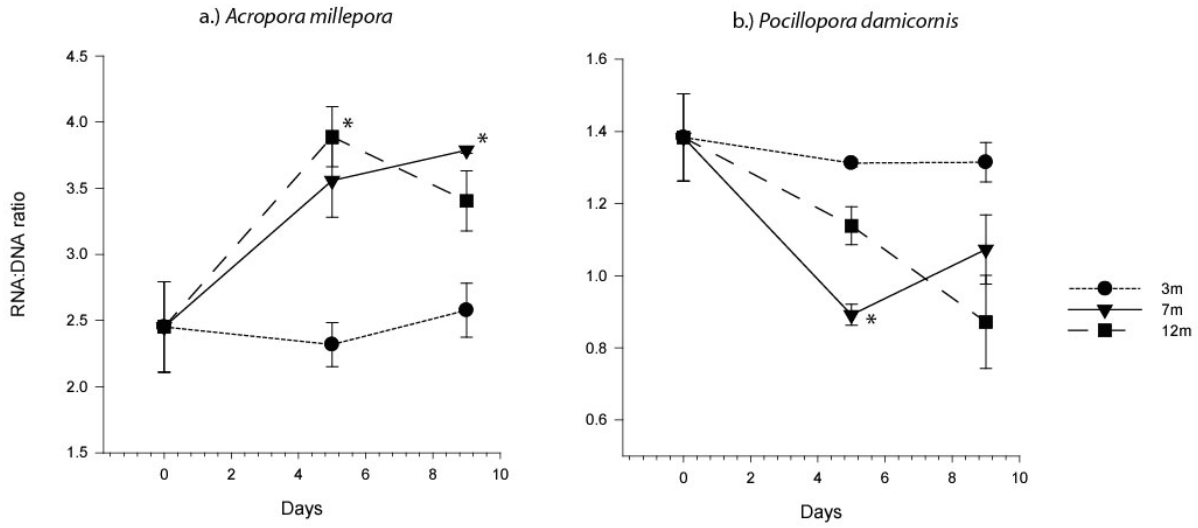

Figure 4.3. Mean RNA:DNA ratio (±s.e.) in corals transplanted to different depths: (A.) *Acropora millepora* and (B.) *Pocillopora damicornis.* * indicates significant differences to corals at 3 m.

Inshore/offshore reef comparison

No *Acropora millepora* was found on the back reef of Bedarra Island. Table 4.2 shows that there was a significant difference in the RNA:DNA ratio of both *A. millepora* and *P. damicornis* between inshore and offshore reefs. *A. millepora* from Gilbey and Wardle Reefs had significantly higher RNA:DNA ratios than *A.millepora* from High Island (Fig. 4.4a). This pattern was the same for *P. damicornis* with corals from Gilbey and Wardle Reefs having significantly higher RNA:DNA ratios than corals from High and Bedarra Islands (Fig. 4.4b). There was no discernable difference detected between the two offshore reefs or between the two inshore reefs.

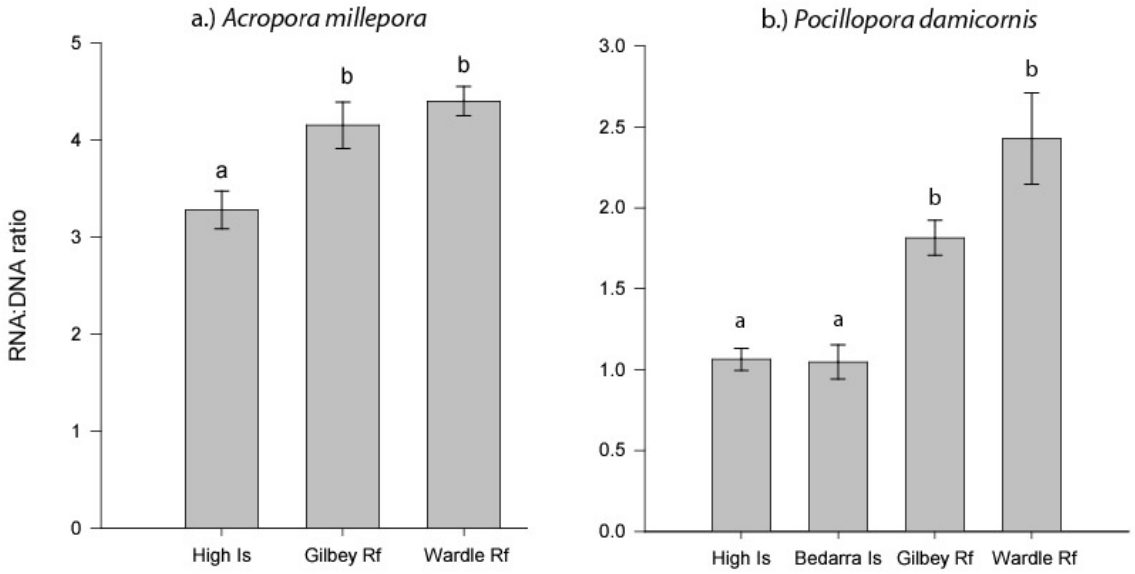

Figure 4.4. RNA:DNA ratio (mean±s.e.) in corals collected from two inshore reefs and two offshore reefs (A.) *Pocillopora damicornis* and (B.) *Acropora millepora.* Bars without a letter in common are significantly different.

Table 4.2. Effects of region and reef on RNA:DNA ratio in *A. millepora* and *P. damicornis*.

	df	MS	F	*p*
(a) *A. millepora*				
Reef (Region)	1	0.1542	0.785	0.3930
Region	1	3.312	16.86	0.0015
(b) *P. damicornis*				
Reef (Region)	2	0.4704	3.49	0.0550
Region	1	5.683	42.22	<0.0001

Handling methods

Results for the handling experiment are presented in Figure 4.5. The study showed that the three different handling methods had no significant effect on the RNA:DNA ratio of *A. millepora* though there was a significant effect due to colony (Table 4.3).

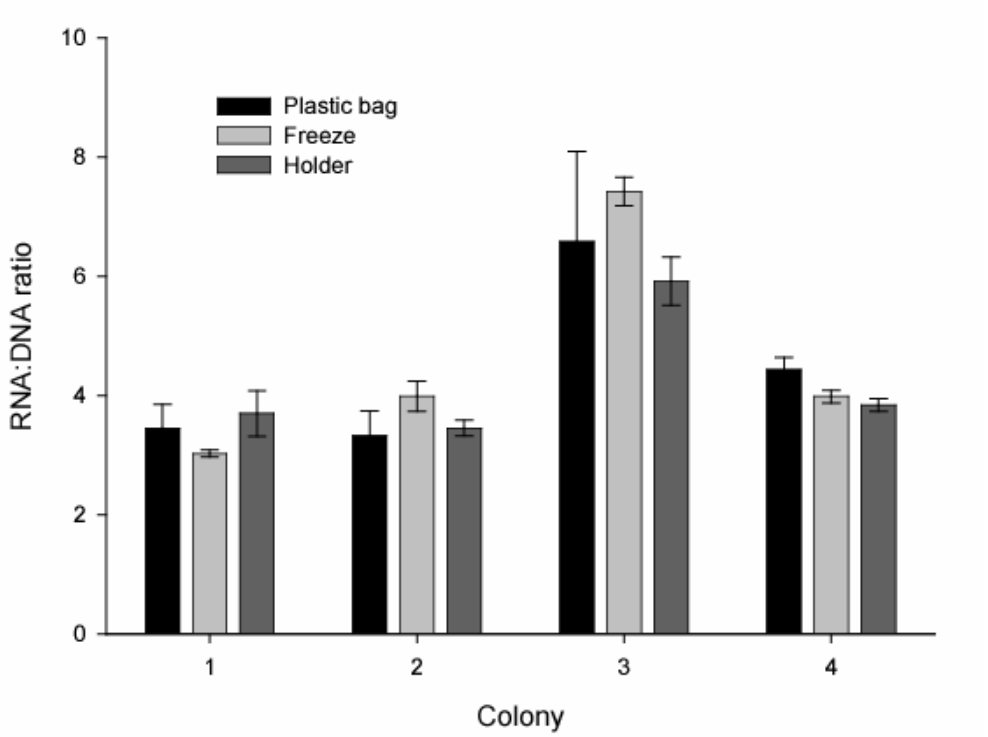

Figure 4.5. RNA:DNA ratios (mean±s.e.) in four *A. millepora* colonies collected and handled in three different ways; placed in a zip-loc plastic bag and carried during the dive, immediately snap frozen in liquid nitrogen and placed in a custom made holder allowing a flow of ambient water around the fragment.

Table 4.3. Effects of colony and handling method on RNA:DNA ratio in *A. millepora.*

	df	MS	F	*p*
Colony	3	40.77	22.61	<0.0001
Handling	2	0.8676	22.62	0.6201
Handling x Colony	6	1.5246	0.84532	0.5402

Inter- and intracolonial variation

The results of the study investigating inter- and intracolonial variations are shown in Figure 4.6. For *P. damicornis* there was a significant difference in the RNA:DNA ratio between colonies (Table 4.4). This was not the case with *A. millepora* where there was no significant difference between colonies (Table 4.4). For *A. millepora* within colony variability increased linearly with increasing colony size (R^2 = 0.963, $F_{(1,3)}$ = 77.309, p < 0.003). Despite colony size having an effect on the variability of the RNA:DNA ratio for *A. millepora*, there was no significant relationship between colony size and RNA:DNA ratio (R^2 = 0.463, $F_{(1,3)}$ = 2.597, p >0.2). There was no relationship between colony size and variation, or between colony size and RNA:DNA ratio in *P. damicornis*.

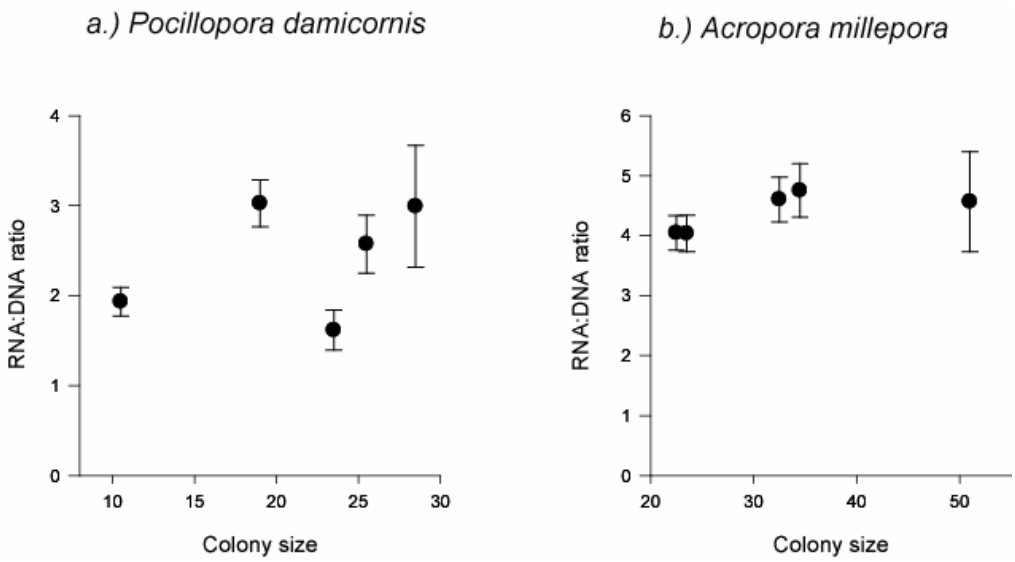

Figure 4.6. Inter- and intracolonial variation in RNA:DNA ratios (mean±s.e.) as a function of colony size: (A.) *Pocillopora damicornis* and (B.) *Acropora millepora*.

Table 4.4. Intercolonial variability of RNA:DNA ratios in *A. millepora* and *P. damicornis.*

	df	MS	F	*p*
(a) *A. millepora*				
Colony	4	2.379	0.9480	0.4393
(b) *P. damicornis*				
Colony	4	8.007	5.316	0.0007

Laboratory experiment

The results for the laboratory study investigating the affects of light and suspended sediment on the RNA:DNA ratio in massive *Porites* are shown in Figure 4.7. No significant difference in the RNA:DNA ratio of the *Porites* was detected between the four different treatments; however, there was a significant difference in the RNA:DNA ratio of corals collected from Princess Charlotte Bay and the Wet Tropics (Table 4.5).

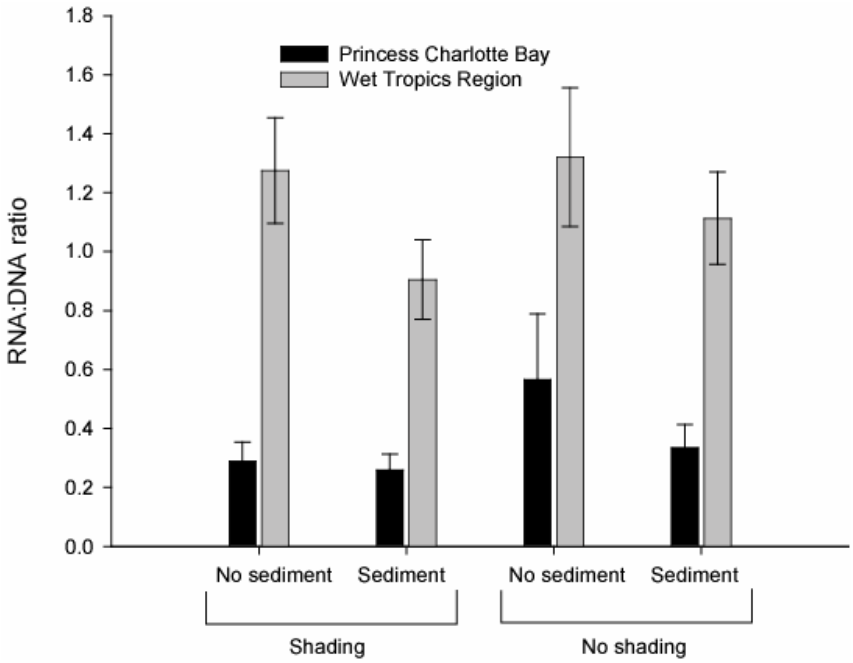

Figure 4.7: RNA:DNA ratio (mean±s.e.) in Porites sp. collected from two regions, Princess Charlotte Bay and the Wet Tropics, exposed to varying treatments of shading and suspended solids.

Table 4.5. Effects of light intensity and suspended particulate matter on RNA:DNA ratio in massive *Porites* cores.

	df	MS	F	*p*
Region	1	14.00	54.04	<0.0001
Sediment	1	0.9825	3.791	0.0549
Light	1	0.5099	1.968	0.1645
Region x Sediment	1	0.1398	0.5393	0.4648
Region x Light	1	0.0135	0.0522	0.8198
Sediment x Light	1	0.0021	0.0081	0.9285
Region x Sediment x Light	1	0.1861	0.7180	0.3994
Error	82	0.2591		

4.4 Discussion

This study looked at the effect of depth, time, location, handling, inter- and intra-colonial variation, light and suspended sediment on the RNA:DNA ratio in several species of coral in an effort to determine the suitability of this measure as an indicator for changes in water quality in the Great Barrier Reef (GBR).

A transplantation experiment where corals were collected at 3 m and transplanted to 7 m and 12 m showed that changes in depth brought about rapid changes in the RNA:DNA ratio in both *P. damicornis* and *A. millepora,* with significant changes being observed within five days, which generally persisted through to the end of the study after nine days. An interesting finding was the differing ways in which these two species responded to changing depth. The RNA:DNA ratio of *P. damicornis* decreased when transplanted to 7 m and 12 m, while the RNA:DNA ratio of *A. millepora* increased. The decrease in RNA:DNA ratio, as exhibited by *P. damicornis* was expected, as the reduced irradiance penetrating to the greater depths would have a marked negative effect on the photosynthetic carbon production by the zooxanthellae, with resulting depression in the overall metabolic activity of zooxanthellae and host. *A. millepora* on the other hand exhibited an increase in the RNA:DNA ratio, which was not expected. This increase may be explained by an increase in protein synthesis reflecting a stress response (Buckley and Szmant 2004). *A. millepora* is not generally found in deeper or more turbid waters (Veron 1986): for example, it was not found below approximately 4-5 m at High Island and not at all at the very turbid Bedarra Island. Hence the rapid decrease in light after transplantation may have induced a stress response to which the coral could not adapt. The *P. damicornis* transplants are unlikely to have exhibited a stress response, as this species is abundant at greater depth in our study region, and previous transplant experiments have show that *P. damicornis* is able to acclimate to light levels as low as 0.8% of incident surface PAR (Titlyanov *et al.* 2002). The varying response of the different species to varying depths again demonstrated that depth is an extremely important ecophysiological factor for corals (McCloskey and Muscatine 1984).

For the RNA:DNA ratio to be a useful measure of coral response to changing environmental conditions it must be able to discriminate between sites with different water quality conditions. To test this, *A. millepora* and *P. damicornis* were collected from both inshore and offshore reefs at constant depth. The RNA:DNA ratio of both species was significantly lower at the inshore reefs sampled, showing that offshore and inshore conditions could be distinguished from the RNA:DNA ratio. It is expected that growth and protein synthesis will be higher at in offshore reefs where light is more intense than in the more turbid waters of inshore reefs. This was confirmed by this study. The differences between the inshore and offshore reefs of this study are relatively large and it is yet to be seen whether the method will be sensitive enough to detect difference between reefs where differences in water quality are not as great. To this end a series of samples have been collected along an established water quality gradient in the Whitsunday region (van Woesik *et al.* 1999), which have yet to be analysed.

There is large interspecific variation in RNA:DNA ratios. Ratios in *A. millepora* were approximately 1.8 fold higher compared with *P. damicornis* (mean = 4.4 and 2.4, respectively) and approximately six fold higher compared with massive *Porites* (mean = 0.7 under laboratory conditions). Buckley and Szmant (2004) found a ~2.4 fold difference between three related species of *Montastraea,* which led them to caution on comparing congeners from different sites. This indicates that phylogenetic differences are likely to overwhelm any differences in RNA:DNA ratios resulting from environmental factors. Also, as shown above in the transplant experiment, species may not only differ in the magnitude of their RNA:DNA ratio, but also in the direction of their response to changes in environmental conditions. Under the same conditions the RNA:DNA ratio of transplanted *A. millepora* increased while that of *P. damicornis* decreased.

Initial work by Gates and Edmunds (1999) on *Madracis mirabilis* showed that RNA:DNA ratios varied by a factor of five among 10 clonal genotypes. The RNA:DNA ratios in 10 colonies of *P. damicornis* sampled from Wardle Reef varied ~1.9 fold (ranges: 1.6 to 3.0) resulting in significant differences between colonies at the same reef. *A. millepora* collected from Wardle Reef showed much smaller variation with the RNA:DNA ratio ranging from ~4.0-4.7 (a ~1.2 fold difference). In comparison, the differences between inshore and offshore reefs were ~ 2 fold for *P. damicornis* while for *A. millepora* it was ~1.3 fold. Interestingly for *A. millepora* the within-colony variation in RNA:DNA ratios increased with increasing colony size (though not affecting mean ratios). This would suggest that in larger colonies, branches from different parts of the colony are likely to grow at differing rates. This in essence reflects the fact that the size and shape of a colony influences water flow around branches and hence gas and nutritional exchange (Patterson *et al.* 1991; Lesser *et al.* 1994), and the availability and quality of light for photosynthesis (Lesser *et al.* 1994). However, when we compared the samples from Wardle Reef with samples collected from High Island for the handling study it was noticed that variability between colonies was much higher at High Island with the RNA:DNA ratio ranging from ~3.0 to 7.4. This is possibly because of the depth distribution the corals were collected from. Despite collecting all samples from similar depths it has been shown that very turbid areas generally have radically compressed biotic zones (Acevedi and Morelock 1988, Dikou and van Woesik 2006). All corals at both reefs were collected within a 2 m range, yet the water at High Island was much more turbid, resulting in relatively larger differences in light between the shallowest and deepest corals collected than at Wardle Reef. This effect of a more rapid change in RNA:DNA ratio with depth in turbid waters than clear waters was also shown by Bak and Meesters (2000).

Changes in light and suspended sediment have been shown to have an effect on coral health (see review by Fabricius 2005). Yet in a laboratory study investigating the effects of light intensity and suspended sediment on *Porites* we were unable to detect any significant differences in the ratio of RNA:DNA between treatments. This is difficult to explain. Light intensity varied from ~830 μE m^{-2} s^{-1} in the filtered seawater with no shading treatment to ~30 μE m^{-2} s^{-1} in the shading and suspended sediment treatment. It would be expected that such large differences in light over the duration of the study would have had some effect on the RNA:DNA ratio considering the rate of change during the transplant experiment over a similar change in light intensity. One possible explanation is photoacclimation. Corals exist in an environment where light varies with depth, turbidity, weather, season, time of day and with latitude (Kirk 1994). As such, corals have developed a number of methods to adjust to changing light regimes through a number of mechanisms including, but not limited to; increasing light absorbance by increasing photosynthetic pigments in zooxanthellae (Falkowski and Dubinsky 1981; Barnes and Chalker 1990), increasing the size of photosynthetic units (Falkowski and Dubinsky 1981), changing numbers of and/or “type” of zooxanthellae (Rowan and Knowlton 1995) and changes in photosynthetic carbon utilisation (Titlyanov *et al.* 2000). These changes have been demonstrated to occur over time periods of days to weeks (Anthony and Hoegh-Guldberg 2003), plenty of time for the corals in this study to have acclimated to the changes in light intensity and reach normal rates of photosynthesis, enabling stable RNA:DNA ratios to be attained. ‘Massive *Porites’* are a species complex, comprising at least five species that are difficult to tell apart in the field. They are a trophically remarkably flexible species, found in a wide range of depths across the whole continental shelf, and occur at high abundances in silty, turbid waters. This suggests that this species complex is particularly able to switch from phototrophy to heterotrophy. No cross-shelf comparison in RNA:DNA ratios was conducted in massive *Porites* in this study. However, the RNA:DNA ratios in massive *Porites* have been found to be higher on some turbid reefs in Indonesia (Bak and Meesters 2000). It has been suggested that such high metabolic activity in turbid water may reflect a phenotypic adaptation in metabolic functioning to turbid environments (Bak and Meesters 2000), and/or it may be due to higher rates of heterotrophy leading to improved nutrient supply for growth (Anthony 2006).

Interestingly, though we were unable to detect differences between treatments there was a significant effect due to region. Ratios in Princess Charlotte Bay region were lower than in the Wet Tropics. The water around the reefs of Princess Charlotte Bay generally has lower mean concentrations of suspended sediments, particulate nitrogen, particulate phosphorous and dissolved nutrients than that found in the Wet Tropics region (Fabricius and De'ath 2004). It remains to be tested whether the corals collected in Princess Charlotte Bay had a different clade of zooxanthellae than those from the Wet Tropics Region, which may contribute to different efficiencies in adapting to laboratory conditions or the irradiance levels of this experiment (Chang *et al.* 1983; Rowan *et al.* 1997). Such a phenomenon has been observed in *A. millepora,* where inshore populations from the central GBR host *Symbodinium* Clade D while *A. millepora* from inshore reefs of Princess Charlotte Bay host *Symbodinium* Clade C (Smith-Keune and van Oppen 2006). Phylogenetic and genotypic differences in coral populations have also been postulated as other factors that may affect RNA:DNA ratios (Meesters *et al.* 2002), though a great deal more work needs to carried out to resolve these issues.

4.5 Conclusions

In this study, a new, simple, rapid and efficient means to process large numbers of sample replicates for RNA:DNA ratio analysis has been developed for use in corals. The use of microplate readers and sensitive new fluorochromes (~200 times more sensitive than traditional ethidium bromide based methods) allow the quantification of RNA and DNA in extremely small samples (~ 100 µg dry weight of tissue). The novel use of nucleases allows the measurement of both RNA and DNA from a single sample. The methods presented here, employing simple and rapid extraction methods and sensitive molecular stains, allows the quick and reliable determination of RNA and DNA in large numbers of coral samples in a short period of time.

This study has shown that the RNA:DNA ratio is sensitive to differences in depth, light and location. In conjunction with other published studies (e.g. Meesters *et al.* 2002; Buckley and Szmant 2004) it indicates that with further research it may be a useful marker for detecting the effects of environmental change on coral ecophysiology, as long as depth of sampling is kept constant, colonies are reliably identified to species level, and samples are taken from the same upper portion of the colony.

Our study suggests that within the GBR, *P. damicornis* is a particularly suitable species for monitoring ecophysiological changes in response to changing water quality conditions: this species is very abundant, easily identified to species level, its RNA:DNA ratio decreases with decreasing light availability, and the difference in RNA:DNA ratios between inshore and offshore is large. However, although the tips of both middle and marginal branches continue to grow throughout the life of the colony, variability between branches is quite large in *P. damicornis*, suggesting within-colony environmental heterogeneity (e.g. self-shading). This re-inforces the need to collect samples within colonies that have comparable exposure to light and water flow. For example, sampling could be restricted to the uppermost 2 cm of protruding tips from the upward oriented part of the colony. Colonies should be collected at sufficient depth (e.g. 5-8 m) so that the shading effect of turbid water becomes relevant, as light is unlikely to be limiting in the uppermost 1-3 m of water even in very turbid conditions. Colonies shaded by adjacent coral outcrops, *Sargassum* or other benthos must be avoided. Further transplantation studies are needed to investigate the differential responses in RNA:DNA ratios in *P. damicornis* exposed to low light versus to high levels of suspended particulate matter.

A. millepora also appeared to be quite suitable for monitoring changes in water quality, as it appears to show lower levels of trophic plasticity than *P. damicornis*. It is very sensitive to low light and high turbidity, and hence likely to show responses to relatively small

environmental changes. Disadvantages are that its distribution in turbid environments is restricted to shallow waters and that it is stressed at low light, suggesting a non-linear response in RNA:DNA ratios (reduced at the onset of turbidity, and enhanced at higher level of stress). Furthermore, several sibling species may exist within this species complex (Wallace and Willis 1994). One advantage in using this species is the low within-colony variability in RNA:DNA ratios. This may be because the digitate *A. millepora* hase a symmetrical and even colony shape, in which new branchlets are generated at the colony edges whereas length and thickness of older branches in the middle of the colony are finite. Furthermore, colonies are almost always oriented upward. Therefore, central branchlets are exposed to quite similar microenvironmental conditions of light and flow, and a consistent collection of central branchlets should reduce the need for sample replicates.

Lastly, existing data suggest that the use of RNA:DNA ratios in massive *Porites* appears less desirable than that of other species, owing to its impressive trophic flexibility and its ability to adapt to highly turbid environments. However, further field studies are needed to confirm this preliminary conclusion.

Despite the promise held out by the proceeding studies there are a number of difficulties in interpreting the data because of the complex interaction between the coral host and symbiotic dinoflagellate. To help clear up these issues and ensure that the RNA:DNA ratio method will become suitable as indicator of coral health, further research needs to be carried out. Future research needs to develop more specific dose-response relationships in the two candidate species *P. damicornis* and *A. millepora*, assessing spatial gradients in the field and seasonal variations. Further research will also need to continue unravelling the mechanisms in which the interaction between coral host and algal symbiont responds to changes in environmental conditions, and investigate complementary areas such as protein synthesis rates and degradation, photoadaptation and the complex interactions between these processes.

4.6 References

Acevedo R, Morelock J. 1988. Effects of terrigenous sediment influx on coral zonation in southwestern Puerto Rico. Proceedings of the 6th International Coral Reef Symposium 2: 189-194

Anthony KRN. 2006. Enhanced energy status of corals on coastal, high-turbidity reefs. Marine Ecology Progress Series 319: 111-116

Anthony KRN, Hoegh-Gludberg O. 2003. Kinetics of photoacclimation in corals. Oceologia 134: 23-31

Bak RPM, Meesters EH. 2000. Acclimatization/adaptation of coral reefs in a marginal environment. Proceedings of the 9th International Coral Reef Symposium 1: 265-272

Barnes DJ, Chalker BE. 1990. Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky Z (Ed). Ecosystems of the World: Coral Reefs. vol 25, pp 109-131. Elsevier, New York

Berdalet E, Dortch Q. 1991. New double-staining technique for RNA and DNA measurement in marine phytoplankton. Marine Ecology Progress Series 73: 295-305

Buckley LJ. 1984. RNA-DNA ratio: an index of larval fish growth in the sea. Marine Biology 80: 291-298

Buckley L, Calderone E, Ong T-L. 1999. RNA-DNA ratio and other nucleic acid-based indicators for growth and condition of marine fishes. Hydrobiologia 401: 265-277

Buckley BA, Szmant AM. 2004. RNA/DNA ratios as indicators of metabolic activity in four species of Caribbean reef-building corals. Marine Ecology Progress Series 282: 143-149

Bulow FJ, Zeman ME, Winningham JR, Hudson WF. 1981. Seasonal variations in RNA-DNA ratios and in indicators of feeding, reproduction, energy storage, and condition in a population of bluegill, *Lepomis macrochirus* Rafinesque. Journal of Fish Biology 18: 237-244

Calderone EM, St. Onge-Burns JM, Buckley LJ. 2003. Relationship of RNA/DNA ration and temperature to growth in larvae of Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 262: 229-240

Chang SS, Prezelin BB, Trench RK. 1983. Mechanisms of photoadaptation in three strains of the symbiotic dinoflagellate *Symbiodinium microadeiaticum*. Marine Biology 76: 37-56

Dell'anno A, Fabiano M, Duineveld GCA, Kok A, Danovaro R. 1998. Nucleic acid (DNA, RNA) quantification and RNA/DNA ratio determination in marine sediments: comparison of spectrophotometric, fluorometric, and high-performance liquid chromatography methods and estimation of detrital DNA. Applied and Environmental Microbiology 64: 3238-3245

Dikou A, van Woesik R. 2006. Survival under chronic stress from sediment load: Spatial patterns of hard coral communities in the southern islands of Singapore. Marine Pollution Bulletin 52: 7-21

Fabricius KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. Marine Pollution Bulletin 50: 125-146

Fabricius KE, De'ath G. 2004. Identifying ecological change and its causes: A case study on coral reefs. Ecological Applications 14: 1448-1465

Falkowski PG, Dubinsky Z. 1981. Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. Nature 289: 172-174

Gates RD, Edmunds PJ. 1999. The physiological mechanisms of acclimatization in tropical reef corals. American Zoologist 39: 30-43

Kirk JTO. 1994. Light and photosynthesis in aquatic ecosystems. Second Edition. Cambridge University Press, Cambridge

Kyle M, Watts T, Schade J, Elser JJ. 2003. A microfluorometric method for quantifying RNA and DNA in terrestrial insects. 7pp. Journal of Insect Science 3:1, Available online: insectscience.org/3.1

Lesser MP, Weis VM, Patterson MR, Jokeil PL. 1994. Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): diffusion boundaries, inorganic carbon limitation, and biochemical plasticity. Journal of Experimental Marine Biology and Ecology 178: 153-179

McCloskey LR, Muscatine L. 1984. Production and respiration in the Red Sea Coral *Stylophora pistallata* as a function of depth. Proceedings of the Royal Society, Series B 1227: 215-230

Meesters EH, Nieuwland G, Duineveld GCA, Kok A, Bak RPM. 2002. RNA/DNA ratios of scleractinian corals suggest acclimatisation/adaptation in relation to light gradients and turbidity regimes. Marine Ecology Progress Series 227: 233-239

Melzner F, Forsythe JW, Lee PG, Wood JB, Piatkowski U, Clemmesen C. 2005. Estimating recent growth in the cuttlefish *Sepia officinalis*: are nucleic acid-based indicators for growth and condition the method of choice? Journal of Experimental Marine Biology and Ecology 317: 37-51

Muscatine L, Falkowski PG, Porter JW, Dubinsky Z. 1984. Fate of photosynthetic fixed carbon in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. Proceedings of the Royal Society of London B222: 181-202

Patterson MR, Sebens KP, Olson RR. 1991. *In situ* measurement of flow effects on primary production and dark respiration in reef corals. Limnology and Oceanography 36: 73-78

Rowan R, Knowlton N. 1995. Intraspecific diversity and ecological zonation in coral-algal symbiosis. Proceedings of the National Academy of Science USA 92: 2850-2853

Rowan R, Knowlton N, Baker A, Jara J. 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature 388: 265-269

Smith-Keune C, van Oppen M. 2006. Genetic structure of a reef-building coral from thermally distinct environments on the Great Barrier Reef. Coral Reefs 25: 493-502

Titlyanov E, Bil' K, Fomina I, Titlyanov T, Leletkin V, Eden N, Malkin A, Dubinsky Z. 2000. Effects of dissolved ammonium addition and host feeding with *Artemia salina* on photoacclimation of the hermatypic coral *Stylophora pistillata*. Marine Biology 137: 463-472

Titlyanov EA, Titlyanov TV, Yamzato K. 2002. Acclimation of symbiotic reef-building corals to extremely low light. Symbiosis 33: 125-143

van Woesik R, Tomascik T, Blake S. 1999. Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: Evidence of recent community changes. Marine and Freshwater Research 50: 427-440

Veron JEN. 1986. Corals of Australia and the Indo-pacific. University of Hawaii Press, Honolulu, USA

Wagner M, Durbin E, Buckley L. 1998. RNA:DNA ratios as indicators of nutritional condition in the copepod *Calanus finmarchicus*. Marine Ecology Progress Series 162: 173-181

Wallace CC, Willis BL. 1994. Systematics of the coral genus *Acropora*: Implications of new biological findings for species concepts. Annual Review of Ecology and Systematics 25: 237-262

Weber LP, Higgins PS, Carlson RI, Janz DM. 2003. Development and validation of methods for measuring multiple biochemical indices of condition in juvenile fishes. Journal of Fish Biology 63: 637-658

Wu RSS, Pollino CA, Au DWT, Zheng GJ, Yuen BBH, Lam PKS. 2003. Evaluation of biomarkers of exposure and effect in juvenile areolated grouper (*Epinephelus areolatus*) on foodborne exposure to benzo[*a*]pyrene. Environmental Toxicology and Chemistry 22: 1568-1573

Chapter 5: Physiological measures in scleractinian corals as potential bioindicators for changing water quality

Tim Cooper

5.1 Introduction

The delivery of land-based sources of pollution from catchments that have been modified over the past 150 years through agriculture and urbanisation is a significant threat to the health of the Great Barrier Reef (GBR) (Haynes and Michalek-Wagner 2000; Alongi and McKinnon 2005). Changes in the relative abundance of susceptible taxa and shifts in the trophic structure of coral reef assemblages have been used to infer the effects of exposure to nutrients and sediments along gradients of water quality on the GBR (van Woesik *et al.* 1999; Fabricius *et al.* 2005). Recognising that physiological responses can provide a valuable insight to the health of corals, recent studies have also documented patterns of spatial variability in some physiological parameters and attributed these to spatial differences in water quality (Anthony and Hoegh-Guldberg 2003b; Anthony 2006). It is not known, however, whether physiological patterns such as these could be used as response indicators of changes in water quality. By investigating the physiological responses in corals along a gradient of water quality, this study aimed to further enhance the understanding of conservation goals required to address the decline in coral reefs around the world (Pandolfi *et al.* 2005).

The types of coral-based indicators that could be used to assess changes in water quality range from physiological responses to community-level measures. At the physiological level, variables such as tissue thickness, skeletal density, linear extension and calcification rates can provide estimates of growth rates of the massive coral *Porites* along cross-shelf and water-quality gradients (Risk and Sammarco 1991; Barnes and Lough 1992; Lough and Barnes 2000). Other physiological measures include determinations of chlorophyll *a* and symbiont densities (Falkowski and Dubinsky 1981; Dubinsky *et al.* 1984; Hoegh-Guldberg and Smith 1989), and determination of lipid and protein content (Harland *et al.* 1992; Anthony and Fabricius 2000; Grover *et al.* 2002). Recently, Siebeck *et al.* (2006) proposed that the saturation of coral colour, which is correlated to the density of symbionts and the amount of pigment they contain, is a simple and appropriate indicator of coral health that can be measured using a 'Coral Health Monitoring Chart'. The chart was developed primarily for monitoring bleaching events, but its potential to detect the effects of changes in water quality on coral physiology is not known, although Fabricius (2006) showed that corals on nearshore reefs of the GBR had a greater saturation of colour (i.e. they were darker) compared with those on outer reefs.

This study comprises two components consisting of a field study followed by two manipulative experiments. First, a field study was done to investigate the spatial variability of the physiological properties of two scleractinian corals *Porites* spp. and *Pocillopora damicornis* along a gradient of water quality in the Whitsunday Islands. This study aimed at understanding physiological variation in the study species and whether any of these patterns were related to spatial differences in water quality. To successfully use any physiological differences as response indicators of coral stress or health, however, required manipulations in differing environmental conditions. The second component, therefore, comprised two manipulative experiments that aimed to validate the field observations of physiological differences to changes in water quality under controlled conditions. Experiment 1 was a tank experiment that examined the responses of corals under controlled conditions with differing

treatments of nutrient and light availability, while Experiment 2 was based on transplantation of corals to different water quality conditions along the gradient in the Whitsunday Islands.

5.2 Materials and methods

Field gradient study

Study sites and sampling

The study was conducted in the Whitsunday Islands (20° 00'-30'S; 148° 45'-149° 15'E) as existing water quality data from a long-term chlorophyll monitoring program (Brodie *et al.* 1997, and our own data presented in Chapter 2) indicated that levels of water column chlorophyll and nutrients increased towards the Australian coast. Two rivers (Proserpine and O'Connell Rivers) flow into Repulse Bay to the south west of the Whitsunday Islands that provide a point-source of terrestrial runoff into the study area (van Woesik *et al.* 1999). The fringing reefs sampled were Repulse, Lindeman, Long, Dent, Whitsunday, Hook, Border and Deloraine Islands; the mid-shelf reefs Bait and Charity Reefs were also sampled for comparison (Fig. 5.1).

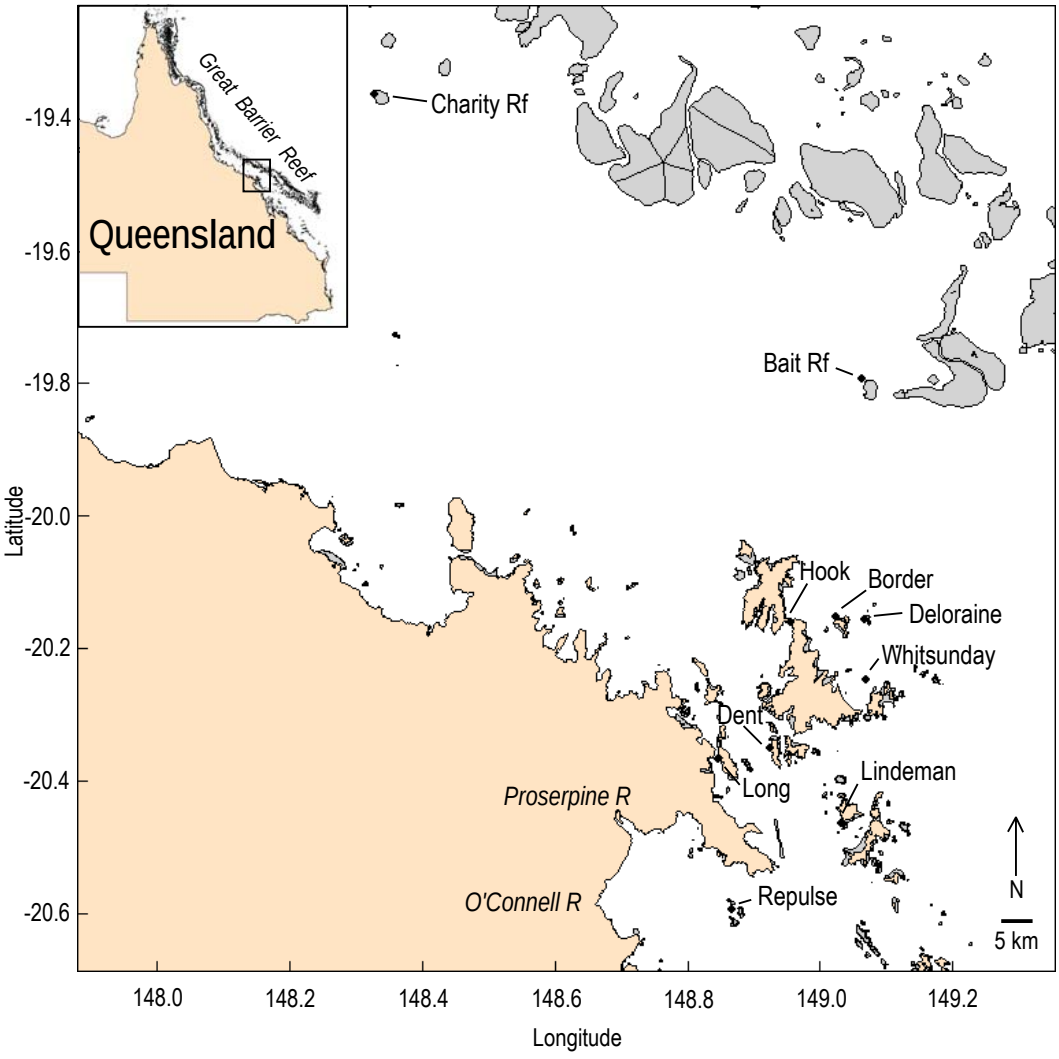

Figure 5.1. Map of study locations in the Whitsunday Islands, Great Barrier Reef.

The physiological parameters coral colour and tissue thickness were measured in massive colonies of *Porites* spp. Using the Coral Health Monitoring Chart (Siebeck *et al.* 2006), the colour saturation of *Porites* spp. was recorded for colonies occurring in each of two belt transects (10 m long x 3 m wide) laid randomly and parallel to the depth contour at two depths (shallow 1-3 m; deep 8-10 m below lowest astronomical tide, LAT) at two sites on each of ten coral reefs, while for tissue thickness, small cores approximately 21 mm diameter x 30 mm length were sampled from the upper surfaces of colonies using a drill with a 25 mm hole-saw attachment (following Barnes and Lough 1992) from five replicate colonies at the depths and sites described above. In the laboratory, each core was sliced in half using a scroll saw and the depth of the tissue layer was measured using vernier calipers at three points along the core. Additional measurements were conducted on *Pocillopora damicornis* as it is ubiquitous in the Whitsunday Islands (Veron 2000). Small branches were collected from each of four colonies selected randomly at the depths and sites described above for analysis of physiological parameters including concentration of chlorophyll *a*, the density of symbiotic dinoflagellates, determinations of protein content and skeletal density (described in detail in Experiment 2). Sampling was done from 8-16 August 2004.

Experiment 1

Collection of corals and suspended particulate matter

The study species for Experiment 1 was the massive coral *Porites lobata.* Small cores were collected from large colonies (> 2 m diameter) using an acrylic template with a central hole (26 mm diameter) as a guide to minimise any damage to the tissue layer of the nubbin (and source colony) during the drilling process. Colonies were selected on the reef flat (1-3 m below LAT) on the back of two islands: Wilkie Island (13˚ 46.5'S, 143˚ 38.0'E) in Princess Charlotte Bay, and High Island (17˚ 10.0'S, 146˚ 00.0'E) adjacent to the Wet Tropics. These two islands are in the Far Northern GBR and Northern GBR, respectively. The sediments used in the laboratory experiment were collected *in-situ* from around the base of coral heads on the leeward side of High Island. These sediments were later sieved and the fine fraction (< 63 μm) retained and used as suspended particulate matter (SPM) for the experiment.

Aquaria system

Experiments were done using a facility with controlled water and air temperatures, controlled light intensities and a constant flow of seawater (Photo 1). The aquaria system comprised eight x 32 L tanks each with a power head to generate water circulation (UniStar POW 100-2, 18W 1000 L h^{-1}), and a seawater inlet set to a constant flow rate of 500 mL min^{-1}. A header tank (500 L) ensured a consistent and even distribution of filtered seawater to each experimental tank.

Light intensities were 650-950 μE m^{-2} s^{-1} (400W Metal Halide) at the water surface, and illumination was provided for 12 h per day. To test hypotheses about the effects of light on the physiological response of corals, shade cloth was used to produce two experimental treatments: Shade and Light. The underwater light regime within the tanks was further characterised with replicate Odyssey data loggers (with a cosine corrected photosynthetic irradiance sensor 400-700 nm) deployed in the experimental treatments for a period of two hours. Similarly, to test hypotheses about the effects of SPM on the physiological response, a dosing system comprising a peristaltic pump (Masterflex L/S digital variable drive), was used to deliver a continuous flow of suspended particulate matter at a concentration of approximately 20 mg L^{-1} resulting in two experimental treatments: SPM (20 mg L^{-1}) and filtered seawater.

The water temperature was set to 25ºC and the air temperature to 22ºC. During the light period, however, water temperature within each tank increased to 28ºC. Each tank was

cleaned once a week to minimise algal growth within the tanks. The experiment ran for a total of 56 days.

Photo 1: Aquarium setup for long-term growth of corals at controlled environmental conditions.

Analysis of water quality

Samples for analysis of water quality were collected at 14 day intervals, although for total suspended solids, samples were collected at 4 day intervals to ensure the dosing system was maintaining concentrations of SPM at 20 mg L^{-1}. Analysis of dissolved inorganic and organic nutrients, total suspended solids (TSS), particulate nitrogen (PN), phosphorus (PP) and particulate organic carbon (POC) followed those described in Chapter 2.

Experiment 2

A manipulative experiment along a water quality gradient in the Whitsunday Islands was done that aimed to validate the responses observed in the laboratory experiment. Corals were transplanted to two depths (shallow: -3 m LAT, and deep: -8 m LAT), and to each of 2 reefs within 2 cross-shelf positions along a water quality gradient (Fig. 5.1): the inner zone (Lindeman and Long Islands), where the coral reefs are exposed to terrestrial runoff from two rivers, and the outer zone (Edward and Deloraine Islands), where conditions are considered to be oligotrophic (Brodie *et al.*, in review). In total, 20 replicate nubbins were sampled from the source colonies and assigned randomly to each of 10 experimental treatments that included a range of procedural controls and treatments to test hypotheses about the effects of light and water quality on coral colour (Table 5.1).

Table 5.1. Summary of experimental treatments used to test hypotheses about the effects of water quality on coral colour.

Treatment	
UN	Sample undisturbed colonies
CO	Control for effects due to coring, nubbin cored and placed back into colony
MO	Control for effects of moving, nubbins moved but returned to source reef
TLS	Control for effects of a site, nubbins moved 25 m on source reef
TLR	Control for effects of a reef, nubbins moved to nearby reef in the same zone
DS	Control for effects of depth, nubbins moved from deep to shallow depth
SD	Control for effects of depth, nubbins moved from shallow to deep depth
TP	Transplant nubbins to new reef in a different water quality zone
TPSD	Transplant nubbins to new reef and depth in a different water quality zone
TPDS	Transplant nubbins to new reef and depth in a different water quality zone

Measurements of coral colour were done using the Coral Health Monitoring Chart (Siebeck *et al.* 2006) and spectral reflectance with an Ocean Optics USB 2000 spectrometer on board a research vessel. Following these measurements, each nubbin had a small hole drilled transversely through the dead portion of the core, and attached into the holders on the transplant units with cable ties. The transplant units were constructed using tiles of natural sandstone as the base (400 x 400 x 20 mm). Four rows of nubbin holders were attached to one side of each tile using stainless steel dyna bolts. Each holder was 350 mm long and constructed from PVC pipe (40 mm diameter) sliced along the longitudinal axis. Into the upper section of each holder, a series of ten holes were drilled (22 mm diameter) to facilitate placement of the small *Porites* cores. All tiles had a small hole drilled through each corner to allow attachment onto the reef using star pickets (600 mm long) and fine gauge stainless steel wire. The transplant units were then deployed at tide-corrected depths adjacent to the source colonies on the back-reef (leeward side) of each island. In total, 480 nubbins were deployed on 22 tiles. Transplanting was done from 8-12 August 2005 and all units were retrieved 4 months later in 14-18 January 2006.

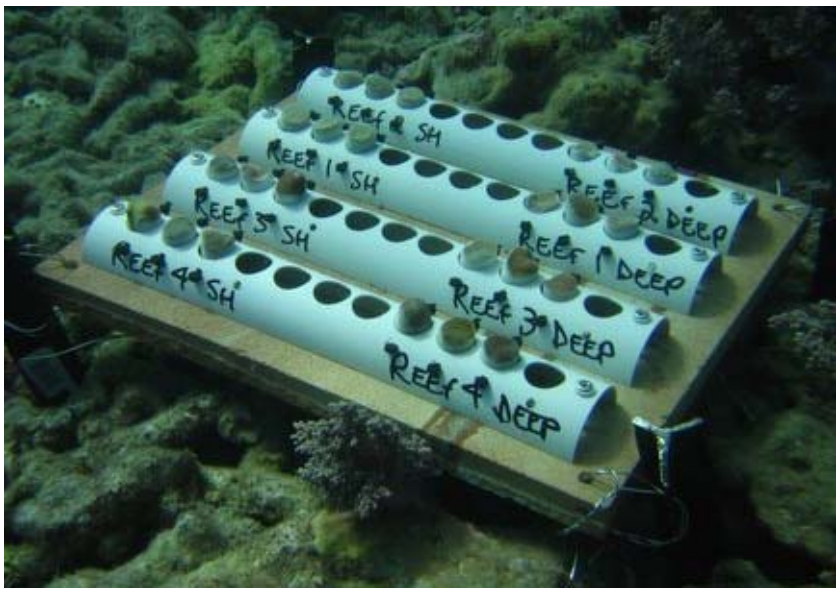

Photo 2: One of the deployment units to transplant Porites nubbins along the water quality gradient in the Whitsundays Islands.

Physiological analyses

In all experiments, corals were processed using the following physiological methods.

Preparation of coral samples

Each coral branch was placed into a plastic bag with filtered seawater (0.2 μm) and blasted with an air gun until the tissue was removed from the skeleton. This technique avoided sampling the tissue of bioeroders and endolithic algae observed within the coral skeletons during collection that may have confounded the results of the analyses. The resulting tissue slurry was then homogenised for 45 seconds using a tissue grinder.

Determination of chlorophyll *a*

A sub-sample of the tissue slurry was centrifuged at 3500 g for 10 minutes at 4°C. The supernatant was discarded and chlorophyll was extracted from the pellet with 100% acetone. After 24 hours, the sample was centrifuged again at 3500 g for 5 minutes at 4°C and the optical properties of the extract measured at 630 nm and 663 nm using a Shimadzu UV1700 Spectrophotometer. All samples were stored on ice and care was taken not to expose them to bright light during the extraction process. The concentration of chlorophyll *a* was determined using the formula from (Jeffrey and Humphrey 1975):

$$\text{Chlorophyll } a = ((11.43 \times E_{663} - 0.64 \times E_{630}) * V_a) \times (V_t / V_s)$$

where V_a = volume of acetone (ml);
V_t = volume of tissue slurry (ml); and
V_s = volume of sub-sample.

Density of dinoflagellate symbionts

The density of symbiont cells was determined using eight replicate counts in a Neubauer Improved Haemocytometer (0.1 mm^3, 0.1mm depth) with an Olympus BH-2 microscope and the 10X objective. For each sample, counts were done on 8 replicate sub-samples and the density of symbionts determined using the formula:

$$D = ((X_r / V_h) \times V_s)/SA$$

where D = density of dinoflagellate symbionts (cells/cm^2);
X_r = mean of 8 replicate counts;
V_h = volume of 1 large square on haemocytometer (1×10^{-4} ml);
V_s = volume of sub-sample corrected for the addition of 1 ml of formaldehyde as a proportion of the total homogenate; and
SA = surface area of the coral branch.

Protein content

The protein content of the coral samples was determined with the standard Bio-Rad DC protein assay using bovine serum albumin (BSA) as the standard. A sub-sample of the tissue slurry was digested in 0.5 M NaOH at 60°C for 5 hours and then spun at low speed in a centrifuge to separate cell-debris from the solution. Protein standards were prepared in the NaOH buffer in a range of concentrations (0, 0.5, 1.0, 1.5 and 2.0 mg ml^{-1}) and placed in a pre-determined configuration in a 96-well plate. To each well, 25 μl of Bio-Rad DC Reagent A and 200 μl Bio-Rad DC Reagent B were added to 5 μl of each sample. Absorbances were measured at 690 nm using a Perkin Elmer spectrophotometer (Wallac Victor^2, 1420 Multilabel Counter). The average of the absorbance of duplicate samples was used to determine the protein content in mg ml^{-1}. Samples were re-analysed if the coefficient of variation between duplicate samples was greater than 10%.

Surface area

The surface area of the coral branches was determined using wax dipping using the technique described by (Stimson and Kenzie III 1991). This involved coating the coral branch (i.e. covering holes in the skeleton) with paraffin wax, which was maintained at a constant temperature of 70°C with a water bath, and recording the initial weight. Each sample was then re-dipped and weighed again. The surface area was calculated using the difference between the two weights and applying a regression coefficient that was determined by repeating the process using a series of acrylic blocks of a known surface area.

The determinations of chlorophyll *a*, density of symbionts, and protein content, were normalised to surface area of the coral branch.

Skeletal density

Skeletal density (ρ_s) of *P.damicornis* was determined using the procedures described by (Anthony *et al.* 2002). Briefly, each sample was rinsed in freshwater and dried at 60°C prior weighing on a Shimadzu AUW 220D balance. The samples were then soaked in freshwater for 3 days and re-weighed while immersed in freshwater to determine buoyant weight. Using Archimedes' Principle, skeletal density was calculated as the ratio between dry and buoyant weight.

Coral colour

A standardised coral colour chart was used both in the field and the laboratory to determine coral colour ('Coral Health Monitoring Chart' University of Queensland, Australia, Siebeck *et al.* 2006), www.CoralWatch.org). The chart comprises six colour categories (1 = almost white, 6 = dark) on a grey-scale to which each of four different hues have been added to assist the colour determination. Only pigment changes related to the symbiotic algae were monitored.

Tissue thickness in massive *Porites*

Small cores (22 mm diameter) were removed from the upper surfaces of massive *Porites* using a pneumatic drill fitted with a 25 mm hole-saw. Colonies greater than 50 cm in diameter were selected for sampling. In the laboratory, each core was sliced in half with a scroll-saw and allowed to air dry for several days, so that the tissue layer could be measured using a vernier calliper to the nearest 0.01 mm.

Statistical analyses

For the field gradient study, the physiological parameters in *P.damicornis* were analysed with 3 factor analyses of variance (ANOVA). The factors were Reefs (10 levels, random), Depth (2 levels, fixed and orthogonal) and Site (2 levels, random and nested). The physiological parameters were further analysed with linear models to determine if relationships existed with a water quality index derived from the z-transformations of water quality parameters (e.g. Fabricius *et al.* 2005) collected over five previous surveys (August 2004 to August 2006, described in more detail in Chapter 2). Experiment 1 tested hypotheses about the effects of exposure to suspended particulate matter on physiological parameters in nubbins of *Porites* with each of two treatments of light (shade and light) and suspended particulate matter (SPM at 20 mg L^{-1} and filtered seawater). The experiment was analysed using a linear mixed effects model with random crossed effects. Experiment 2 tested hypotheses about the effects of light and water quality on nubbins manipulated along a water quality gradient in the Whitsunday Islands. Due to mortality among some of the nubbins (see below), differences among the experimental treatments were examined using a 1 factor ANOVA. For all ANOVAs, Cochran's C-Test was used to test for deviations from the assumption of homogeneity of variances, and data were transformed if necessary. Means for significant

factors in the ANOVA were compared using Student Newman Keuls (SNK) tests. Statistical analyses were done using the statistical software R (R Development Core Team 2006).

5.3 Results

Field gradient study

The colour of massive *Porites* varied significantly among locations in the Whitsunday Islands (Table 5.2). The *Porites* were darker at Repulse Island (4.33 ± 0.16 colour chart units) compared with the other locations, which were not different from each other (3.0 ± 0.2 to 3.55 ± 0.17 colour chart units). The thickness of the tissue layer in *Porites* varied inconsistently among locations and between depths (Table 5.2). At the shallow depth, the tissue layer was thinner at Lindeman Island (3.13 ± 0.31 mm) followed by Long and Repulse Islands (not significantly different from each other) compared with Dent, Whitsunday, Hook, Border Islands and Charity Reef (not different from each other) with the tissue layer being thickest at Bait Reef and Deloraine Island (7.18 ± 0.52 mm). Similarly, at the deep depth, the tissue layer was thinnest at Lindeman Island (3.05 ± 0.27 mm), followed by Repulse Island, compared with the other locations, which did not differ from each other (4.65 ± 0.33 to 5.90 ± 0.20 mm).

The physiological parameters in *P.damicornis* were analysed to investigate patterns of variability between depths and among the locations in the Whitsunday Islands. With few exceptions, all the physiological parameters varied inconsistently among locations and between depths (indicated by Loc x Dep interactions, Table 5.2). For example, at the shallow depth, there was more chlorophyll *a* per cm^{-2} in *P.damicornis* at Repulse Island (8.98 ± 1.02 µg cm^{-2}) compared with the other locations, but no differences where detected elsewhere (range 2.43 ± 0.48 to 6.20 ± 0.84 µg cm^{-2}) (Table 5.2). There were more symbionts per cm^{-2} at the deep depth at Long (2.51 ± 0.57 x 10^6 cells cm^{-2}) and Lindeman Islands (1.83 ± 0.53 x 10^6 cells cm^{-2}) compared with the other locations, which did not differ from each other (0.66 ± 0.07 to 1.09 ± 0.15 x 10^6 cells cm^{-2}). At the shallow depth, there were more symbionts per cm^{-2} at Repulse Island (2.40 ± 0.13 x 10^6 cells cm^{-2}) compared with the other locations (0.55 ± 0.09 to 1.67 ± 0.48 x 10^6 cells cm^{-2}) (Table 5.2). The protein content per cm^{-2} at the shallow depth was lowest at the shallow depth at Long Island (0.60 ± 0.10 mg cm^{-2}) compared with the other locations, which were not different from each other (0.90 ± 0.16 to 1.96 ± 0.22 mg cm^{-2}) (Table 5.2). In contrast, the skeletal density of the *P.damicornis* varied significantly among locations. The skeleton of *P.damicornis* was least dense at Repulse Island (2.06 ± 0.07 g cm^{-3}) compared with the other locations, which were not different from each other (2.18 ± 0.07 g cm^{-3} to 2.48 ± 0.03 g cm^{-3}) (Table 5.2). The patterns of variability of physiological parameters in massive *Porites* and *P.damicornis* were therefore generally dominated by inconsistent variation among locations and between depths. There were some patterns, however, such as coral colour in *Porites* spp and skeletal density in *P.damicornis* that indicated physiological differences existed at larger scales among locations in the Whitsunday Islands.

Table 5.2. Summary of ANOVAs comparing select physiological parameters in (a–b) massive *Porites* and (c–f) *Pocillopora damicornis* among locations and between depths in the Whitsunday Islands, August 2004. Significant *P* values in bold, * denotes term eliminated at *P*>0.25. For *post hoc* tests, abbreviations: Rep = Repulse Is, Lind = Lindeman Is, Long Is, Dent Is, Whit = Whitsunday Is, Hook Is, Bord = Border Is, Del = Deloraine Is, Bait Reef, Char = Charity Reef.

Variate	Source of variation	df	MS	*F*	*P*	*Post hoc* tests
a) Coral colour *Porites*	Location	9	3.2714	4.18	**0.0179**	Loc: Whit=Hook=Del=Bait=Long=Bord=Dent=Char=Lind<Rep
	Site(Loc)	10	0.7828	1.71	0.0832	
	Depth	1	0.0968	0.08	0.7828	
transform: none	*Loc x Dep	9	0.6635	0.55	0.8090	
C=0.1280 (ns)	Dep x Site(Loc)	10	1.2068	2.63	**0.0054**	
	Residual	160	0.4586			
b) Tissue thickness *Porites* (mm)	Location	9	22.432	2.87	0.0581	
	Site(Loc)	10	7.822	5.41	**<0.0001**	Loc x Dep
	Depth	1	0.1897	0.05	0.8249	Shallow: Lind=Long=Rep<Dent=Whit=Hook=Bord=Char<Bait=Del Deep: Lind=Rep<Dent=Long=Del=Whit=Hook=Bord=Char=Bait
transform: none	Loc x Dep	9	3.6578	2.53	**0.0097**	
C=0.1280 (ns)	*Dep x Site(Loc)	10	0.8805	0.61	0.8042	
	Residual	160	1.4446			
c) Chlorophyll *a* (µg cm^{-2})	Location	9	1.089	1.59	0.2393	
	Site(Loc)	10	0.684	2.11	**0.0270**	Loc x Dep
	Depth	1	0.010	0.03	0.9426	Shallow: Whit=Bord=Long=Del=Hook=Lind=Char=Bait=Dent<Rep; Deep: Hook=Dent=Bait=Char=Whit=Del=Bord=Lind=Long
transform: ln(x)	Loc x Dep	8	1.809	5.58	**<0.0001**	
C=0.0945 (ns)	*Dep x Site(Loc)	9	0.291	0.90	0.5287	
	Residual	146	0.324			
d) Symbionts (10^6 cells cm^{-2})	Location	9	0.366	45.16	0.1150	
	Site(Loc)	10	0.008	0.23	0.6300	Loc x Dep
	Depth	1	0.121	0.65	0.7441	Shallow: Del=Whit=Bord=Long=Hook=Bait=Char=Lind=Dent<Rep; Deep: Del=Bord=Whit=Hook=Bait=Char=Dent<Lind=Long
transform: sqrt(x+1)	Loc x Dep	8	0.187	3.67	**0.0346**	
C=0.0810 (ns)	Dep x Site(Loc)	9	0.051	1.46	0.1682	
	Residual	146	0.035			

Variate	Source of variation	df	MS	*F*	*P*	*Post hoc* tests
e) Protein (mg cm^{-2})	Location	9	1.306	1.93	0.1602	
	Site(Loc)	10	0.677	2.81	**0.0033**	Loc x Dep
	Depth	1	1.007	1.27	0.2927	Shallow: Long<Whit=Dent=Bord=Hook=Lind=Del=Char=Bait Deep: Dent=Hook=Whit=Long=Char=Bord=Del=Bait=Lind
transform: ln(x)	Loc x Dep	8	0.794	3.56	**0.0017**	
C=0.0916 (ns)	*Dep x Site(Loc)	9	0.223	0.93	0.5051	
	Residual	146	0.241			
f) Skeletal density (g cm^{-3})	Location	9	0.283	3.07	**0.0477**	Loc: Rep<Dent=Long=Lind=Bait=Whit=Del=Hook=Char=Bord
	Site(Loc)	10	0.092	3.62	0.0002	
	Depth	1	0.024	0.42	0.5354	
transform: none	Loc x Dep	8	0.057	0.62	0.7454	
C=0.1280 (ns)	Dep x Site(Loc)	9	0.093	3.65	**0.0004**	
	Residual	146	0.025			

Linear models were used to further examine the patterns of variation of the physiological parameters and determine if any of the variability could be explained by relationships to a water quality index. Significant relationships occurred between the water quality index and the saturation of colour of massive *Porites* spp and tissue thickness, explaining 71% and 53% of the variance, respectively (Table 5.3). As the water quality index increases, the massive *Porites* become progressively darker in colour, and their tissue layer became thinner, compared with conspecifics occurring on reefs where the water quality index is lower and the water column characterised by lower concentrations of nutrients, suspended solids and a greater light availability (Fig. 5.2). All of the physiological parameters in *P.damicornis* showed significant, but variable, relationships with the water quality index (Table 5.3). As the water quality index increased, i.e. from the clear water mid-shelf reefs and outer islands toward those in the more turbid coastal zone, the density of symbionts and concentration of chlorophyll *a* in *P.damicornis* increased by 54% and 31%, respectively (Fig. 5.2). In contrast, the skeletal density in *P.damicornis* decreased by approximately 12%, and interestingly, there was a modal response in the protein content, with increases in the water quality index (Fig. 5.2).

These results indicated that there were spatial differences in selected physiological parameters in *P.damicornis* and massive *Porites* spp. in the Whitsunday Islands that correlated with a water quality index developed for the region. Whether these physiological patterns could be used as response indicators of differences in water quality was explored with a dose-response experiment (Experiment 1) and a manipulative experiment in the field (Experiment 2).

Table 5.3. Summary of linear models testing relationship between select physiological parameters in (a-b) massive *Porites* spp. and (c-f), *Pocillopora damicornis* and a water quality index. Second order polynomials were used for all models. Significant *P* values shown in bold. Degrees of freedom for the *F*-values 2, 14, except for (a–b) where df 2, 15.

Variate	**R^2**	**F**	***P***
(a) Colour *Porites*	0.71	18.00	**0.0001**
(b) TTL *Porites* (mm)	0.53	8.38	**0.0036**
(c) Chlorophyll *a* (µg cm^{-2})	0.45	5.75	**0.0150**
(d) Symbionts (10^6 cells cm^{-2})	0.60	10.57	**0.0016**
(e) Protein content (mg cm^{-2})	0.49	6.62	**0.0095**
(f) Skeletal density (g cm^{-3})	0.52	7.67	**0.0056**

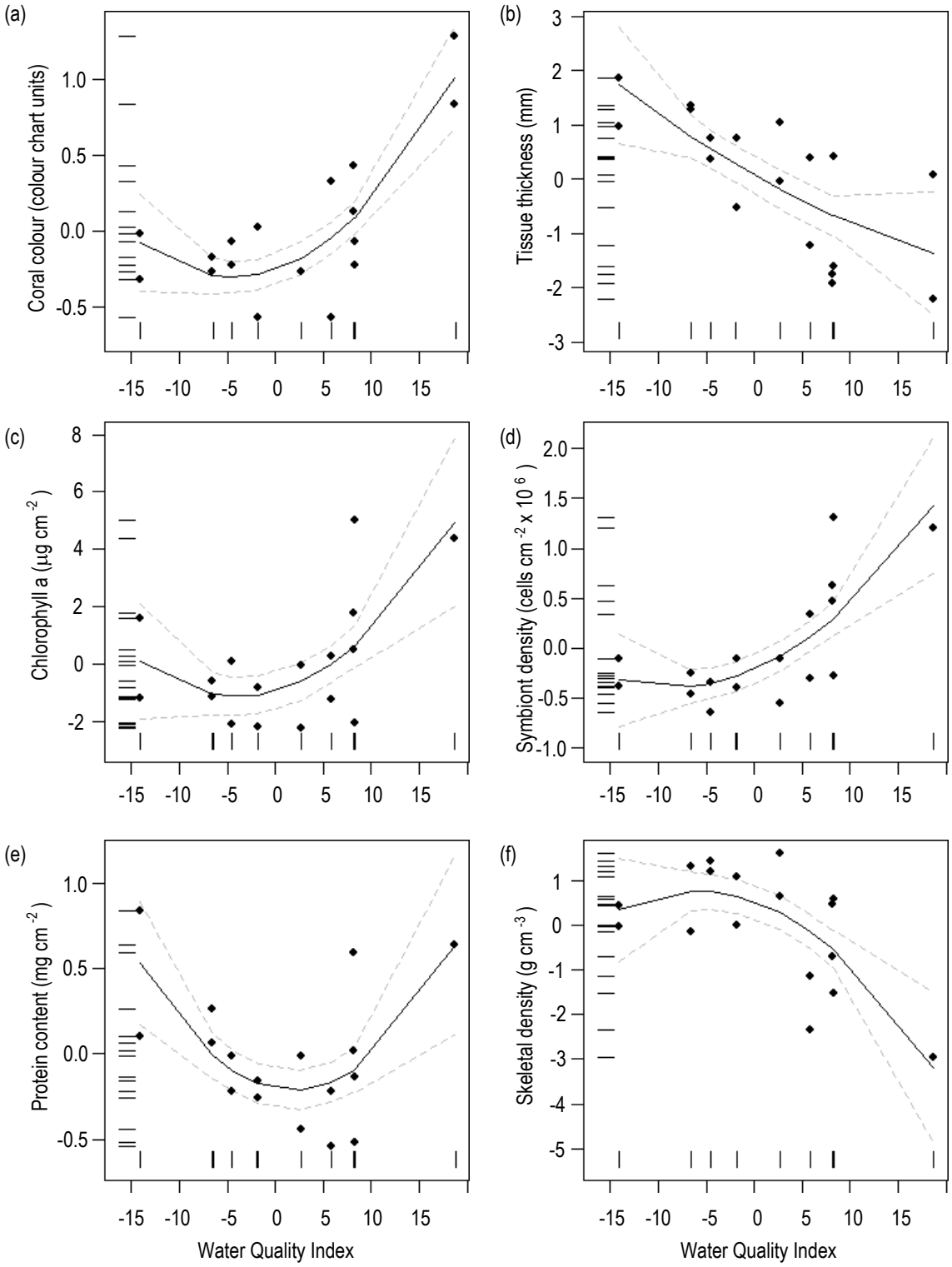

Figure 5.2. Plot of spline terms in models of the relationships between physiological parameters in (a–b) massive *Porites* spp. (±SE, n=10), and (c–f) *Pocillopora damicornis* (±SE, n=8) and a water quality index for the Whitsunday Islands. Index derived from five surveys between August 2004 and August 2006; large positive numbers correspond to nearshore reefs in the coastal zone, negative numbers correspond to outer islands and mid-shelf reef. Data are z-transformed.

Experiment 1

General

The *Porites* nubbins sampled from Wilkie and High Island were maintained successfully in the experimental set-up for 56 and 32 days, respectively, with no mortality. The shorter exposure time for the nubbins from High Island was due to a longer acclimation period prior to the commencement of the experiment as some nubbins became 'paler' after collection and transportation to the laboratory. Interestingly, some nubbins from Wilkie Island appeared to be less efficient at rejecting sediment compared with colonies from High Island. Despite having a thin layer of sediment on their upper surface after the first week of exposure, these colonies did not show any visible adverse affects of smothering, i.e. there was no partial mortality or bleaching. The light regime differed among the experimental treatments. The mean light intensity ($\pm$ SE, n=2) was greatest in filtered seawater (FSW) and no shade (835 $\pm$ 4 μE m^{-2} s^{-1}), followed by suspended particulate matter (SPM) and no shade (598 $\pm$ 2 μE m^{-2} s^{-1}), FSW and shade (56 $\pm$ 0.3 μE m^{-2} s^{-1}), with the lowest levels recorded in the SPM and shade treatment (32 $\pm$ 0.2 μE m^{-2} s^{-1}). In general, shading and SPM produced a 93% and 94% reduction in the underwater light intensity, respectively.

There were few differences between the experimental treatments for levels of dissolved inorganic and organic nutrients. Levels of nitrate (NO_3), nitrite (NO_2) and dissolved inorganic nitrogen (DIN) were, however, generally two-fold greater in the SPM compared with filtered-seawater treatment (Fig. 5.3). Levels of particulate nitrogen, phosphorus and organic carbon differed two to three-fold between the water quality treatments indicating that particulate nutrients in the experiment were more elevated than dissolved nutrients in the SPM compared with FSW treatment (Fig. 5.3). Levels of total suspended solids were maintained in the range of 20 mg L^{-1} above background levels (approximately 4 mg L^{-1}) for the duration of the experiment (Fig. 5.3).

Coral colour

The colour of the *Porites* from both Wilkie and High Island differed significantly among the experimental treatments (Fig. 5.4). The Wilkie Island nubbins commenced the experiment with a colour saturation of approximately 4.0 colour chart units as determined with the Coral Health Chart. By Day 10 of the experiment, clear differences in the saturation of coral colour among the treatments were apparent. Nubbins in the FSW and no-shade treatment (i.e. control) had maintained a colour of 3.7 $\pm$ 0.1 colour chart units, but corals in all the other treatments were noticeably darker and had increased by approximately one colour score. At Day 20, nubbins in the no SPM, no shade treatment were still within the colour saturation range that they started the experiment with (3.9 $\pm$ 0.2 colour chart units), whereas the corals placed into the shaded treatments had increased a further colour score and were within the range of 6.0 colour chart units. Corals placed in the SPM and light treatment appeared to stabilise in colour saturation and maintained a colour score of approximately 5.0 colour chart units until the completion of the experiment. All nubbins appeared to stabilise their colour saturation within approximately 20 days and they maintained the values recorded at Day 20 until the exposure was stopped on Day 56. It was noteworthy that the colour response in the turbid water treatment (i.e. SPM and normal light) was rapid and clearly discernible after Day 10 of the experiment.

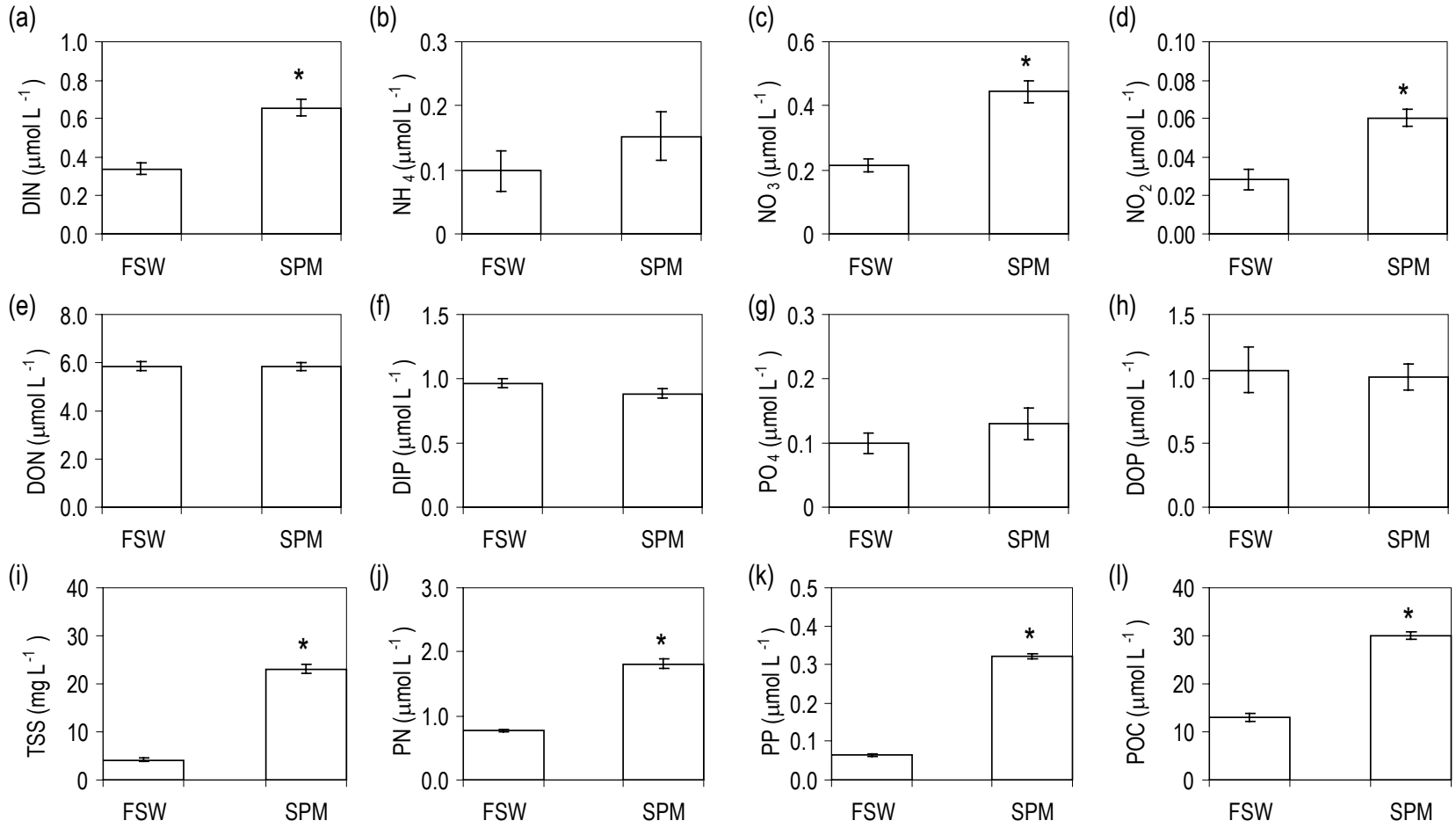

Figure 5.3. Mean concentration of water column parameters in Experiment 1 to examine physiological response of *Porites* nubbins exposed to suspended particulate matter (values averaged over 56 days). (a–h) dissolved nutrients (n=20), suspended solids and particulate nutrients (n=40). Treatments: FSW = filtered seawater and SPM = suspended particulate matter. * denotes statistical significance a $P < 0.05$. Abbreviations: DIN, dissolved inorganic nitrogen; DON, dissolved organic nitrogen; DIP, dissolved inorganic phosphorus; DOP, dissolved organic phosphorus; TSS, total suspended solids; PN, particulate nitrogen; PP, particulate phosphorus; POC, particulate organic carbon.

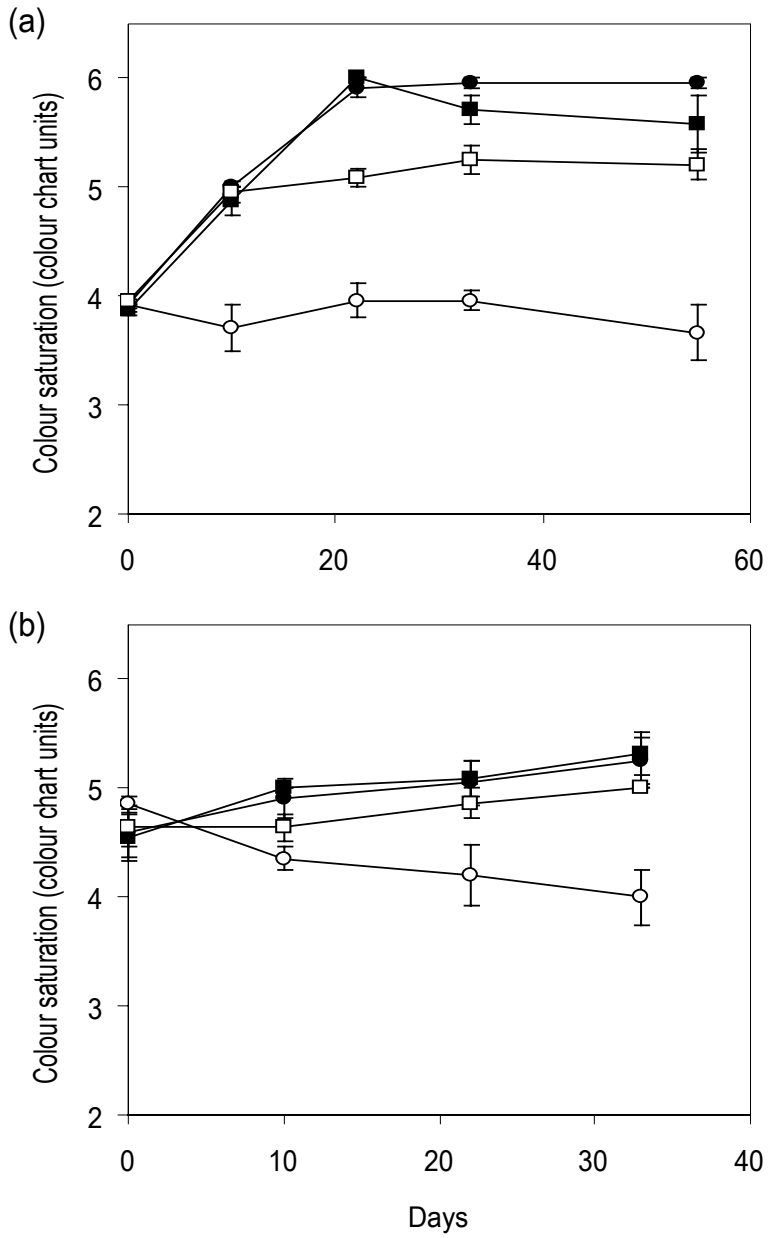

Figure 5.4. Mean saturation (±SE) of coral colour for nubbins of *Porites* from a) Wilkie Island (n=12), and b) High Island (n=10) exposed to different treatments of nutrient and light availability. Symbols: circles = filtered seawater; squares = SPM; open symbols = light; dark symbols = shade. The shorter exposure time for the nubbins from High Island was due to a longer acclimation period prior to the commencement of the experiment as some nubbins became 'paler' after collection and transportation to the laboratory

Thickness of the tissue layer, chlorophyll a and density of symbionts

The thickness of the tissue layer of the Wilkie Island nubbins varied significantly between SPM treatments after 56 days of exposure (Table 5.4). The tissue layer of the nubbins in the SPM treatment was thicker (5.52 ± 0.31 mm) compared with those in the FSW treatment (4.69 ± 0.21 mm). There were no differences in tissue thickness between SPM and light treatments for the High Island nubbins. The concentration of chlorophyll *a* cm^{-2} varied inconsistently between the light and water quality treatments for colonies sampled from Wilkie and High Islands (Table 5.4). Under high light, there was more chlorophyll *a* cm^{-2} in nubbins placed in the SPM compared with the FSW treatment, but there was no difference between treatments in low-light conditions (Fig. 5.5). There were no differences in the density of symbionts among treatments for nubbins from either Wilkie of High Island (Table 5.4).

In summary, the *Porites* nubbins responded physiologically to differences in water quality in an experimental tank setup. Of the responses that were detected, the most interesting appears to be the response of coral colour. The response was rapid as differences among the nubbins were noticeable within 10 days of the onset of exposure to suspended particulate matter and adaptation to endpoint levels had occurred after 20 days of exposure. Furthermore, the differences among treatments measured using the colour chart were supported by the results of the pigment extractions with significantly less chlorophyll *a* occurring in nubbins placed in the control treatment compared with those placed in SPM and full light (i.e. simulating turbid conditions and thus poor water quality) or the shaded treatments.

These results indicated that indeed physiological responses to differences in water quality could be detected in laboratory experiments. These responses needed to be examined with a further manipulative experiment under field conditions (Experiment 2).

Table 5.4. Summary of ANOVAs comparing physiological parameters in *Porites* nubbins from two different regions exposed in a laboratory experiment to different treatments of nutrients and light availability after exposure. Nubbins from Wilkie Island exposed for 56 days, nubbins from High Island exposed for 32 days. Significant *P*-values in bold, * denotes term eliminated at $P > 0.25$. For *post hoc* tests, means (±SE) are untransformed and in ascending order. FSW = filtered seawater, SPM = suspended particulate matter.

Variate	Source of variation	df	MS	*F*	*P*	*Post hoc* tests			
Coral colour									
a) Colour - Wilkie Is.	Light	1	30.88	1.70	0.4162	Shade		Light	
	SPM	1	8.76	0.48	0.6134	FSW = SPM		FSW < SPM	
transform: none	Light X SPM	1	18.13	64.14	**<0.0001**	5.96	5.58	3.13	5.21
C = 0.7169 (*P*<0.01)	Residual	44	0.283			(0.04)	(0.26)	(0.07)	(0.14)
b) Colour – High Is.	Light	1	5.625	2.25	0.3743	Shade		Light	
	SPM	1	2.500	1.00	0.5000	FSW = SPM		FSW < SPM	
transform: none	Light X SPM	1	2.500	6.55	**0.0149**	5.25	5.25	4.00	5.00
C=0.4346 (ns)	Residual	36	0.382			(0.21)	(0.20)	(0.26)	(0.00)
Tissue thickness									
c) TTL (mm) – Wilkie Is.	Light	1	0.864	0.50	0.4831	SPM			
	SPM	1	8.411	4.87	**0.0326**	FSW < SPM			
transform: none	*Light X SPM	1	1.768	1.02	0.3171	4.69	5.53		
C = 0.4356 (ns)	Residual	44	1.727			(0.21)	(0.31)		
d) TTL (mm) – High Is.	Light	1	0.054	0.31	0.5795				
	SPM	1	0.064	0.39	0.5382				
transform: none	*Light X SPM	1	0.115	0.70	0.4094				
C = 0.4207 (ns)	Residual	36	0.164						
Chlorophyll *a*									
e) Chlorophyll *a* (ug cm^{-2}) – Wilkie Is.	Light	1	29.01	1.03	0.4956	Shade		Light	
	SPM	1	15.75	0.56	0.5916	FSW = SPM		FSW < SPM	
transform: none	Light X SPM	1	28.22	4.68	**0.0360**	7.16	6.77	4.07	6.75
C = 0.4453 (ns)	Residual	44	6.03			(0.95)	(0.68)	(0.32)	(0.75)

Variate	Source of variation	df	MS	*F*	*P*	*Post hoc* tests			
f) Chlorophyll *a* (ug cm^{-2}) – High Is.	Light	1	10.69	0.78	0.5401	Shade		Light	
	SPM	1	40.59	2.95	0.3357	FSW = SPM		FSW < SPM	
transform: none	Light X SPM	1	13.77	4.48	**0.0413**	5.74	6.58	3.53	6.72
C = 0.3721 (ns)	Residual	36	3.07			(0.57)	(0.68)	(0.24)	(0.63)
Density symbionts									
g) Symbionts (x10^6 cells cm^{-2}) – Wilkie Is.	Light	1	1.5E+13	4.40	0.2831				
	SPM	1	1.2E+13	3.67	0.3064				
transform: none	Light X SPM	1	3.4E+12	1.97	0.1671				
C = 0.4243 (ns)	Residual	44	1.7E+12						
h) Symbionts (10^6 cells cm^{-2}) – High Is.	Light	1	4.4E+12	4.50	0.2804				
	SPM	1	3.7E+12	3.77	0.3028				
transform: none	Light X SPM	1	9.8E+11	2.54	0.1197				
C = 0.4011 (ns)	Residual	36	3.8E+11						

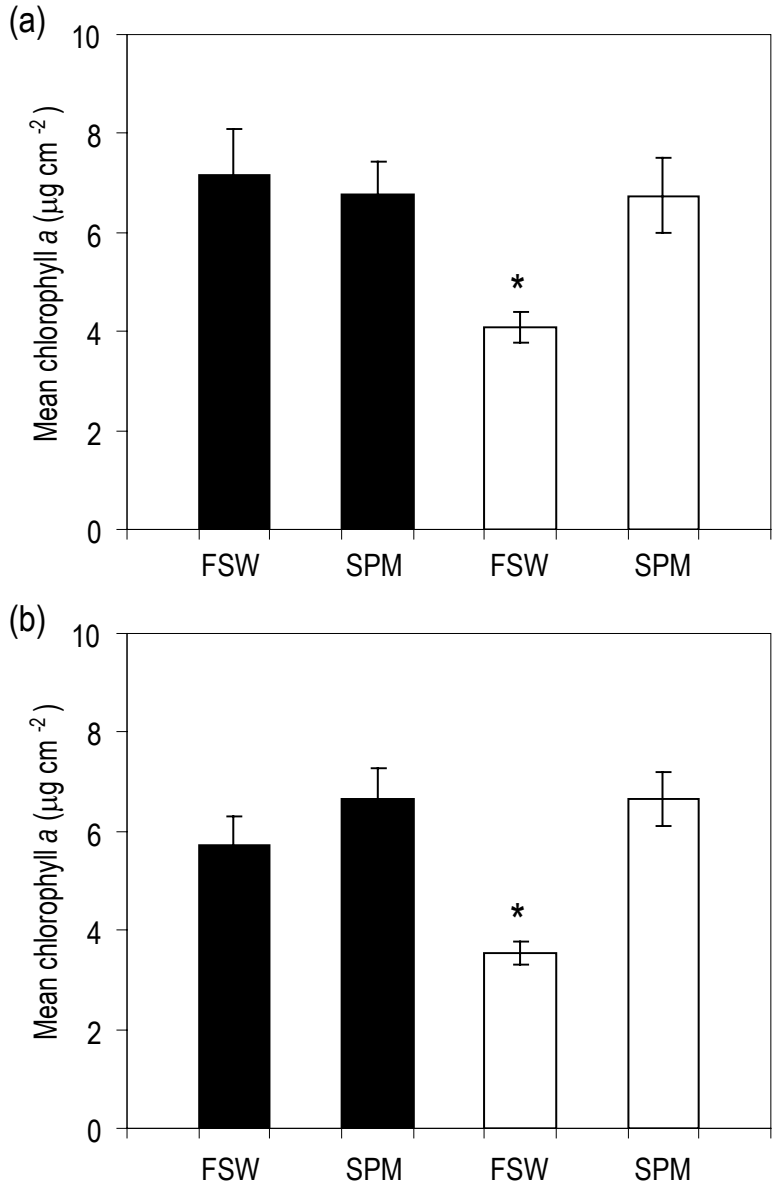

Figure 5.5. Mean concentration (±SE) of chlorophyll *a* in *Porites* nubbins from (a) Wilkie Island (n=12) and (b) High Island (n=10) exposed to different treatments of nutrient and light availability (Experiment 1). Wilkie Island nubbins exposure time was 56 days, High Island was 32 days. Symbols: closed bars = shade; open bars = light; FSW = filtered seawater; SPM = suspended particulate matter.

Experiment 2

In the 4-month field transplantation experiment, approximately 50% of nubbins were retrieved undamaged, while the others showed signs of mortality most likely caused by parrotfish (Scaridae). Whilst this level of mortality precluded more sensitive statistical tests of the effects of water quality on coral colour, enough nubbins were retrieved to pool each of the inner and outer zone treatments, i.e. 9 experimental treatments for each water quality zone. The TLS treatment, i.e. nubbins translocated 25 m from the source colony to examine the effects of Site on the saturation of colour, was not included in the analyses due to a high level of mortality.

In general, there was a decrease in the saturation of colour for nubbins in all experimental treatments sourced from the inner zone (Fig. 5.6). This included treatments that were transplanted to a new water quality zone, i.e. from the inner (elevated nutrients and SPM) to the outer zone (lower nutrients and SPM), but also for the procedural controls that remained in the inner zone. A similar pattern occurred for nubbins in most experimental treatments sourced from the outer zone where there was also a general decrease in the saturation of colour (Fig. 5.6). There were, however, two treatments where the saturation of colour increased during the experiment. Nubbins transplanted from the outer to inner zone (OI treatment) at the same depth commenced the experiment with a colour score of 4.2 $\pm$ 0.1 colour chart units increasing to 4.5 $\pm$ 0.2 colour chart units at the completion of the experiment. The greatest increase in colour saturation occurred for nubbins moved from the outer shallow to the inner deep (OSID treatment) that commenced with a colour score of 3.5 $\pm$ 0.1 colour chart units and increased to 4.6 $\pm$ 0.2 colour chart units by the end of the deployment (Fig. 5.6).

Analysis of chlorophyll *a* per cm^{-2} showed that there was considerable variation within treatments for nubbins from the inner zone but there were significant differences among treatments for outer zone nubbins (Table 5.5). There was more chlorophyll *a* per cm^{-2} in nubbins transplanted from the outer shallow to the inner deep depth (OSID treatment) compared with the other treatments, which were not different from each other (Fig. 5.7). Similarly, the spectral reflectance of the nubbins differed among treatments for the outer zone nubbins but no differences occurred for those from the inner zone (Table 5.5). Nubbins transplanted from the outer shallow to the inner deep depth (OSID treatment) that had responded with an increase in the concentration of chlorophyll *a*, reflected less light compared with nubbins in the other treatments, but no differences occurred among the other experimental treatments (Fig. 5.8).

Table 5.5. Summary of ANOVAs comparing concentrations of pigments and spectral reflectance among experimental treatments for coral nubbins manipulated along a water quality gradient in the Whitsunday Islands. Significant *P*-values given in bold.

Variate	Source of variation	df	MS	*F*	*P*
a) Chlorophyll *a*: inner nubbins	Treatment	5	24.10	1.54	0.1824
	Residual	111	132.30		
b) Chlorophyll *a*: outer nubbins	Treatment	5	119.27	3.22	**0.0121**
	Residual	62	37.09		
c) Reflectance: inner nubbins	Treatment	5	0.0042	1.25	0.2927
	Residual	112	0.0034		
d) Reflectance: outer nubbins	Treatment	5	0.0073	2.69	**0.0289**
	Residual	63	0.0027		

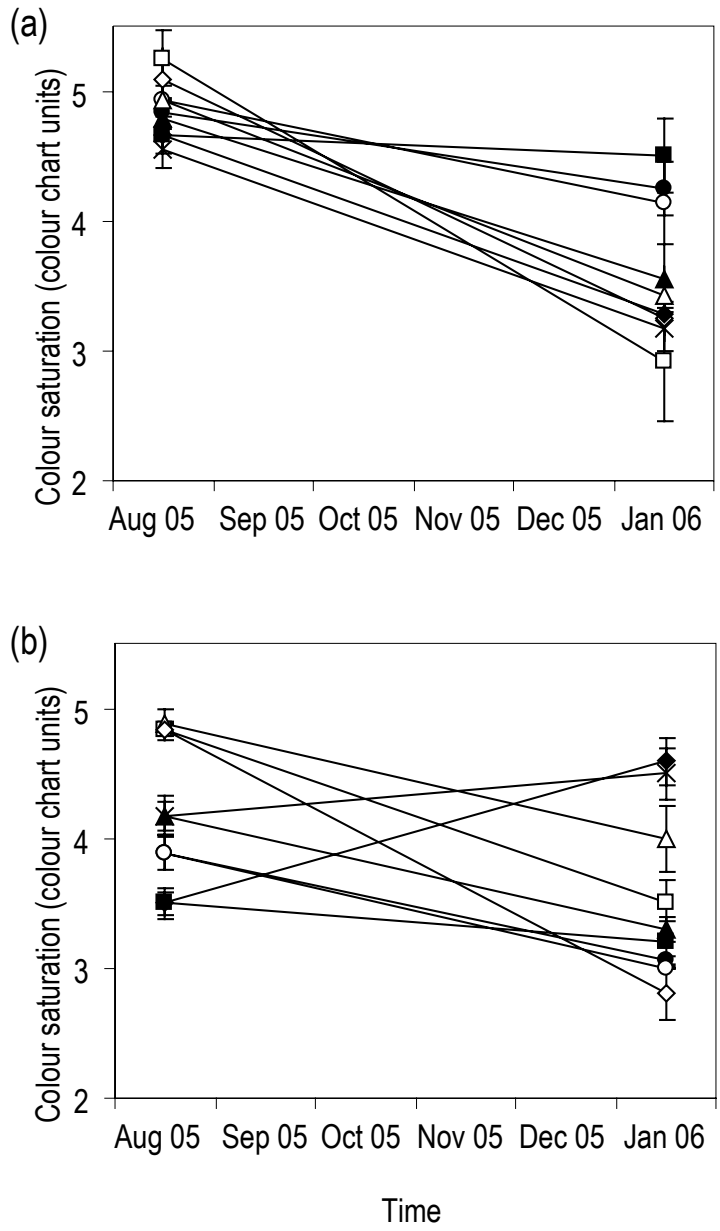

Figure 5.6. Mean saturation of colour (± SE) of coral nubbins sourced from (a) inner zone, and (b) outer zone, and transplanted along a water quality gradient in the Whitsunday Islands. Colour saturation measurements made using Coral Health Monitoring Chart from Siebeck *et al.* (2006). Symbols: ● undisturbed; ○ cored; ▲ moved; □ translocate deep to shallow; ■ translocate shallow to deep; △ translocate reef; ✕ transplant inner to outer/outer to inner; ◆ transplant inner shallow to outer deep/outer shallow to inner deep; ◊ transplant inner deep to outer shallow/outer deep to inner shallow.

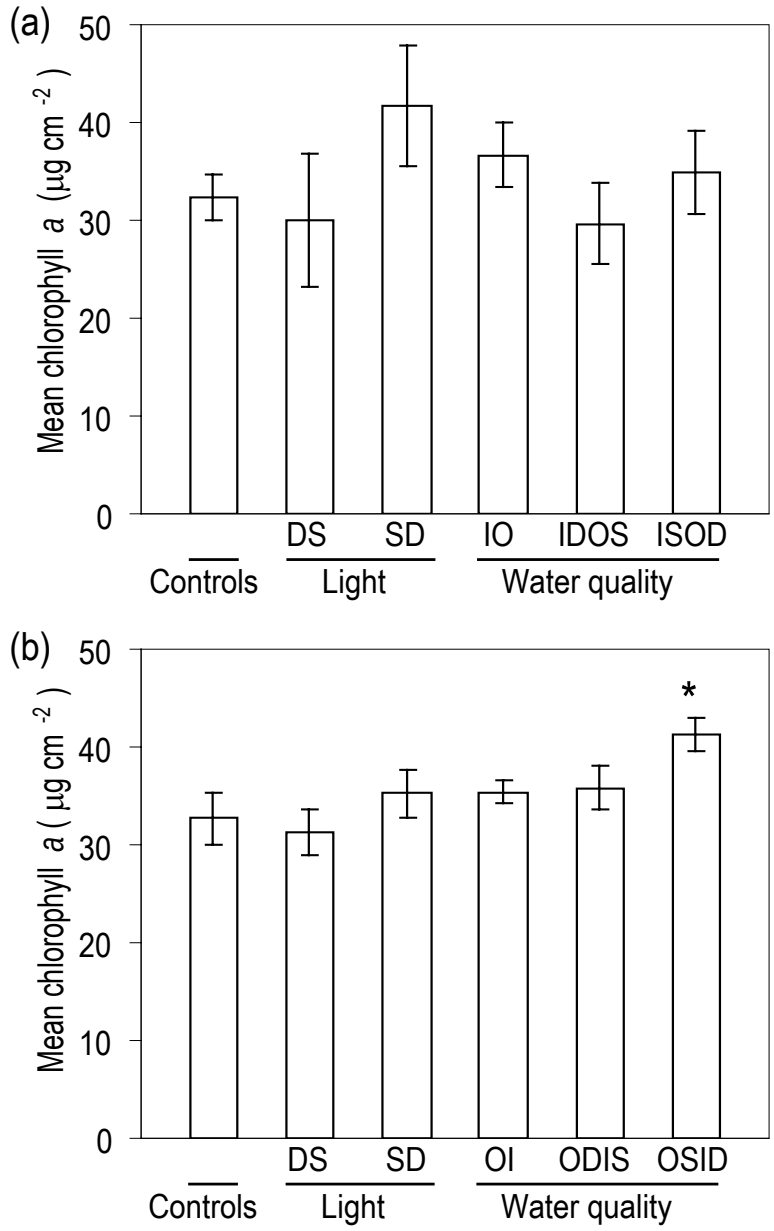

Figure 5.7. Mean concentration of chlorophyll *a* (μg cm^{-2}, ± SE) for coral nubbins sourced from (a) inner zone, and (b) outer zone, and transplanted along a water quality gradient in the Whitsunday Islands. Abbreviations: DS = deep to shallow; SD = shallow to deep; IO = inner to outer; OI = outer to inner; transplant treatments are combinations of these. * denotes statistical significance $P<0.05$.

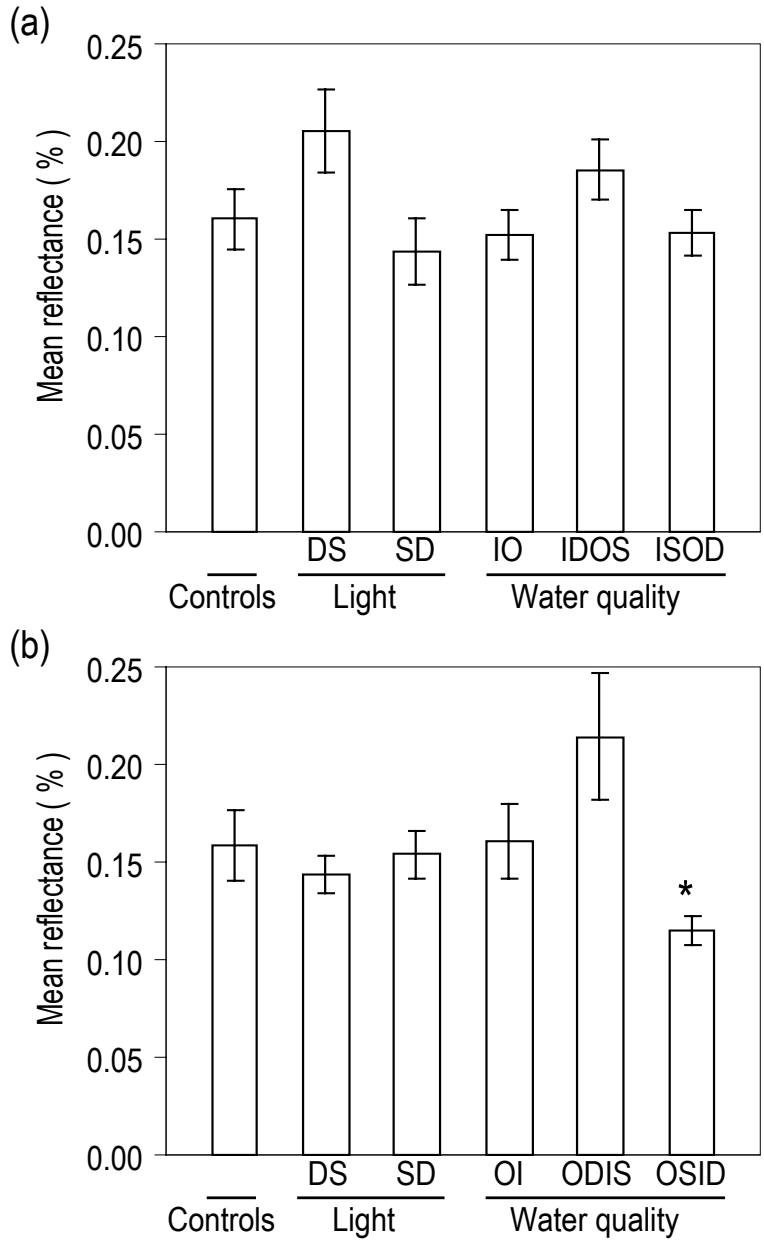

Figure 5.8. Mean reflectance (± SE) of coral nubbins sourced from (a) inner zone, and (b) outer zone, and transplanted along a water quality gradient in the Whitsunday Islands. Abbreviations: DS = deep to shallow; SD = shallow to deep; IO = inner to outer; OI = outer to inner; transplant treatments are combinations of these. * denotes statistical significance $P<0.05$.

5.4 Discussion

Physiological responses in the two scleractinian corals investigated here can be used as bioindicators of differences in water quality over comparatively small spatial scales. In the Whitsunday Islands, the patterns of variability of physiological parameters in massive *Porites* and *P.damicornis* were generally dominated by inconsistent variation among locations and between depths. When this variation existed, however, it was common for the corals sampled from the inner islands to differ significantly from those occurring on fringing reefs of the outer Whitsunday Islands and the nearby mid-shelf reefs. This pattern of variability could potentially be attributed to differences in water quality and was supported by the results of the linear models that showed significant relationships existed between the physiological parameters and a water quality index.

All of the physiological parameters in *Porites* spp. and *P.damicornis* showed significant, but variable, relationships with the water quality index. As the water quality index increases toward the coastal zone, the massive *Porites* become progressively darker in colour with a decreasing thickness of tissue layer. Similarly, in *P.damicornis*, concentrations of chlorophyll *a* and the density of symbionts per cm^{-2} increase, but the density of the skeleton decreases, compared with conspecifics on reefs where the water column is characterised by lower concentrations of nutrients, suspended solids and a greater light availability (Figure 5.). These patterns are consistent with other studies that have found physiological differences including increases for symbiont density and chlorophyll *a* concentrations when corals are exposed to elevated levels of dissolved nutrients (Hoegh-Guldberg and Smith 1989; Stambler *et al.* 1994; Marubini and Davies 1996) or increases in the relative abundance of photopigments in under low irradiance (Falkowski and Dubinsky 1981; Anthony and Hoegh-Guldberg 2003a). Similarly, Risk and Sammarco (1991) suggested that inshore to offshore differences in the skeletal density of massive *Porites* were potentially due to inhibition of calcification due to exposure of nutrients in the coastal zone or by increased light availability on the offshore reefs. There are clear differences in the water column characteristics between inner and outer conditions in the Whitsunday Islands. For example, there was a two to three-fold increase in the nutrient parameters such as concentrations of chlorophyll *a* and total suspended solids, and a corresponding decrease in the irradiance parameters Secchi and optical depth, moving along the gradient from offshore locations toward those in the coastal zone (Chapter 2). Given that nutrient and irradiance parameters are likely to co-vary with increasing distance away from the coast, it is not possible to determine which of these parameters is responsible for the physiological patterns observed in the field gradient study. An important finding, however, was that the physiological differences in two coral species were related to a water quality index spanning a relatively small spatial scale (i.e. ~ 50 km) suggesting that there are physiological features in corals that are sensitive to changes in water quality.

It is noteworthy that the water quality index was derived from data collected from only five surveys and it is possible that relationships between the index and the physiological parameters may have improved, i.e. explained more of the variance, had it been possible to characterise the water column characteristics on more occasions. Nevertheless, the water quality index is an appropriate explanatory variable in the models as other parameters such as distance to the mainland and nearby rivers were correlated with each other making it impossible to separate the effects of one from the other. Other studies have used this approach and identified population and community level responses along water quality gradients (Fabricius and De'ath 2004). The results of this study add a further level of evidence, i.e. a physiological level, to the population and community-level responses reported in other spatial comparisons (van Woesik *et al.* 1999; Fabricius *et al.* 2005), of the effects of changes in water quality on corals and coral reef assemblages in the coastal zone of the GBR.

In Experiment 1, the response of the saturation of colour in massive *Porites* to changes in water quality was rapid and occurred within 10 days of the commencement of dosing with suspended particulate matter. Hoegh-Guldberg and Smith (1989) used a similar experimental approach to examine the effects of ammonium on coral symbionts and reported that corals in the nutrient treatments were darker compared with those in the controls, although this colour response was not quantified. Using a simple Coral Health Monitoring Chart (Siebeck *et al.* 2006), it has been possible to quantify the colour saturation in corals exposed to differing treatments of nutrient and light limitation in the laboratory. Corals in the no SPM, no shade treatments maintained a consistent saturation of colour throughout the experiment, while corals were up to 2 colour chart scores darker after 56 days of exposure to suspended particulate matter and nutrients coupled with reduced light regimes. Moreover, the colour difference among the treatments was detectable as a difference in concentrations of the photopigment chlorophyll *a*. Corals exposed to elevated levels of suspended particulate matter and normal light regimes, which simulated turbidity events on a coral reef such as those that might occur during flood plumes (Devlin *et al.* 2001) or resuspension events (Larcombe *et al.* 1995), contained concentrations of chlorophyll *a* that were comparable to corals placed in both the shaded treatments. Further experiments are required to determine if this response was because of photoacclimation to the reduced light intensity owing to absorption and dispersion of incident light by the suspended particles, or whether it was as a result of increased nutrient availability associated with the sediments (Falkowski and Dubinsky 1981; Dubinsky and Jokiel 1994; Anthony and Hoegh-Guldberg 2003a). Notwithstanding, an important finding from Experiment 1 was that a response to changes in water quality was detected after less than four weeks using both the colour chart and extraction of pigments.

Using an experimental design for a manipulative experiment that incorporated appropriate procedural controls, the results of the tank experiment were further tested under field conditions and confirmed (on a preliminary basis) that coral colour responds to changes in water quality. The limitation to this finding was that a low-level bleaching event (i.e. < 10% of coral cover) occurred in the Whitsunday region during 2005/06 (Great Barrier Reef Marine Park Authority 2006) confounding results that could be attributed to an improvement in water quality, e.g. the response of corals relocated from reefs in the coastal zone to the outer islands that decreased in their colour saturation and became lighter. This may also explain the trend for the procedural controls to become lighter throughout the experiment, although some degree of 'paling' was expected due to seasonal variation in the density of the symbionts (Stimson 1997; Fitt *et al.* 2000). Despite this bleaching event, however, corals in the treatment relocated from the outer shallows (low nutrients, high irradiance) to the inner deep depth (elevated nutrients, low irradiance, Chapter 2) went against this overall trend and increased their saturation of colour and were noticeably darker. This response was measured using the colour charts, and detected as a treatment effect by (i) a greater concentrations of the pigment chlorophyll *a*, and (ii) lower spectral reflectance, of nubbins in this treatment compared with nubbins in the other experimental treatments. A further limitation to Experiment 2 was the mortality of a number of nubbins by grazing from fishes that precluded more sensitive tests of hypotheses about the effects of water quality on physiological responses in *Porites lobata*. Nevertheless, by relocating coral nubbins from an outer zone in the Whitsunday Islands, which are characterised by low levels of nutrients and suspended solids to a nearshore zone where water conditions are more turbid (Chapter 2), and measuring a response to a darker saturation of colour with three different methods, indicates that the saturation of coral colour could be used as a valid 'early warning' bioindicator of the effects of water quality on coral reefs. Further and better experiments are required to confirm this and the results presented here should be tested in the Austral winter when bleaching events are less likely to confound the results, and consideration should be given to the use of barriers to reduce the mortality of the nubbins from grazing by fish. In doing so, consideration would need to be given to the experimental artefacts associated with

the any barriers on the physiological responses in the corals, and accordingly, these would need to be controlled for in the experimental design (e.g. Rodrigues and Hughes 2004).

On the basis of the results from field sampling in the Whitsunday Islands and the manipulative experiments, the physiological indicator that demonstrates the greatest potential for incorporation into monitoring programs is a change in the saturation of coral colour. In the Whitsunday Islands, the strongest correlation (R^2 = 0.78) between the physiological parameters and a water quality index was for colony colour in massive *Porites*. The patterns of variation of most of the other physiological indicators in *P.damicornis* and *Porites* were dominated by inconsistent variation among locations and depths, which was problematic and suggests that some of these indicators might respond to natural differences in the environment as much as they could show a response to a change in water quality. This was not the case, however, for coral colour where significant location effects were detected in the Whitsunday Islands. The *Porites* had a darker saturation of colour at Repulse Island, which is within the coastal zone of the GBR lagoon and nearest the effects of terrestrial runoff from two nearby rivers, compared with the other locations. The model that corals appeared darker in the coastal zone of the Whitsunday Islands due to exposure to nutrients and/or altered light regimes was further supported by the experimental manipulation of suspended particulate matter and light availability, with corals placed in turbid water treatment responding within a short 'response time' by increasing their saturation to a darker colour. The model that changes in the saturation of coral colour could be used as a response indicator to differences in water quality were partly supported by the results of the transplantation experiment in the Whitsunday Islands, in particular, the corals that became darker despite the low-level bleaching event was encouraging, but this needs to be confirmed by experiments at other times of the year and that take into account the potential of mortality due to grazing by fish.

Of the methods that were used to record the colour response, the colour chart developed by Siebeck *et al.* (2006) is arguably the simplest to use. Notwithstanding this, the chart was developed as a tool for assessing bleaching events and based on the principal that a change to a paler colour is related to the expulsion of pigment-containing symbionts when seawater temperatures are elevated beyond the thermal tolerances of the coral holobiont. Prior to this study, little was known about the usefulness of the Coral Health Monitoring Chart for assessing the effects of water quality on coral reefs, although in an assessment of the effects of colony colour on the temperature of the boundary layer surrounding corals, Fabricius (2006) showed that corals on nutrient-exposed nearshore reefs were darker compared with those on oligotrophic offshore reefs of the GBR. Indeed, the results of this study support the hypothesis that the saturation of coral colour does in fact respond to changes in water quality.

5.5 References

Alongi DM, McKinnon AD. 2005. The cycling and fate of terrestrially-derived sediments and nutrients in the coastal zone of the Great Barrier Reef shelf. Marine Pollution Bulletin 51: 239-252

Anthony KRN. 2006. Enhanced energy status of corals on coastal, high-turbidity reefs. Marine Ecology Progress Series 319: 111-116

Anthony KRN, Connolly SR, Willis BL. 2002. Comparative analysis of energy allocation to tissue and skeletal growth in corals. Limnology and Oceanography 47: 1417-1429

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

Anthony KRN, Hoegh-Guldberg O. 2003a. Kinetics of photoacclimation in corals. Oecologia 134: 23-31

Anthony KRN, Hoegh-Guldberg O. 2003b. Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys? Functional Ecology 17: 246-259

Barnes DJ, Lough JM. 1992. Systematic variations in the depth of skeleton occupied by coral tissue in massive colonies of *Porites* from the Great Barrier Reef. Journal of Experimental Marine Biology and Ecology 159: 113-128

Brodie JE, Furnas MJ, Steven ADL, Trott LA, Pantus F, Wright M. 1997. Monitoring chlorophyll in the Great Barrier Reef Lagoon: trends and variability. Proceedings of the 8th International Coral Reef Symposium, Panama. Pp 797-802.

Devlin MJ, Brodie J, Waterhouse J, Mitchell A, Audas D, Haynes D. 2001. Flood plumes in the Great Barrier Reef: spatial and temporal patterns in composition and distribution. Great Barrier Reef Marine Park Authority, Townsville.

Dubinsky Z, Falkowski PG, Porter JW, Muscatine L. 1984. Absorption and utilisation of radiant energy by light- and shade-adapted colonies of the hermatypic coral *Stylophora pistillata*. Proceedings of the Royal Society London, Series B 222: 203-214

Dubinsky Z, Jokiel PL. 1994. Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. Pacific Science 48: 313-324

Fabricius KE. 2006. Effects of irradiance, flow and colony pigmentation on the temperature microenvironment around corals: implications for coral bleaching? Limnology and Oceanography 51: 30-37

Fabricius KE, De'ath G. 2004. Identifying ecological change and its causes: a case study on coral reefs. Ecological Applications 14: 1448-1465

Fabricius KE, De'ath G, McCook L, Turak E, Williams DM. 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Marine Pollution Bulletin 51: 384-398

Falkowski PG, Dubinsky Z. 1981. Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. Nature 289: 172-174

Fitt WK, McFarland FK, Warner ME, Chilcoat GC. 2000. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnology and Oceanography 45: 677-685

Great Barrier Reef Marine Park Authority. 2006. Final Bleaching Summary Report 2005/2006, www.gbrmpa.gov.au/corp_site/info_services/science/climate_change/conditions_report.html

Grover R, Maguer JF, Reynaud-Vaganay S, Ferrier-Pages C. 2002. Uptake of ammonium by the scleractinian coral *Stylophora pistillata*: Effect of feeding, light, and ammonium concentrations. Limnology and Oceanography 47: 782-790

Harland AD, Davies PS, Fixter LM. 1992. Lipid content of some Caribbean corals in relation to depth and light. Marine Biology 113: 357-361

Haynes D, Michalek-Wagner K. 2000. Water quality in the Great Barrier Reef World Heritage Area: Past perspectives, current Issues and new research directions. Marine Pollution Bulletin 41: 428-434

Hoegh-Guldberg O, Smith GJ. 1989. Influence of the population density of zooxanthellae and supply of ammonium on the biomass and metabolic characteristics of the reef corals *Seriatopora hystrix* and *Stylophora pistillata*. Marine Ecology Progress Series 57: 173-186

Jeffrey SW, Humphrey GF. 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie der Pflanzen 167: 191-194

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

Lough JM, Barnes DJ. 2000. Environmental controls on growth of the massive coral *Porites.* Journal of Experimental Marine Biology and Ecology 245: 225-243

Marubini F, Davies PS. 1996. Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. Marine Biology 127: 319-328

Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, Sala E. 2005. Are U.S. Coral Reefs on the Slippery Slope to Slime? Science 307: 1725-1726

R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Risk MJ, Sammarco PW. 1991. Cross-shelf trends in skeletal density of the massive coral *Porites lobata* from the Great Barrier Reef. Marine Ecology Progress Series 69: 195-200

Rodrigues M, Hughes TP. 2004. Effects of overfishing on coral dynamics: A large-scale experimental approach. 10th International Coral Reef Symposium, Okinawa, Japan.

Siebeck UE, Marshall NJ, Klueter A, Hoegh-Guldberg O. 2006. Monitoring coral bleaching using a colour reference card. Coral Reefs 25: 453-460

Stambler N, Cox EF, Vago R. 1994. Effect of ammonium enrichment on respiration, zooxanthellar densities, and pigment concentrations in two species in Hawaiian corals. Pacific Science 48: 284-290

Stimson J. 1997. The annual cycle of density of zooxanthellae in the tissues of field and laboratory-held *Pocillopora damicornis* (Linnaeus). Journal of Experimental Marine Biology and Ecology 214: 35-48

Stimson J, Kenzie III RA. 1991. The temporal patterns and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linneaus) under nitrogen-enrichment and control conditions. Journal of Experimental Marine Biology and Ecology 153: 63-74

van Woesik R, Tomascik T, Blake S. 1999. Coral assemblages and physio-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. Marine and Freshwater Research 50: 427-440

Veron JEN. 2000. Corals of the World. Australian Institute of Marine Science, Townsville, Queensland, Australia

Chapter 6: Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis

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6.1 Introduction

Around the world, water quality in coastal areas is changing in response to rapidly increasing fertiliser use and land clearing (Vitousek *et al.* 1997; Tilman *et al.* 2001; Smith *et al.* 2003). Annual nitrogen fertiliser use has increased globally more than six-fold since 1960 (Matson *et al.* 1997), land clearing continues at a rate of 1% of the earth's surface per year (GESAMP 2001), and coastal urbanisation is expanding disproportionally to human population growth. Oxygen-depleted seafloor zones, caused primarily by river-borne agricultural nitrogen and phosphorus, have doubled in number and expanded in size since 1990, presenting clear evidence that many coastal waters are becoming more eutrophic (GESAMP 2001). Coastal coral reefs, like other marine coastal ecosystems, are increasingly exposed to growing loads of nutrients, sediments and pollutants discharged from the land. Terrestrial runoff is therefore a growing concern for most of the 104 nations endowed with coral reefs (Bryant *et al.* 1998; Spalding *et al.* 2001).

Field studies have provided a large body of information showing that sedimentation, nutrient enrichment and turbidity can degrade coral reefs at local scales (Table 6.1). At regional scales, it has often been difficult to assess causal relationships between increasing terrestrial runoff and reef degradation, because pollution effects and other disturbances are typically confounded, historical data are often missing, and reef communities change naturally along gradients from oceanic conditions (low siltation, high water clarity, generally low nutrient levels except during upwelling periods) to terrestrially influenced conditions (fluctuating salinity, variable or high silt and nutrient levels, variable or reduced water clarity). As nutrients increase, coral reef communities change from dominance of nutrient-recycling symbiotic organisms such as corals (in oligotrophic oceanic waters), to increasing proportions of macroalgae (on eastern continental margins naturally exposed to river runoff), and further to heterotrophic filter feeders (in nutrient-enriched areas of upwelling or lagoons) (Birkeland 1987). Although coastal coral reefs can flourish at relatively high levels of particulate matter and siltation (Fabricius *et al.* 2005), they tend to be restricted to the upper 4 to 10 m depth of well-flushed wave-sheltered locations in turbid water, while extending to >40 m in clear oceanic waters (Yentsch *et al.* 2002).

This review compiles the current state of knowledge on runoff-specific responses in coral reefs, in order to aid assessment of the effects of terrestrial runoff at regional scales. Inorganic nutrients and particulate material, although not 'classical' pollutants, are arguably the most important contaminants at national and regional levels (GESAMP 2001), and this review will focus on assessing the effects of these materials on reef communities. However, contamination by pesticides, heavy metals, hydrocarbons or other human-made pollutants can also significantly affect the health of exposed reefs at local scales (Guzman and Holst 1993). For example, heavy metals such as copper and zinc and some hydrocarbons have been linked to reduced fertilization, fecundity and growth in adult corals (Heyward 1988; Brown 1987; Loya and Rinkevich 1987; GESAMP 2001). Some herbicides (e.g. diuron and atrazin) cause rapid (but reversible) photophysiological stress in corals after short-term exposure at environmentally relevant concentrations of <1 $\mu g\ L^{-1}$ (Owen *et al.* 2003; Jones and Kerswell 2003; Jones *et al.* 2003; Negri *et al.* 2005); their effects at chronic low-level exposures are still largely unknown. Other studies, too numerous to be listed here, document the uptake of a variety of human-made pollutants by adult corals; the effects of these substances on coral reefs are beyond the scope of this review.

Table 6.1. List of some of the more comprehensively documented field assessments on the effects of enhanced terrestrial runoff, and other forms of pollution, on the ecology of coral reefs.

Location	Agent	Response	Source
Northern Gulf of Aqaba (Eilat), Red Sea	50% increase in nutrients from floating fish farms	50% coral mortality from benthic algal blooms, 3-4 fold reduced reef calcification, 50% increased P/R ratio.	Loya, 2004
	Sewage discharge, spillage of phosphate dust	Increased algal growth trapping sediment; four-fold increased mortality in *Stylophora pistillata,* possibly from reduced light, inhibition of calcification, and increased sedimentation.	Walker and Ormond, 1982
Reunion Island, Indian Ocean	Coastal urbanisation, groundwater enriched with nutrients from untreated sewage	Higher coral cover, coral diversity, fish diversity and density of sea urchins, and lower macroalgal density on reefs away from nutrient enrichment and in the 1970s before nutrient enrichment, than on nutrient-enriched reefs. High bioerosion, calcification slower than reef erosion on nutrient enriched reefs.	Cuet *et al.*, 1988; Montaggioni *et al.*, 1993; Naim, 1993; Chazottes *et al.*, 2002
Hong Kong	Excess pollutants, nutrients, sediment dredging	Low coral recruitment, few zooxanthellate octocorals, disappearance of giant clams (*Tridacna* spp.), high bioerosion.	Morton, 1994; Hodgson and Yau, 1997
Japan	Eutrophication and sedimentation	Declining coral cover.	Shimoda *et al.*, 1998
	Gradients away from rivers	Change in coral community composition away from source.	West and Van Woesik, 2001
Philippines	Excess sedimentation from logging	Declining coral cover, declining biodiversity due to disappearance of sediment-sensitive species over 12 months, inhibition of coral settlement.	Hodgson, 1990a; Hodgson and Walton Smith, 1993
Indonesia	Excess nutrients and sedimentation	Low coral cover, reduced coral diversity, unaltered vertical extension but low skeletal density in massive corals, increased bioerosion.	Edinger *et al.*, 2000; Tomascik *et al.*, 1997; Edinger *et al.*, 1998; Holmes *et al.*, 2000
Great Barrier Reef	Gradient in nutrients and turbidity	Increased macroalgal cover and richness (esp. red and green macroalgae), reduced octocoral richness.	Fabricius and De'ath, 2004; Fabricius *et al.*, 2005;
	Gradient away from river	Reduced coral cover, richness; increased filter feeders and macroalgae near source.	van Woesik *et al.*, 1999
	Turbidity	Decreasing richness of zooxanthellate octocorals.	Fabricius and De'ath, 2001b
	Inshore-offshore gradient, terrestrial runoff	Increasing density of internal macro-bioeroders towards the coast.	Hutchings and Peyrot-Clausade, 2005

Location	Agent	Response	Source
	Sedimentation gradient	Decreasing cover of crustose coralline algae.	Fabricius and De'ath, 2001a
Kanehoe Bay, Hawaii	Nutrients	Reduced coral cover, increased filter feeders, increased macroalgal cover.	Smith *et al.*, 1981; Hunter and Evans, 1995; Stimson and Larned, 2000; Stimson *et al.*, 2001
Barbados	Eutrophication gradient	Photosynthetic pigments increase with increasing nutrient enrichment. Convex modal responses in gross photosynthesis, respiration, linear extension, calcification (enhanced by nutrients, depressed by turbidity).	Marubini, 1996; Tomascik and Sander, 1985; Tomascik, 1990
		Reduced species diversity, probably due to differences in sediment rejection abilities, combined with feeding and reproductive strategies, altered community structure; increased bioerosion in coral rubble.	Tomascik and Sander, 1987b; Holmes, 2000
		Reduced gamete formation, larval development and settlement, reduced recruit and juvenile density and diversity, juveniles larger, increased juvenile mortality.	Tomascik and Sander, 1987a; Tomascik, 1991; Hunte and Wittenberg, 1992; Wittenberg and Hunte, 1992
Grand Cayman Island	Untreated fecal sewage, six-fold increased bacterial biomass	Five-fold increased internal bioerosion by the boring sponge *Cliona delitrix*.	Rose and Risk, 1985
Costa Rica (2 sites)	Sedimentation	Low live coral cover, low species diversity, and large average colony diameters, high acid-insoluble residues incorporated in skeleton on exposed reef.	Cortes and Risk, 1985
Brazil (2 sites)	Eutrophication	High macroalgal abundances, high density of heterotrophs.	Costa Jr *et al.*, 2000
U.S. Virgin Islands	Turbidity, sedimentation	Coral-growth rates determined by depth, light, turbidity and sedimentation.	Hubbard and Scaturo, 1985; Hubbard, 1986
Puerto Rico	Turbidity, sedimentation	Reduced coral cover and diversity.	Loya, 1976

This paper systematically reviews and synthesises the available information on the direct effects of terrestrial runoff on (1) calcification, tissue growth, zooxanthellae populations and photosynthesis in adult hard corals, (2) the six main stages of coral reproduction and recruitment, and (3) six groups of other reef organisms that affect hard coral abundances. The latter group includes those organisms that affect coral larval settlement, bioeroding filter feeders that weaken the structural strength of reefs, macroalgae, heterotrophic filter feeders and octocorals competing for space with corals, disease pathogens, and coral predators. Responses of each of these groups are assessed separately against exposure to the four main water quality parameters, namely: (1) dissolved inorganic nutrients, (2) suspended particulate organic matter, (3) light reduction from turbidity and (4) sedimentation. This separation disregards additive or synergistic effects, but helps to understand the mechanisms for change in the field where many contaminants and responses co-occur. Furthermore, the paper identifies geographic and biological properties influencing the level of resistance and resilience of reefs to degradation.

6.2 Direct effects of terrestrial runoff on hard corals: (1) Colony calcification, tissue growth and symbiosis

Dissolved inorganic nutrients

Considerable effort has gone into experiments studying the direct effects of elevated dissolved inorganic nitrogen (DIN, as nitrate or ammonium) and phosphate (DIP) on coral calcification, tissue growth and zooxanthellae. Table 6.2a, and detailed reviews by Dubinsky and Stambler (1996) and Szmant (2002) show that most experiments were conducted at environmentally unrealistically high levels, and that significant inconsistencies exist across studies that are as yet unresolved. Many studies found that high levels of DIN and DIP both reduce calcification up to 50%, while other studies found no change in growth rates, or reported slightly increased rates of calcification and linear extension but reduced skeletal densities (Table 6.2a). Effects of DIN on tissue growth and composition vary across studies, with some reporting reduced lipids (Koop *et al.* 2001), and others finding enhanced zooxanthellae protein but unaltered host protein (Marubini 1996). Increased DIP appears to have little effect on tissue growth. Most studies found that increased DIN increases zooxanthellae density, increases the contents of nitrogen and chlorophyll a per zooxanthellae, and increases photosynthetic rates. In contrast, high levels of DIP did not affect zooxanthella densities. In experimental studies, colony survival was generally unaffected by DIN and DIP, while coral mortality increased, for unknown reasons, in one species after a 1-years field exposure to high daily pulses of both DIN and DIP (Koop *et al.* 2001); however, such high and frequent nutrient pulses are unlikely to be encountered in nature for sustained periods except near sewage outfall sites.

Zooxanthellae are typically nitrogen-limited at high irradiance when ample photosynthetically fixed carbon is available (C / N ratios are up to 30), whereas they may not be nitrogen-limited at lower irradiance (C / N ratios about 10; Falkowski *et al.* 1984; Dubinsky and Jokiel 1994). Zooxanthellae densities increase in response to enhanced DIN availability because this nutrient is preferentially used for zooxanthellae growth rather than the growth of host tissue (in contrast to nutrients derived from zooplankton feeding which increase both tissue and zooxanthellae growth; Dubinsky and Jokiel 1994). Reduced calcification at elevated DIN has been explained as follows: zooxanthellae populations increase after release of N limitation, these cells have preferential access to the available CO2 which they use for photosynthesis, hence less CO2 is available for calcification and CO2 becomes a limiting factor (Marubini and Atkinson 1999; Marubini and Thake 1999). Evidence for this hypothesis is provided by data that show that DIN causes no growth reduction in the presence of high levels of bicarbonate (Marubini and Thake 1999). Reduced calcification at higher DIP availability seems to ce caused by another, as yet not fully understood mechanism (Marubini and Davies 1996). Hypotheses focus on the reduced chemical CaCO3 crystal formation in the presence of phosphate (Simkiss, 1964), or experimental artifacts based on lowered pH from using unbuffered PO_4. Possibly due to the presence of

two different mechanisms, simultaneous increases of DIN and DIP generally do not result in interactive effects on calcification rates (Table 6.2a, Marubini and Davies 1996).

In the field, both DIN and DIP are quickly taken up by phytoplankton and bacteria and benthic food webs. Hence elevated nutrients are available in their dissolved inorganic form only for short periods of time over relatively limited areas. Severe direct effects of dissolved inorganic nutrients on corals appear restricted to heavily polluted, poorly-flushed locations such as semi-enclosed lagoons and bays, where they are linked to reduced reef calcification, coral cover and biodiversity (Table 6.1). Away from the coast, regions that regularly experience the upwelling of cool waters (i.e., rich in dissolved inorganic nutrients but no sedimentation or light reduction) have also been used to assess the effects of DIN and DIP on calcification. Coral calcification can be up to 50% reduced in upwelling regions, which has been attributed to elevated nutrients as well as to cool temperatures (Kinsey and Davies 1979; Wellington and Glynn 1983). Reef formation is noticeably restricted in places where upwelling is a common occurrence, such as along western tropical and subtropical land masses (Birkeland 1987; Achituv 1990). This has lead to the conclusion that reduced calcification from exposure to periodic or chronically elevated dissolved inorganic nutrients can substantially alter coral populations and communities (Kinsey and Davies 1979; Hallock 1988; Wilson *et al.* 2003); however cool temperatures may to a large part explain such low calcification (e.g. calcification declines by 50% with every 3 degrees temperature in massive *Porites*; Lough and Barnes 2000).

In summary, the available information suggests that short-term exposure to high levels of unprocessed DIN and DIP does not kill or greatly harm individual coral colonies, however chronically increased levels of dissolved inorganic nutrients may alter reef metabolism and reef calcification sufficiently to cause noticeable changes in coral communities. Existing data indicate (Fig. 6.1) that: (a) there is strong evidence that zooxanthellae numbers, chlorophyll per unit surface area, and photosynthetic rates increase with increasing DIN (but not DIP), affecting the transfer of energy, CO_2 and nutrients between zooxanthellae and host; (b) there is little evidence that dissolved inorganic nutrients alter tissue thickness, lipids or coral protein per unit surface area; and (c) while some studies found increased or unaltered skeletal growth (measured as linear skeletal extension, skeletal density and/or calcification), many controlled experimental studies found a reduction in growth at elevated levels of DIN and/or DIP. Combining the few existing physiological data with environmental data leads to the suggestion that coral growth (calcification) declines gradually with increasing dissolved inorganic nutrient availability (Fig. 6.2a), but levels of dissolved inorganic nutrients will often not greatly increase along pollution gradients. In reality, response curves are likely to be more complex, for the following reasons: (1) there are complex interactions between the growth of tissue, zooxanthellae and calcification, (2) nutrient limitation occurs predominantly at high irradiance where carbon is available in overabundance, hence nutrient addition may be only of consequence in high-light environments; (3) other limitations such as that of CO_2 co-occur; and (4) nutrient uptake rates are partly mass transfer limited, hence not only a function of concentrations but also of water currents (Hearn *et al.*, 2001). All these factors are insufficiently considered in most experimental studies, and may contribute to explaining the inconsistencies between results.

Table 6.2. List of some representative studies of direct effects of terrestrial runoff on adult corals (see also Figs. 6.1 and 6.2).

Parameter	Response	Source
a) Enrichment with dissolved inorganic nutrients		
NH_4, NH_4 plus PO_4^{3-}	Increased zooxanthellae density, increased protein synthesis by zooxanthellae.	Muscatine *et al.*, 1989
NH_4 (15 μM)	After 8 weeks, increased zooxanthellae density, increased chlorophyll and N per zooxanthella.	Snidvongs and Kinzie, 1994
NO_3 (0, 1, 2, 5, 20 μM)	Calcification decreases with increasing NO_3 to 50% of controls, effects significant at ≥1 μM. After 30 - 40 days: at ≥1 μM, increased N per zooxanthellae, increased zooxanthellae density. At ≥5 μM NO_3, increased zooxanthellae size, chlorophyll per zooxanthellae, photosynthesis, increased coral protein through greater zooxanthellae biomass. At 20 μM NO_3, 30% increased chlorophyll and zooxanthellae density, reduced respiration per unit protein.	Marubini, 1996
NH_4 (10 μM and 20 μM)	After 9 weeks: Unaltered buoyant weight gain at 10 μM, reduced buoyant weight gain (-60%) at 20 μM.	Ferrier-Pages *et al.*, 2000
NO_3 (2 μM)	No change in zooxanthellae density or rate of photosynthesis. Reduced buoyant weight gain (-34%) after 3 weeks.	Ferrier-Pages *et al.*, 2001
NH_4 (10 or 20 μM)	Inconsistent effects on linear extension and buoyant weight after 1 year: 10 to 20% reduction, or no effect, or slight increase. Reduced lipids.	Koop *et al.*, 2001
NH_4	Increased zooxanthellae density, chlorophyll concentration. Decreased linear extension.	Stambler *et al.*, 1991
NO_3 (15 μM)	After 2 weeks, reduced primary production, unaltered zooxanthellae density and chlorophyll concentrations. Temperature effects enhanced by presence of nitrate.	Nordemar *et al.*, 2003
PO_4^{3-} (2 μM)	Increased photosynthesis, reduced calcification.	Kinsey and Davies, 1979
PO_4^{3-}	No effect on zooxanthellae density or their protein production.	Muscatine *et al.*, 1989
PO_4^{3-} (1.2 μM)	Slowed calcification, unaltered zooxanthellae density, lower C and P per zooxanthella.	Snidvongs and Kinzie, 1994
PO_4^{3-} (0, 0.2, 1, 5 μM)	After 30 days: no change in photosynthesis, organic productivity, zooxanthellae density or size, tissue biomass; calcification up to 20% decreased in one species with increasing PO_4, unaltered in another.	Marubini, 1996
PO_4^{3-} (2 μM)	After 9 weeks, reduced buoyant weight gain (-60%), increased gross photosynthesis (up to +150% increase).	Ferrier-Pages *et al.*, 2000

Parameter	Response	Source
PO_4^{3-} (2 or 4 μM)	Inconsistent effects on growth rates after 1 year: increased calcification, linear extension and/or reduced skeletal density in some species. Increased lipids.	Koop *et al.*, 2001
PO_4^{3-}	No effects on zooxanthellae density or linear extension.	Stambler *et al.*, 1991
NH_4 (10 or 20 μM) plus PO_4^{3-} (2 μM)	Reduced buoyant weight gain (-60%), increased gross photosynthesis (up to +150% increase).	Ferrier-Pages *et al.*, 2000
NH_4 plus PO_4^{3-} (20 and 4 μM)	Increased mortality in *Pocillopora damicornis* after 1 year.	Koop *et al.*, 2001
b) Enrichment with suspended particulate matter		
Increased particulate and dissolved nutrients from fish excretions	Increased linear extension.	Meyer and Schultz, 1985
Artemia food	No effect on density of zooxanthellae.	Muscatine *et al.*, 1989
Particulate and dissolved nutrients released from fish farm	In adult corals, increased growth, oocyte and testes numbers, unaltered survival. In small coral fragments, reduced growth probably due to physical effects (burial by settled particulate matter, light reduction).	Bongiorni *et al.*, 2003b; Bongiorni *et al.*, 2003a
Suspended particulate matter (SPM), sedimentation, eutrophication gradient	Increased linear extension at moderate SMP, reduced linear extension at high SMP due to smothering, reduced light levels and reduced zooxanthellae photosynthesis. Small average colony size. No effect on partial mortality.	Tomascik and Sander, 1985; Lewis, 1997
1-32 mg l^{-1} SPM	Increased SPM feeding, covering up to 50% carbon and 30% nitrogen required for tissue growth at high particle concentrations. No effect on calcification.	Anthony, 1999
1-16 mg l^{-1} SPM	After 4 weeks exposure: unaltered calcification. Increased tissue biomass but unaltered lipids in one species; convex modal change in tissue biomass and lipids in response to SPM in a second species.	Anthony and Fabricius, 2000
Cross-self gradient	Increased linear extension, reduced skeletal density towards inshore environments. Highest annual calcification inshore, lowest offshore.	Lough and Barnes, 1992
c) Light reduction from turbidity		
Reduced light, excess phosphate, sedimentation	Reduced calcification, increased mortality.	Walker and Ormond, 1982

Parameter	Response	Source
Turbidity	Changed coral community structure and life forms, reduced species richness, compressed depth zonation.	Loya, 1976; Acevedo and Morelock, 1988; Fabricius and De'ath, 2001b; Crabbe and Smith, 2002
Shading	After 5 weeks, reduced growth, net primary productivity and respiration. Altered community structure after bleaching and death in several coral species.	Rogers, 1979
Turbidity	High turbidity (28-30 NTU) increased mucus production, depressed P:R ratio to below 1.0, possibly due to increased respiration.	Telesnicki and Goldberg, 1995
Shading (plus 1-16 mg l^{-1} SPM)	After 4 weeks exposure: reduced calcification, reduced tissue biomass, reduced lipids in 2 species. In 1 species, feeding on 16 mg L^{-1} SPM annulled shading effects.	Anthony and Fabricius, 2000
d) Sedimentation		
Low sedimentation	Increased respiration, reduced net photosynthesis; Species-specific rejection efficiency.	Abdel-Salam *et al.*, 1988
Sedimentation	Coral cover and coral species diversity increase with distance from the sediment source. Partial or total burial of colonies, bleaching and surface colonisation by filamentous blue-green algae.	Acevedo and Morelock, 1988
Sedimentation	Low/brief sedimentation: reduced photosynthetic yield; high/prolonged sedimentation: loss of zooxanthellae, partial mortality, but species-specific tolerances.	Philipp and Fabricius, 2003
Sedimentation (30 mg cm^{-2})	Species-specific rejection efficiency.	Hodgson, 1990b,
Sedimentation (50-1000 mg cm^{-2} of four particle sizes, and 200 mg cm^{-2})	Species-specific rejection efficiency: rejection rates positively correlated with calice size, and faster for medium-fine (63 - 250 μm) than for coarse (500 - 1000 μm) sediment. Bleaching and partial mortality within 48 h in some species, but clearance times generally <2 days.	Stafford-Smith and Ormond, 1992; Stafford-Smith, 1993
Sedimentation (up to 14 mg cm^{-2} d^{-1})	Passive sediment removal more successful for fine grain sizes, tall polyps, and convex colonies, active removal independent of colony morphology.	Lasker, 1980
Heavy sedimentation (>10 mg cm^{-2} d^{-1} and >10 mg l^{-1})	Reduction in coral species, live coral cover, coral growth rates, calcification, net productivity of corals, and rates of reef accretion; increased proportion in branching forms. Species-specific capabilities for particle rejection and for surviving lower light levels.	Rogers, 1990
High sedimentation	Reduced linear extension: growth inversely related to sediment resuspension.	Cortes and Risk 1985; Dodge *et al.*,1974
Sedimentation	Loss of zooxanthellae, reduced calcification.	Bak, 1978

Parameter	Response	Source
Sedimentation	Reduced mean colony sizes (through stunted growth and/or reduced life expectancy).	Van Woesik and Done, 1997
Sedimentation	Increased mean colony sizes (through reduced recruitment).	Wesseling *et al.*, 2001; Cortes and Risk, 1985; Tomascik and Sander, 1985
Terrestrial runoff and sedimentation	Partial mortality: High proportion of injured or algae infested corals, and/or high soft coral cover, and/or high proportion of rocky substrate suitable for, but unoccupied by, living corals.	van Katwijk *et al.*, 1993
Sedimentation	Partial mortality: Colony lesion densities increase with sedimentation, wave exposure, colony size, and intensity of human reef exploitation. Colony size, live coral cover and *Acropora* cover decrease with intensity of human reef exploitation.	Wesseling *et al.*, 2001
Sedimentation	Reduced coral cover.	Loya, 1976; Cortes and Risk, 1985; Acevedo and Morelock, 1988; Brown *et al.*, 1990; Chansang *et al.*, 1981; Morelock *et al.*, 1983
Sedimentation	Changed coral community structure and life forms, reduced species richness.	Loya, 1976; Morelock *et al.*, 1983; Pastorok and Bilyard, 1985; Acevedo and Morelock, 1988; Rogers, 1990; Brown *et al.*, 1990; Edinger *et al.*, 1998; West and Van Woesik, 2001

	DIN	DIP	POM	Light reduction	Sedimentation
Calcification	↓	↓	↑	⬇	⬇
Tissue thickness	–	–	↑	↓	⬇
Zooxanthellae density	⬆	–	↑	↑	↓
Photosynthesis	↑	↑	↑	⬇	⬇
Adult colony survival	–	–	↑	↓	⬇

Figure 6.1. Synthesis of documented direct effects (Tables 6.1 and 6.2) of the four main parameters of terrestrial runoff on the growth and survival in adult corals, based on published studies or known biological properties and processes. The arrows indicate the relative strength and direction of the response (arrows pointing up or down = increasing or decreasing, thick arrow = strong, medium = moderate, thin = weak effect); a dash indicates that a response is unlikely; empty cells indicate that insufficient data are available.

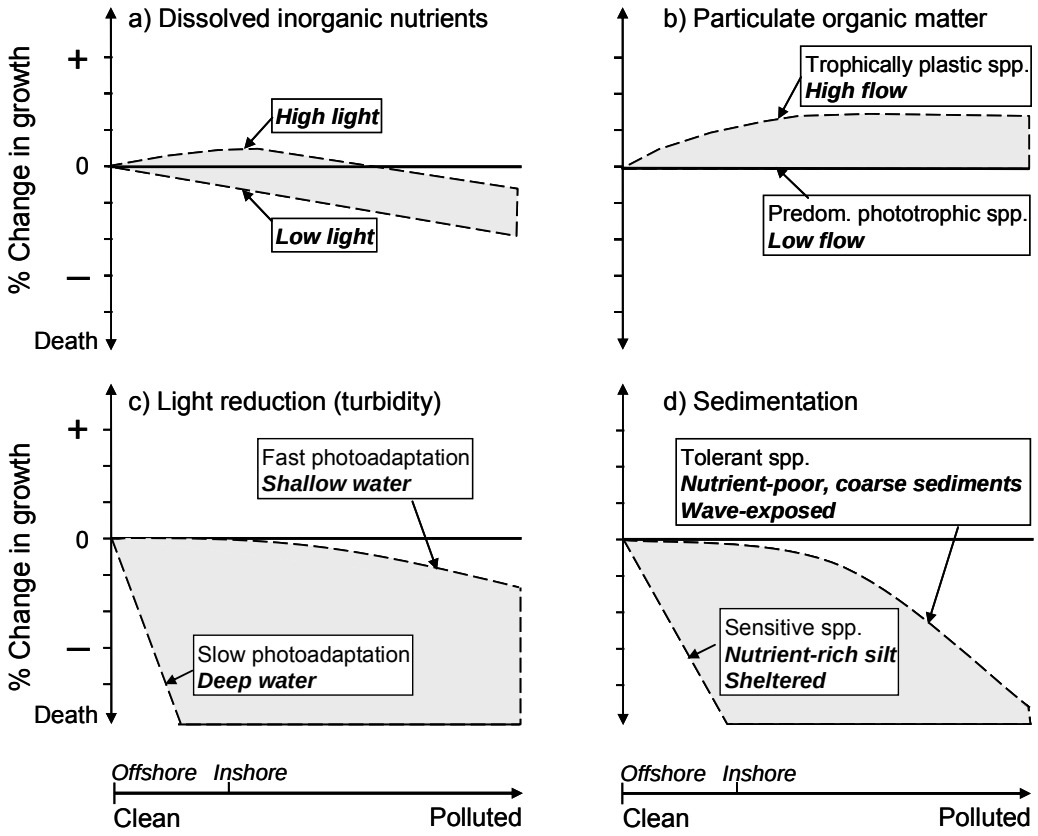

Figure 6.2. Schematic representation of direct effects of terrestrial runoff on coral growth (measured as change in calcification and/or linear extension, i.e., addition of skeletal biomass) and survival along environmental gradients. Plotted are changes in coral growth in response to a) uptake of dissolved inorganic nutrients, b) feeding on suspended particulate organic matter, c) light reduction from turbidity, hence reduction in gross photosynthesis, and d) disturbance by sedimentation. The x-axis represents a hypothetical water quality gradient from offshore water quality to polluted conditions, also indicting the relative positions of offshore and inshore conditions unaltered by human activities. The y-axis scale represents relative units of changes in growth, with severe long-term reduction in growth effectively representing 'colony death'. Grey shading is used to approximate typical response envelopes due to species-specific differences (normal font) and local environmental conditions (bold italic font).

Particulate organic matter

Particulate organic matter (POM) greatly contributes to nutrient availability in many coastal regions, because a majority of nutrients are discharged to the marine environment in particulate form, and much of the dissolved inorganic nutrients can be taken up and converted into particulate form within hours to days (Furnas 2003). Suspended particulate matter in areas of high sediment resuspension can have a nutrient content of >5%, either contained in the bacteria, phytoplankton, zooplankton and detritus, or absorbed to the surfaces of fine inorganic particles; the nutrient content is even higher offshore where less inert material is suspended from the seafloor. POM can be used by a range of benthic organisms including corals (Lewis 1976; Anthony 1999). However the ability to utilize POM varies widely between coral species, and a number of species are naturally restricted to clear water habitats (Veron 2000). Depending on species, feeding saturation may occur at low to moderately high levels of POM: some species become mixotrophic at high turbidity, while others remain mostly phototrophic and gain a small proportion of their energy demand from particle feeding (Anthony and Fabricius 2000). Rates of POM intake furthermore depend on water current speeds, with intake rates being generally higher at moderate to fast flow than in sheltered locations.

Moderate loads of POM have been linked to increases in tissue thickness in some species (Tables 6.1, 6.2b). Linear skeletal extension may double while skeletal density may be up to 20% reduced in response to POM feeding, with varying effects on overall calcification rates. In fragile branching species, increased linear skeletal extension may be partly offset by greater breakage due to reduced skeletal density. Zooxanthellae densities appear to increase to a lesser extent in response to organic enrichment than in response to dissolved inorganic nutrients, possibly because POM promotes the growth both of host and zooxanthellae, in contrast to dissolved inorganic nutrients that are preferentially used for zooxanthellae rather than host tissue growth (Dubinsky and Jokiel 1994).

In the field, coral calcification and growth appears to change in a modal fashion along eutrophication gradients: in areas of intermediate turbidity where particulate and dissolved nutrient loads were high, corals had higher concentration of photosynthetic pigments, calcification, gross photosynthesis and respiration compared to a cleaner site (Tomascik and Sander 1985; Marubini 1996). At the most eutrophic site, pigment concentration was even higher than at the intermediate site, however light reduction from turbidity annulated the growth advantages from POM feeding, consequently calcification, gross photosynthesis and respiration was lower at the most eutrophic site than at the intermediate site (Marubini 1996). Photosynthetic pigment concentrations in corals have therefore been suggested as the most linear and hence most useful early-warning indicator for nutrification (Marubini 1996).

In summary, the limited existing data suggest that moderate concentrations of POM can provide substantial energy and growth benefits for some, but not all coral species, especially at high water flow and high irradiance (Fig. 6.2b). Overall, of the four parameters of terrestrial runoff considered, POM is the one parameter that can enhance growth in some species, at moderate levels compensating for growth reduction from the other three parameters. At higher levels of POM, feeding saturation prevents additional energy gains, while losses from the associated light reduction, dissolved inorganic nutrients and sedimentation outweigh the benefits of POM feeding.

Light reduction

The availability of light decreases directly as a function of particle concentration and water depth, but also depends on the nature of the suspended particles (Te 1997). Fine clays and organic particles are easily suspended from the sea floor, reducing light for prolonged periods while undergoing cycles of deposition and resuspension. Increased nutrient runoff into semi-enclosed seas accelerates phytoplankton production to the point that it also increases turbidity and reduces light penetration (Abal and Dennison 1996). In areas of nutrient-enrichment, light for benthic organisms can be additionally severely reduced by dense stands of large frondose macroalgae (see below), and to a minor extent by particles settling on colony surfaces.

Shading temporarily reduces photosynthesis by zooxanthellae, leading to lower carbon gain, slower calcification and thinner tissues (Table 6.2c; Rogers 1979; Telesnicki and Goldberg 1995; Anthony and Hoegh-Guldberg 2003). Within 5–10 days, many corals can adjust to somewhat lower light by increasing the size and amount of chloroplasts in zooxanthellae (not altering zooxanthellae densities per unit area), a process known as photoacclimation. However, light exposure on inshore reefs fluctuates through a 5-fold range on a time scale of days to weeks as a result of tides, resuspension and clouds (Anthony and Hoegh-Guldberg 2003). Under such variable conditions, photoacclimation does not significantly enhance gross productivity, because delays in upward- and downward-regulation of photosynthesis in response to altered light are symmetrical and compensate for each other over longer periods (Anthony and Hoegh-Guldberg 2003). Therefore, the maximum depth for photocompensation (the depth range within which corals can survive or maintain active reef growth) diminishes as a direct function of turbidity from >40 m to <4 m depth (Birkeland 1987; Yentsch *et al.* 2002).

In the field, the effects of light reduction on species richness are strongly depth-dependent, as light requirements greatly vary between species. Few species can tolerate the low light levels at deep depths or at high levels of turbidity. On the other hand, in high-irradiance conditions many slower-growing species are out-competed by fast-growing phototrophic species, hence species richness is often highest at intermediate light levels (Cornell and Karlson 2000).

Historic data on water clarity in coastal marine systems are sparse. Indeed, only few records of changes in water clarity exist, and these are from places where research stations are located, or in areas of extreme pollution. Reduced visibility has been linked to phytoplankton blooms around a sewage outfall site in Kanehoe Bay, Hawaii (Hunter and Evans 1995), and around floating fish farms in the Northern Red Sea (Loya 2004). Some researchers argue that resuspension, governed by water depth and wave height, is the best predictor of turbidity over a sediment-covered seafloor, and nearshore water clarity therefore won't substantially increase due to increased sediment discharges from the land (Larcombe and Woolfe 1999). In contrast, other researchers point out that biological processes such as water column productivity can also reduce water clarity, and that nepheloid layers can form and reduce water clarity offshore at regional scales, such as described off a mud-enriched coastline along the central Great Barrier Reef (Wolanski *et al.* 2003). Given the strong link between turbidity, light reduction and lower depth limits for coral reefs, more research is needed to understand conditions leading to long-term changes in water clarity in tropical coastal systems.

In summary, the effects of shading from turbidity are minimal in shallow water and progressively increase with increasing depth, but effects greatly vary between species (Fig. 6.2c). The main symptoms in the field are more compressed depth distribution zones, low biodiversity at deeper depths, and an overall more shallow lower depth limit for reef growth.

Sedimentation

Enhanced levels of sedimentation from coastal erosion have severely degraded many coastal reefs around the world (Table 6.2d, Rogers 1990). Most sediments are imported into coastal marine systems via rivers, with >95% of the larger sediment grain fractions being deposited within a few kilometres of the river mouth, while fine grains may be transported over longer distances. Near the source, benthic communities are easily smothered by sedimentation (e.g. Golbuu *et al.* 2003), as high sedimentation rates (accumulating to >100 mg dry weight cm^{-2} deposits) can kill exposed coral tissue within a period of a few days (Riegl and Branch 1995). Lower (<100 mg cm^{-2}) sedimentation levels reduce photosynthetic yields in corals (Philipp and Fabricius 2003), and the removal of settled particles increases metabolic costs (Telesnicki and Goldberg 1995). In coral colonies, sedimentation stress increases linearly with the duration and amount of sedimentation: for example, a certain amount of sediment deposited on the coral for one time unit exerts the same measurable photophysiological stress as twice the amount deposited for half the time (Philipp and Fabricius 2003).

Coral damage appears to not only depend on the amount and duration of sedimentation, but also strongly depends on the sediment type. For example, tissue damage under a layer of sediment increases with increasing organic content and bacterial activity, and with decreasing grain sizes (Hodgson 1990b; Weber *et al.* 2004). Low-level sedimentation (~12 mg cm^{-2}) when combined with transparent exopolymer particles (polysaccharides possibly exuded by bacteria and diatoms, called 'marine snow') kills newly settled coral recruits, whereas the same amount of sediment without the addition of marine snow does not reduce their short-term survival (Fabricius *et al.* 2003). Marine snow aggregates are found in high concentrations in coastal and inshore areas of the central Great Barrier Reef. These and similar data demonstrate the critical (but as yet poorly understood) interactions between sediment quality and quantity on coral damage (Fabricius and Wolanski 2000). They also show that short exposure to sediments (few days) can cause long-term effects in populations, by removing cohorts of young corals and thus retarding reef recovery after a disturbance.

In the field, sedimentation is greatest on sheltered, wave-protected lagoons, bays or deeper reef slopes, whereas sediment deposition is minimal in wave-exposed shallow-water areas. Sedimentation has been linked to profound changes in coral population structures, such as altered size frequencies, declining mean colony sizes, altered growth forms, and reduced growth and survival (Table 6.2d; Rogers 1990). However, sedimentation tolerances greatly vary among coral species. Large colonies or those with branching growth forms or thick tissues are more tolerant of sedimentation, whereas small colonies or species with thin tissues and flat surfaces are often highly sensitive (Rogers 1990). Some species with thick tissues can remove particles from their surfaces by tissue extension, mucus production or ciliary movement (such as found in *Fungia*) and are therefore quite sediment tolerant (Stafford-Smith and Ormond 1992). As tolerance of sedimentation varies widely among species, a reduction in biodiversity is a common outcome of sedimentation stress, with fewer sensitive species and persistence of more tolerant species (such as massive *Porites*) in the coral communities (Table 6.2d).

In summary, sedimentation effects greatly vary between coral species, but also between sediment types and between environmental conditions (Fig. 6.2d). Only few species can persist in wave-protected regions where silt-sized, nutrient-enriched sediments are deposited. In contrast, more wave-exposed areas, or areas with nutrient-poor or coarse-grained sediments will support a wider range of species even at moderate levels of sedimentation.

6.3 Direct effects of terrestrial runoff on hard corals: (2) Reproduction and recruitment

In most cases where terrestrial runoff causes reef degradation, disturbances other than eutrophication were the proximate causes of coral mortality, and runoff effects only became obvious when hard corals failed to re-establish after such disturbances (see Tables 6.1 and 6.3 for references). This indicates that coral reproduction and/or recruitment are affected by terrestrial runoff. Indeed, sedimentation and eutrophication have commonly been related to decreased juvenile densities on reefs (for references see Table 6.3). This section presents a brief literature overview to resolve how the four main parameters of terrestrial runoff affect the six main pre- and post-settlement processes, namely (1) gamete production, (2) egg fertilisation, (3) embryo development and larval survival, (4) larval settlement and metamorphosis, (5) recruit survival, and (6) juvenile growth and survival.

The limited available experimental data suggest that the three main pre-settlement stages of coral reproduction (gamete production, egg fertilization, and larval development and survival), as well as larval settlement rates, are sensitive to dissolved inorganic nutrients (Table 6.3). In acroporid corals, fecundity, egg sizes, egg fertilisation rates and embryo development are all reduced, and the occurrence of irregular embryos increased, at slightly elevated levels of dissolved inorganic nutrients (from 1 μM NH_4 and 0.1 μM PO_4, i.e., at <10% of concentrations that detrimentally affect adult corals; Ward and Harrison 2000, Harrison and Ward 2001). Furthermore, spat densities were reduced at elevated levels of nitrogen (Ward and Harrison 1997). Other observed effects include failed planulation in the brooding coral *Pocillopora damicornis*, and reduced egg sizes in *Montipora* that releases zooxanthellate eggs, after four months of exposure to elevated ammonium levels (Cox and Ward 2002). The underlying mechanisms for such surprisingly high levels of sensitivity are presently not understood.

Laboratory experiments show that POM can inhibit egg fertilization rates, larval development, larval survival, settlement and metamorphosis (Gilmour 1999). It is unknown to what extent juveniles (like adult colonies, see above) benefit from feeding on POM. Light affects both reproduction and recruitment, as coral fecundity decreases in low-light conditions, and coral larvae use light quantity and quality to choose their settlement site. At low light levels, corals preferentially settle on upper surfaces, where the risk of sedimentation damage is high, rather than on vertical of downward facing surfaces (Birkeland *et al.* 1981). At highly turbid conditions, coral recruits may undergo reverse metamorphosis, indicating conditions are unsuitable for continued development and growth (Te 1992). Light reduction from turbidity is therefore likely to result in compressed depth zonations. Finally, sedimentation also strongly inhibits successful coral reproduction, especially coral settlement and recruit and juvenile survival. Sedimentation mortality thresholds for coral recruits are an order of magnitude lower than those for larger colonies (loads of tens rather than hundreds of mg cm^{-2}; Fabricius *et al.* 2003). Few coral larvae settle on sediment-covered surfaces, and survival on such surfaces is minimal. At moderate to high rates of sedimentation, successful larval settlement is restricted to downward-facing surfaces where growth and survival are negatively affected by low light.

In summary, existing data suggest that coral reproduction and recruitment are far more sensitive to changes in water quality than adult corals, and are highly dependent on clean water and low sedimentation. Each of the four water quality parameters affect different stages of coral recruitment, and each of the effects is a negative one (Fig. 6.3): dissolved inorganic nutrients inhibits fecundity, fertilization, embryo and larval development, and possibly larval settlement; suspended particulate matter reduces pre-settlement survival; shading alters larval settlement, and sedimentation inhibits settlement and increases post-

settlement mortality. However, more experimental studies are needed to verify and complement the data synthesis of Figure 6.3.

	Dissolved inorg. nutr.	POM	Light reduction	Sedimentation
Fecundity	↓		↓	↓
Fertilization	⇓	↓	—	—
Embryo develop./ larval surv.	⇓	↓	—	—
Settlement / metamorphosis	↓	↓	⇓	⇓
Recruit survival			↓	⇓
Juvenile growth / survival			↓	↓

Figure 6.3. Synthesis of documented direct effects (Table 6.3) of the four main parameters of terrestrial runoff on the six main processes associated with coral reproduction and recruitment (Table 6.3). Symbols as in Figure 6.1.

Table 6.3: Summary of reported effects of water quality on coral reproduction and early life stages in corals (see also Fig. 6.3).

Agent	Response	Source
≥1 μM NH_4 and/or ≥1 μM PO_4	Reduced egg fertilisation rates in *Acropora,* increased rate of abnormally formed embryos.	Harrison and Ward, 2001
NH_4 (11 to 36 μM m^{-3}) and/or PO_4 (2 - 5 μM m^{-3})	Reduced spat densities on tiles in NH_4 enriched, but not in PO_4 enriched treatments.	Ward and Harrison, 1997
NH_4 (11 to 36 μM m^{-3}) and/or PO_4 (2 - 5 μM m^{-3})	Smaller and fewer eggs per polyp, reduced egg fertilization, increased proportion of irregular embryos.	Ward and Harrison, 2000
20 μM NH_4 for 4 months	Failed planulation in *Pocillopora damicornis*. Reduced egg size, but no difference in fecundity and fertilisation in *Montipora* with zooxanthellate eggs.	Cox and Ward, 2002
Increased nutrients from floating fish farms	Reduced coral planulation.	Loya *et al.*, 2004
Eutrophication gradient	Reduced gametogenesis, larval development, larval settlement, recruit and juvenile density and diversity, increased juvenile mortality.	Tomascik and Sander, 1987a; Tomascik, 1991; Hunte and Wittenberg, 1992; Wittenberg and Hunte, 1992
Suspended sediment (50 and 100 mg l^{-1})	Reduced fertilisation, uninhibited post-fertilisation embryonic development, reduced larval survival and larval settlement.	Gilmour, 1999
Turbidity by SPM (0, 10, 100, 1000 mg l^{-1})	Unaltered settlement rates, but increased rates of reversed metamorphosis after settlement ("polyp bail-out") at 100 and 1000 mg L^{-1}.	Te, 1992
Turbidity, sedimentation	Reduced fecundity.	Kojis and Quinn, 1984
Shading	Reduced fecundity.	Carlon, 2002
Shading	Species-specific effects on settlement and metamorphosis.	Mundy and Babcock, 1998; Babcock and Mundy, 1996

Agent	Response	Source
Sedimentation	Reduced larval settlement on upper surfaces, especially when sediments are trapped by thick turf algae.	Hodgson, 1990a; Babcock and Davies, 1991; Te, 1992; Babcock and Mundy, 1996; Babcock and Smith, 2002; Birrell *et al.*, 2005.
Sedimentation (1 to 11.7 mg cm^{-2} d^{-1})	Reduced recruit survival.	Babcock and Smith, 2002
Muddy marine sediments (14 mg cm^{-2}), with and without enrichment with marine snow	After 48 h, reduced recruit survival in sediments enriched with marine snow.	Fabricius *et al.*, 2003
Sedimentation	Increased juvenile mortality (abrasion, smothering, competition with algae).	Birkeland, 1977; Sato, 1985; Sammarco, 1991; Wittenberg and Hunte, 1992
Eutrophication, sedimentation	Increased mean colony sizes (interpreted as sign of low recruitment rates).	Cortes and Risk, 1985; Tomascik and Sander, 1985
Terrestrial runoff, heavy sedimentation (>10 mg cm^{-2} d^{-1} and >10 mg l^{-1})	Reduced coral recruitment.	Pastorok and Bilyard, 1985; Rogers, 1990, Richmond, 1997
Water from creek runoff (28 ppt salinity)	Reduced fertilisation (-86%), reduced larval development (up to -50%).	Richmond and Walton Smith, 1993
Gradient in exposure to terrestrial runoff	Reduced recruit and juvenile density.	Smith *et al.*, 2005

6.4 Effects of terrestrial runoff on benthic organisms that affect corals and coral communities

Abundances of a large number of invertebrates and algae in coral reef communities change along environmental gradients influenced by terrestrial runoff. This section focuses on the responses of those organism groups that profoundly affect health and abundance of corals; hence changes in their abundances in response to terrestrial runoff induce secondary or indirect effects on corals. The six main groups of organisms are those that (1) facilitate coral settlement (especially crustose coralline algae), (2) alter the structural strength of the reef substratum (internal bioeroders), (3) compete for space with corals (macroalgae), (4) do not contribute to reef calcification (heterotrophic filter feeders and octocorals), (5) infect corals with diseases, and (6) predate on corals (the crown-of thorns starfish *Acanthaster planci*).

Organisms that determine coral settlement

Substratum availability, and especially the presence of certain species of crustose coralline algae (CCA) and the absence of sediment layers are essential for coral settlement (Harrington *et al.* 2004). Few experimental data exist to assess the effects of terrestrial runoff on substratum availability and suitability for coral settlement. Some experiments and field data suggest that sedimentation may be a major factor influencing CCA abundances. CCA cover on reefs is negatively related to sedimentation (Kendrick 1991), with cover decreasing from >30% in some low sedimentation habitats to 1% at high sedimentation on the Great Barrier Reef (Fabricius and De'ath 2001b). Laboratory experiments suggest that some coral reef associated CCA survive burial under coarse inorganic sediments for days to weeks, but their survival is compromised if sediments are fine-grained (<0.63 m) or organically enriched (Harrington *et al.* 2005). The responses of CCA to sediments is complicated by their interaction with turf algae that efficiently trap sediments (Purcell, 2000), and by this means not only smother and replace CCA (Steneck 1997) but also make the surrounding substratum less suitable for coral settlement (Birrell *et al.* 2005). Light also affects CCA abundances, however responses are species-specific, with high-irradiance species being replaced by low-light species as light availability decreases. Laboratory studies show that elevated levels of orthophosphate can reduce calcification in tropical CCA (Brown *et al.* 1977; Björk *et al.* 1995), but field experiments found no responses by either CCA or turf algae to enrichment with dissolved inorganic nutrients (Koop *et al.* 2001).

Organisms that determine structural strength of the substratum

By far the largest proportion of filter feeders lives below the reef surface. Some types, especially sponges, bryozoans, ascidians, molluscs and some polychaetes, colonise existing cracks and crevices of the substratum. Others actively bore into or chemically erode the inorganic reef substratum and the calcium carbonate skeletons of live corals. These are internal macro-bioeroders that can reach densities of thousands of individuals m^{-2} reef area, weakening the structure of coral reefs and affecting their susceptibility to storm damage (Rose and Risk 1985). The main groups are sponges such as the boring sponge *Cliona* spp., and bivalves such as the date mussel *Lithophaga* spp., the latter known to re-dissolve up to 40% of skeletons of living coral by direct boring and by changing alkalinity around the bore holes (Loya, 1991). The boring activity of these filter feeders is complemented by internal micro-boring green and blue-green microalgae. Several studies have documented increased abundances of internal macro- and microbioeroders in response to enhanced nutrient availability (Rose and Risk 1985; Hallock and Schlager 1986; Hallock 1988; Cuet *et al.* 1988; Holmes 2000; Chazottes *et al.* 2002). For example, abundances of the boring sponge *Cliona delitrix* increased five-fold in an area exposed to untreated fecal sewage (Rose and Risk 1985). Similarly, erosion by microalgae and other microbes is enhanced 10-fold by fertiliser application (Carriero-Silva *et al.* 2004). While certain borers are detrimentally affected by

sedimentation (Hutchings *et al.* 2005), abundances of most internal macrobioeroders are highest in the more productive inshore environments than offshore (Sammarco and Risk 1990; Edinger and Risk 1996). Of greatest concern is that increased bioerosion in areas of nutrient enrichment, combined with reduced coral growth, skeletal densities and recruitment rates, can lead to conditions where reef erosion exceeds calcium carbonate accretion (Montaggioni *et al.* 1993; Edinger *et al.* 2000; Pari *et al.* 2002; Carriero-Silva *et al.* 2004).

Organisms in competitive interaction with corals: macroalgae

Hard corals are competitive in low-nutrient environments because of efficient internal recycling of nutrients and energy between host and zooxanthellae, and because they occupy almost all available trophic levels simultaneously: they are efficient in photosynthesis, they take up dissolved inorganic and organic nutrients, feed on primary producers such as large phytoplankton, capture and prey upon herbivorous and predatory zooplankton, and also feed on decompositional material such as detritus (Lewis 1976; Rosenfeld *et al.* 1999). Additionally, corals show considerable trophic plasticity in response to light and food availability. Such remarkable ability to gain energy at most trophic levels simultaneously allows hard corals to grow in nutrient-poor as well as quite productive environments. This trophic flexibility contrasts with the more specialised feeding strategies of other major benthic groups on coral reefs, the most important ones being macroalgae and heterotrophic filter feeders.

Macroalgal communities are an integral and often diverse component of inshore reef systems. However at certain environmental conditions, some macroalgal species can form dense mats that overgrow or damage large areas of coral by trapping sediment, restricting gas exchange, and creating anoxic conditions when mats age and collapse. For example, mats of the ephemeral green filamentous *Enteromorpha* sp. can smother adult corals by depleting oxygen at night. A 50% local increase in nutrients in the northern-most part of the Red Sea (Eilat, Gulf of Aqaba) has led to such blooms, reducing coral cover by 50% and reef ecosystem calcification by a factor of 3 to 4 since 1990 (Loya 2004). Other, fleshy perennial species such as *Sargassum* spp. seasonally grow to form up to 2 m tall forests. Such forests shade corals underneath and their fronds can cause some tissue abrasion in coral. Rather than directly smothering adult corals, they tend to establish after corals are killed by other disturbance, however once established, they can become a major factor retarding coral recovery (Schaffelke *et al.* 2005). Both types of macroalgae (low ephemeral mats and fleshy perennial stands) inhibit coral recruitment by space occupancy, allelopathy, silt trapping or shading (Sammarco 1980; Connell *et al.* 1997; Hughes and Tanner 2000; Szmant 2002; Schaffelke *et al.* 2005).

Macroalgae cover their carbon demand by photosynthesis, and their nutrient demand by uptake of dissolved inorganic nutrients, plus in some species by decomposing particulate organic matter deposited on their fronds (Schaffelke 1999b). In the absence of grazing control, the growth and productivity of certain groups of macroalgae is nutrient limited and increases with slight increases in dissolved inorganic nutrients and POM (Schaffelke 1999a, Schaffelke *et al.* 2005). High standing biomass of fleshy, silt-trapping macroalgae has been reported around many point nutrient sources (Table 6.1), such as Kaneohe Bay (Smith *et al.* 1981), Brazil (Costa Jr *et al.* 2000) or the Bahamas (Lapointe *et al.* 2004). On inshore reefs of the central and northern Great Barrier Reef, total macroalgal cover (especially red and green algae) increases by up to 50% from reefs in water with lowest nutrient and particle loads to those in least clean water (van Woesik *et al.* 1999; Fabricius and De'ath 2004; Fabricius *et al.* 2005). Time series data of sites where macroalgal cover expanded with increasing nutrients from coastal runoff on Reunion Island (Cuet *et al.* 1988), and where macroalgal cover decreased after sewage diversion in Kaneohe Bay (Smith *et al.* 1981), add evidence for a causal link between increasing macroalgal abundances with increasing nutrient availability. The prevalence of macroalgae on eastern sides of large land masses

from which most rivers originate (Birkeland 1987), the increase of both macroalgal biomass and nutrients with latitude (Johannes *et al.* 1983), and the high abundances of macroalgae found in areas of nutrient upwelling (Birkeland 1988), add further strong evidence to the conclusion that nutrients can limit macroalgal biomass, and that they can have a negative effects on reef development. However, interactions between macroalgae and nutrients are complicated by the fact that macroalgal biomass is co-limited by grazing (McCook 1997; Hughes *et al.* 1999), and in turbid or deeper water by light availability. The link between nutrients and macroalgal productivity is further complicated by the fact that nutrient uptake is mass transfer limited and increases with water flow (such as in wave zones) as well as with nutrient concentrations.

Surface occupying organisms that do not calcify: heterotrophic filter feeders and octocorals

Filter feeders (predominantly sponges, bivalves, ascidians, bryozoans and barnacles) that occupy the reef surface also increase in densities in response to nutrient enrichment (Birkeland 1977; Smith *et al.* 1981; Costa Jr *et al.* 2000). Most actively pumping benthic filter feeders are asymbiotic, feeding on a narrow size range of plankton particles, and are often unable to obtain a positive carbon balance in oligotrophic waters (Birkeland 1988). Again, heterotrophic filter feeders contribute to the biodiversity of coral reefs, and indeed only few examples exist of filter feeders (in particular some sponges; Aerts 1997; Aronson *et al.* 2002) directly competing with corals for space, replacing corals and preventing further reef growth. Such take-over seems restricted to areas of low light, high phytoplankton concentrations and organic enrichment (Smith *et al.* 1981; Brock and Smith 1983). Other filter feeders are sensitive to sedimentation and therefore disadvantaged by terrestrial runoff. Unlike macroalgae that directly compete with corals for well-lit habitats, surface-inhabiting heterotrophic filter feeders are generally low in profile, and tend to monopolise space only in poorly lit, highly productive environments that are *per se* marginal or unsuitable for corals. It therefore seems that, with few locally restricted exceptions involving one or few fast-growing species, the decline of corals and the spread of filter feeders are largely independent symptoms of high nutrient loads in the water, driven by organic enrichment rather than by competition between the two disparate groups.

Octocorals are also suspension feeders, however most of the more abundant genera with larger colonies tend to be zooxanthellate and therefore depend on light. There are some reports of zooxanthellate soft corals monopolizing space in productive waters (Fabricius and Dommisse 2000) or after hard coral disturbance (Nishihira 1981), but this is probably not a widespread phenomenon (Fabricius 1998). Exceptions are found in some species of the families Alcyoniidae (especially the genus *Sinularia*), Briareidae and Clavulariidae that can locally establish space dominance at moderate concentrations of suspended particulate matter (Fabricius 1998; Fabricius and Dommisse 2000), but their success in space competition with hard corals tends to be restricted to high-irradiance, high-current and wave-protected inshore reefs. Indeed, octocorals appear to be overall more strongly affected by declining water quality than hard corals are (Fabricius *et al.* 2005): octocoral species richness declines by up to 60% along a gradient of increasing turbidity, mostly due to the disappearance of zooxanthellate octocorals (Fabricius and De'ath 2001a). Some octocorals are also more sensitive to sedimentation than hard corals (Riegl and Branch 1995).

Organisms that cause diseases in corals

Bacteria, cyanobacteria, fungi and protists cause diseases in coral reef organisms, and some of these are now major factors threatening coral and octocoral populations in the Caribbean (Linton *et al.* 2002). Slow-release fertiliser experiments have demonstrated that infection rates and the spread of certain coral and octocoral diseases are accelerated by

experimentally enhancing concentrations of inorganic nutrients (Bruno *et al.* 2003). On regional scales, disease prevalence has been attributed to increasing seawater temperatures as well as to sedimentation, pathogens transported via air-borne dust from expanding deserts, eutrophication and pollution (Sutherland *et al.* 2004). Overall, more data are needed to test for the potential links between water quality and disease prevalence and virulence in coral reef organisms.

Organisms that predate on corals

Another indirect, and particularly severe effect of water quality on the status of the wider coral reef ecosystem is the apparent link between frequencies of population outbreaks of the coral eating crown-of-thorns starfish *Acanthaster planci*, and terrestrial runoff. A strong spatial and temporal relationship exists between drought-breaking floods around high continental Indo-Pacific islands and outbreaks of *A. planci* (Birkeland 1982). Experimental studies document faster development and enhanced survival of the planktotrophic larvae of *A. planci* when concentrations of large phytoplankton are sufficiently high (Lucas 1982; Okaji *et al.* 1997). Large phytoplankton groups tend to be nutrient-limited and bloom in response to nutrification events. New research further strengthens the evidence that higher outbreak frequencies of *A. planci* are linked to terrestrial runoff, while acknowledging that the removal of predators of *A. planci* can further enhance the likelihood of outbreaks (Brodie *et al.* 2005; De'ath *et al.* unpub. data). The offsprings of the primary *A. planci* outbreak that formed in a region with high phytoplankton concentrations are moved by currents to more remote offshore reefs, hence new *A. planci* outbreaks can form even in areas that are far away from sources of terrestrial runoff.

In summary, the different groups of organisms that interact with corals are inhibited or promoted in diverse ways by the four water quality variables (Fig. 6.4). Dissolved inorganic nutrients affect at least three of the five groups, especially macroalgae. However, dissolved inorganic nutrients are also responsible to organically enriched suspended particulate matter, and hence in this way, promote the growth of filter feeding bioeroders, larvae of *A. planci* and heterotrophic filter feeders. Sedimentation strongly inhibits some crustose coralline algae, but can also interfere with certain bioeroders and space competitors. Overall, two of these indirect effects, namely increased abundances of macroalgae and increased frequencies of outbreaks of *A. planci*, arguably affect adult corals more than do the direct effects of nutrient enrichment.

	Dissolved inorg. nutr.	POM*	Light reduction	Sedimentation
Crustose coralline algae	↓			⇓
Bioeroders	↑	⇑		↓
Macroalgae	⇑	↑	⇓	↓
Heterotrophic filter feeders		⇑	⇑	↓
Coral diseases	↑			↑
Coral predators		⇑		

* including phytoplankton

Figure 6.4. Synthesis of effects of the four main parameters of terrestrial runoff on the five main groups of organisms that affect coral cover. High abundances crustose coralline algae as settlement substrata promote coral populations, whereas high abundances of the other groups are assumed to negatively affect coral populations. Symbols as in Figure 6.1.

6.5 Reef properties related to resistance, resilience and risk

Inshore reefs vary considerably in their resistance against detrimental effects from terrestrial runoff and their resilience after exposure. Understanding properties of reefs or regions that contribute to their resistance and resilience could underpin management decisions, e.g. by prioritizing protection of reefs that have the greatest chance of withstanding degradation by terrestrial runoff. This section provides an assessment of the physical, hydrodynamic, spatial and biological properties that may contribute to protecting coral reefs from deterioration at local and regional scales (Table 6.4). This list of risk factors is preliminary and qualitative, based on previously discussed ideas as well as commonalities that emerged by comparing the better-described regions (Tables 6.1 to 6.3); a formal risk analysis is needed to confirm the contributions of the properties identified.

An important factor that has been previously identified to determine the risk of degradation is the level of exposure (concentration and duration) to terrestrial runoff of a reef system. This exposure is spatially determined by the downstream distance between a reef and the major sources of discharge, the mean annual pollutant load from the source, and dilution processes (West and Van Woesik 2001; Bourke *et al.* 2002; Devlin *et al.* 2003). Exposure is also determined by the rate of retention of pollutants in the ecosystem: any mechanism that promotes retention will enhance exposure and hence the risk of degradation. Retention and removal depend on hydrodynamic processes (flushing rates, dilution), hydrology (e.g. accumulation and slow discharge via groundwater) as well as biological processes (e.g. absorption and storage of pollutant spikes in tissues, altering the organisms' physiology throughout a whole growing season).

Table 6.4. Spatial, physical and hydrodynamic, and biological properties of coral reefs, affecting reef resistance and resilience to degradation by exposure to poor water quality from terrestrial runoff.

Most affected reef areas	Mechanism	Least affected reef areas
a) Spatial, physical and hydrodynamic properties		
Short distance and/or downstream location relative to discharge source	More frequent exposure to less diluted discharges.	Far away or upstream of source of discharge
Shallow surrounding seafloor on wide continental shelf	Resuspension, retention.	Deep or precipitating surrounding seafloor
Small (<2 m) tidal range; or very large (>4 m) tidal range	Retention of pollutants and sedimentation, esp. in bays at small tides; or chronic resuspension/turbidity and low capacity for photoacclimation at very large tidal ranges.	Intermediate tidal range (2-4 m)
Low current area	Retention of pollutants, sedimentation, slow dilution.	Current-swept front reef, flank or channels
Embayment, lagoon	Small water volume hence low dilution.	Large, open water body
No waves; or high wave exposure	Retention of pollutants, sedimentation; or storm damage and bioerosion due to low skeletal densities in corals.	Moderate wave exposure
Deeper reef slope	Low light, slow growth rates, high sediment deposition.	Reef crest, upper reef slope
b) Biological properties		
Overfished area	Reduced macroalgal grazers and predators of *A. planci*.	Healthy abundances of herbivores and predators (fish, molluscs)
Region prone to frequent or severe disturbances	Removal of adult populations, slow recovery.	Region with low disturbance regime
Poor connectivity to larval pools	Low recruitment, slow recovery.	High connectivity to larval pools
Region of low biodiversity	Low species redundancy, less functional replacement.	Region of high biodiversity

At regional scales, tides are important factors determining rates of pollutant removal. Estuarine areas with <2 m tidal amplitudes are more vulnerable to eutrophication than those with large tides (Monbet 1992). However, extreme tidal ranges also inhibit reef growth by causing continuous sediment resuspension and chronic turbidity (Kleypas 1996). A shallow and wide continental shelf is also likely to enhance retention and hence susceptibility of reefs to degradation. This is because material undergoes cycles of deposition and resuspension from a shallow sea floor, whereas the same material is rapidly removed from reefs surrounded by deep water. For example, the shallow and wide northeast Australian continental shelf may play an important role in determining the level of susceptibility of the Great Barrier Reef to terrestrial runoff. A large proportion of the imported material remains in its inshore system for prolonged periods of time due to wave-driven currents and the Coriolis force, and the fine particle fraction (which carries most of the nutrients) is repeatedly resuspended from the shallow sea floor. Possibly as a consequence, although nutrient enrichment on the Great Barrier Reef is less severe than in many other regions, reef

communities clearly change along water quality gradients (van Woesik *et al.* 1999; Fabricius *et al.* 2005, Fabricius and De'ath 2004).

At local scales, current-swept reef fronts, flanks and channels are likely to experience relatively low levels of retention, as pollutants are rapidly carried away and diluted. In contrast, poorly flushed bays and lagoons with small water volumes are most likely to be damaged by terrestrial runoff (e.g. Kaneohe Bay, Smith *et al.* 1981). Upper reef slopes and crests are also less affected by turbidity and sedimentation than deeper areas (Fig. 6.2). This is because light becomes limiting for corals at greater depths, and sediment deposition is normally greater below the reach of surface waves than on reef crests (except in sheltered bays). Locations with moderate wave action also facilitate coral growth, as waves prevent sediment retention, but strong wave action may result in coral breakage in nutrient-rich areas where coral skeletal densities are weak. Current-swept areas and well-lit reef crests with moderate wave action are therefore likely to be the locations with best coral growth and fastest recovery from disturbance. For example, reef development on the most turbid inshore reefs of the Great Barrier Reef is naturally restricted to sheltered bays, whereas exposed headlands and depositional back reef areas do not support reef accretion. However, current flow, waves and light also facilitate macroalgal growth, as nutrient uptake is flow-dependent, and areas with high light and wave-enhanced nutrient fluxes are also the zones where competition with macroalgae is likely to be most intense.

Biological properties of reefs can also enhance the resistance and resilience of coral reefs. In particular, healthy populations of herbivores help controlling algal or prey populations, hence regions that have high grazer abundances are less likely to respond to deteriorating water quality with macroalgal dominance (McCook 1999). Importantly, regions that are prone to severe or frequent disturbances (e.g. from coral bleaching, storms, cold water upwelling, or outbreaks of crown-of-thorns starfish) are also likely to be more prone to degradation than less frequently disturbed regions. This is because poor water quality often does not directly kill the adult coral populations (see above), but retards coral recruitment and hence the speed of recovery from such unrelated disturbances. Consequently, connectivity due to lateral transport by currents will contribute to enhancing resilience, as reefs that are well connected to upstream larval sources will recover more quickly from disturbance than reefs that are poorly connected. The role of biodiversity in supporting resistance and resilience is comparatively less understood and needs further research. It appears plausible that regions of high biodiversity have more functional redundancy, and structural changes in diverse regions may be prevented by species replacement when some species disappear in response to changing water quality. In contrast, regions of lower biodiversity may not have suitable species to replace the loss of sensitive species, and are more likely to undergo structural and functional change in their communities (Bellwood *et al.* 2004). At present it is unknown whether marginal reefs at high latitudes, with their higher macroalgal biomass, lower coral biodiversity and low calcification rates differ in their resistance and resilience to degradation by poor water quality to those at low latitudes.

In summary, reefs that are surrounded by a shallow sea floor, reefs in poorly flushed bays or lagoons, deeper reef slopes, and frequently disturbed reefs are likely to experience changes even at low levels of pollution, in particular when populations of herbivores are low. In contrast, well-flushed shallow reef crests surrounded by deep sea floors or in areas of moderate tides are likely to have the highest level of resistance and resilience, especially when inhabited by healthy populations of herbivores that protect against overgrowth by sediment-trapping macroalgae.

6.6 Conclusions

Models of the global scale of pollution around coral reefs estimate that 22% of all coral reefs worldwide are classified as at high (12%) or medium (10%) threat from inland pollution and soil erosion (Bryant *et al.* 1998). The percentage of reefs at risk is highest in countries with widespread land clearing, such as Taiwan and Vietnam with 50% of their reefs at risk from terrestrial runoff, or the Philippines with 35% (Bourke *et al.* 2002). The models also classify 30% of reefs as threatened from coastal development (proximity to cities, mines and resorts), and 12% at threat from marine pollution (distance to ports, oil tanks, oil wells and shipping areas; Bryant *et al.* 1998). On a global scale, pollution is therefore rated as a threat to coral reefs similar in severity and scale to coral bleaching, overfishing and destructive fishing (Spalding *et al.* 2001). On local scales, it can be the single most significant pressure on coastal and inshore coral reefs (Table 6.1).

This literature review indicates that four fundamentally different processes have to be distinguished when assessing the effects of terrestrial runoff on coral reefs:

1. Dissolved inorganic nutrients can reduce coral calcification and fertilization rates, and increase macroalgal abundances (Figs. 6.2a, 6.3 and 6.4). In the field however, dissolved inorganic nutrients disappear so quickly that their main role may that of curbing organic enrichment of benthos, sediments and suspended POM, except in areas of upwelling and near sewage outfalls.
2. Enrichment with POM enhances feeding rates and growth in some corals, providing a growth advantage that can partly or fully compensate for light reduction, especially in high-flow environments (Fig. 6.2b). However, while some corals can benefit from POM, heterotrophic filter feeders will benefit even more than corals do, hence the competitive advantage shifts from corals that can grow at extremely low food concentrations to simpler, more heterotrophic communities. A promotion of the growth and survival of filter feeding larvae of *A. planci* has also profound negative consequences for coral populations (Fig. 6.4).
3. Turbidity-related light limitation reduces gross photosynthesis (Fig. 6.2c). Light limitation increases with depth and under macroalgae, but will not occur in shallow water, even in very turbid environments. The effects of light limitation are more severe for phototrophic than mixotrophic species, while heterotrophic species such as filter feeders may be promoted. Light limitation also greatly reduces coral recruitment (Fig. 6.3).
4. Sedimentation represents a severe disturbance for coral reefs. It reduces growth and survival in a wide range of coral species, although responses differ substantially between species and also between different sediment types (Fig. 6.2d). Smothering by sedimentation or sediment-trapping macroalgae is the main factor affecting recruitment and the survival of early life stages in corals: settlement rates are near-zero on sediment-covered surfaces, and sedimentation tolerance in coral recruits is at least one order of magnitude lower than for adult corals (Fig. 6.3). Some of the bioeroding and space-competing groups of organisms are also sensitive to sedimentation by fine silt, and so are crustose coralline algae, with negative consequences for coral recruitment (Fig. 6.4).

The type and severity of response to terrestrial runoff at any particular location depends on whether changes occurred predominantly in sedimentation, turbidity, POM or dissolved inorganic nutrients, and also depend on the physical, hydrodynamic, spatial and biological properties of a location. In most places, reduced recruitment success in corals, together with the promotion of macroalgae and *A. planci*, arguably represent the most significant direct effect of terrestrial runoff on coral reefs. In severe conditions, the overall outcome is reduced reef calcification, shallower photosynthetic compensation points, changed coral community structure, and greatly reduced species richness. Hence reef ecosystems increasingly simplify

with increasing exposure to terrestrial runoff, compromising their ability to maintain essential ecosystem functions at the presently increasing frequencies of human-induced disturbances.

6.7 References

Abal EG, Dennison WC. 1996. Seagrass depth range and water quality in southern Moreton Bay, Queensland, Australia. Marine and Freshwater Research 47: 763-771.

Abdel-Salam H, Porter JW, Hatcher BG. 1988. Physiological effects of sediment rejection on photosynthesis and respiration in three Caribbean reef corals. In: Choat JH, Barnes D, Borowitzka MA, Coll JC, Davies PJ, Flood P, Hatcher BG, and Hopley D (Eds) Proceedings of the Sixth International Coral Reef Symposium, Townsville (Australia), Vol. 2: 285-292.

Acevedo R, Morelock J. 1988. Effects of terrigenous sediment influx on coral reef zonation in southwestern Puerto Rico. In: Choat JH, Barnes D, Borowitzka MA, Coll JC, Davies PJ, Flood P, Hatcher BG, and Hopley D (Eds) Proceedings of the Sixth International Coral Reef Symposium, Townsville (Australia), Vol. 2: 189-194.

Achituv Y, Dubinksy Z. 1990. Evolution and zoogeography of coral reefs. In: Dubinsky Z (Ed) Ecosytems of the World 25: Coral Reefs. Elsevier, Amsterdam, pp. 1-9.

Anthony KR. 1999. Coral suspension feeding on fine particulate matter. Journal of Experimental Marine Biology and Ecology 232: 85-106.

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

Anthony KR, Hoegh-Guldberg O. 2003. Kinetics of photoacclimation in corals. Oecologia 134: 23-31.

Anthony KR, Hoegh-Guldberg O. 2003. Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys? Functional Ecology 17: 246-259.

Aronson RB, Precht WF, Toscano MA, Koltes KH. 2002. The 1998 bleaching event and its aftermath on a coral reef in Belize. Marine Biology 141: 435-447.

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

Babcock R, Mundy C. 1996. Coral recruitment: Consequences of settlement choice for early growth and survivorship in two scleractinians. Journal of Experimental Marine Biology and Ecology 206: 179-201.

Babcock RC, Smith L. 2002. Effects of sedimentation on coral settlement and survivorship. In: Kasim Moosa MK, Soemodihardjo S, Nontji A, Soegiarto A, Romimohtarto K, Sukarno, Suharsono (Eds) Proceedings of the Ninth International Coral Reef Symposium, Bali, Indonesia, October 23-27 2000. Ministry of Environment, the Indonesian Institute of Sciences and the International Society for Reef Studies, 245-248.

Bak RPM. 1978. Lethal and sublethal effects of dredging on reef corals. Marine Pollution Bulletin 9 14-16.

Bellwood DR, Hughes TP, Folke C, Nyström M. 2004. Confronting the coral reef crisis. Nature 429: 827-833.

Birkeland C. 1977. The importance of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. In: Taylor DL (Ed) Proceedings of the Third International Coral Reef Symposium, Miami, Florida, 15-21.

Birkeland C. 1982. Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). Marine Biology 69: 175-185.

Birkeland C. 1987. Nutrient availability as a major determinant of differences among coastal hard-substratum communities in different regions of the tropics. In: Birkeland C (Ed) Comparison between Atlantic and Pacific tropical marine coastal ecosystems: community structure, ecological processes, and productivity. UNESCO Reports in Marine Science, 45-97.

Birkeland C. 1988. Geographic comparisons of coral-reef community processes. In: Choat JH, Barnes D, Borowitzka MA, Coll JC, Davies PJ, Flood P, Hatcher BG, and Hopley D (Eds) Proceedings of the Sixth International Coral Reef Symposium, Townsville (Australia), 211-220.

Birkeland C, Rowley D, Randall RH. 1981. Coral recruitment patterns at Guam. In: Gomez ED, Birkeland CE, Buddemeier RW, Johannes RE, Marsh JA, Tsuda RT (eds), The reef and man. Proceedings of the Fourth International Coral Reef Symposium. Manila (Philippines), Vol. 2: 339-344.

Birrell CL, McCook JL, Willis BL. 2005. Effects of algal turfs and sediment on coral settlement. Marine Pollution Bulletin 51: 408-414.

Björk M, Mohammed SM, Björklund M, Semesi A. 1995. Coralline algae, important reef-builders threatened by pollution. Ambio. Stockholm 24: 502-505.

Bongiorni L, Shafir S, Rinkevich B. 2003a. Effects of particulate matter released by a fish farm (Eilat, Red Sea) on survival and growth of *Stylophora pistillata* coral nubbins. Marine Pollution Bulletin 46: 1120-1124.

Bongiorni L, Shafir S, Angel D, Rinkevich B. 2003b. Survival, growth and gonad development of two hermatypic corals subjected to in situ fish-farm nutrient enrichment. Marine Ecology Progress Series 253: 137-144.

Bourke L, Selig E, Spalding M. 2002. Reefs at risk in Southeast Asia. World Resources Institute, Cambridge, 72 pp.

Brock RE, Smith SV. 1983. Response of coral reef cryptofaunal communities to food and space. Coral Reefs 1: 179-183.

Brodie J, Fabricius KE, De'ath G, Okaji K. 2005. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. Marine Pollution Bulletin 51: 266-278.

Brown BE. 1987. Heavy metals pollution on coral reefs. In: Salvat B (Ed) Human impacts on coral reefs: facts and recommendations. Antenne de Tahiti Muséum E.P.H.E., Moorea, 119-134.

Brown BE, Le Tissier MDA, Scoffin TP, Tudhope AW. 1990. Evaluation of the environmental impact of dredging on intertidal coral reefs at Ko Phuket, Thailand, using ecological and physiological parameters. Marine Ecology Progress Series 65: 273-281.

Brown V, Ducker SC, Rowan KS. 1977. The effect of orthophosphate concentration on the growth of articulated coralline algae (Rhodophyta). Phycologia 16: 125-131.

Bruno J, Petes LE, Harvell D, Hettinger A. 2003. Nutrient enrichment can increase the severity of coral diseases. Ecology Letters 6: 1056-1061.

Bryant DG, Burke L, McManus J, Spalding M. 1998. Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, Washington DC.

Carlon DB. 2002. Production and supply of larvae as determinants of zonation in a brooding tropical coral. Journal of Experimental Marine Biology and Ecology 268: 33-46.

Carriero-Silva M, McClanahan T, Kiene W. 2005. The role of inorganic nutrients and herbivory in controlling microbioerosion of carbonate substrate. Coral Reefs 24:214-221.

Cervino JM, Hayes RL, Honovitch M, Goreau TJ, Jones S, Rubec PJ. 2003. Changes in zooxanthellae density, morphology, and mitotic index in hermatypic corals and anemones exposed to cyanide. Marine Pollution Bulletin 46: 573-586.

Chansang H, Boonyanate P, Charuchinda M. 1981. Effect of sedimentation from coastal mining on coral reefs on the northwestern coast of Phuket Island, Thailand, In: Gomez ED, Birkeland CE, Buddemeier RW, Johannes RE, Marsh JA, Tsuda RT (eds) The reef and man. Proceedings of the Fourth International Coral Reef Symposium. Manila (Philippines), Vol. 1: 129-136.

Chazottes V, Le Campion-Alsumard T, Peyrot-Clausade M, Cuet P. 2002. The effects of eutrophication-related alterations to coral reef communities on agents and rates of bioerosion (Reunion Island, Indian Ocean). Coral Reefs 21: 375-390.

Connell JH, Hughes TP, Wallace CC. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67: 461-488.

Cornell HV, Karlson RH. 2000. Coral species richness: ecological versus biogeographical influences. Coral Reefs 19: 37-49.

Cortes JN, Risk MJ. 1985. A reef under siltation stress: Cahuita, Costa Rica. Bulletin of Marine Science 36: 339-356.

Costa Jr, OS, Leao ZM, Nimmo M, Attrill MJ. 2000. Nutrification impacts on coral reefs from northern Bahia, Brazil. Hydrobiologia 440: 370-415.

Cox EF, Ward S. 2002. Impact of elevated ammonium on reproduction in two Hawaiian scleractinian corals with different life history patterns. Marine Pollution Bulletin 44: 1230-1235.

Crabbe MJC, Smith DJ. 2002. Comparison of two reef sites in the Wakatobi Marine National Park (SE Sulawesi, Indonesia) using digital image analysis. Coral Reefs 21: 242-244.

Cuet P, Naim O, Faure G, Conan JY. 1988. Nutrient-rich groundwater impact on benthic communities of La Saline fringing reef (Reunion Island, Indian Ocean): Preliminary

results. In: Choat JH, Barnes D, Borowitzka MA, Coll JC, Davies PJ, Flood P, Hatcher BG, Hopley D (Eds) Proceedings of the Sixth International Coral Reef Symposium, Townsville (Australia), Vol. 2: 207-212.

Devlin M, Brodie J, Waterhouse J, Mitchell A, Audas D, Haynes D. 2003. Exposure of Great Barrier Reef inner-shelf reefs to river-borne contaminants, 2nd National Conference on Aquatic Environments: Sustaining Our Aquatic Environments – Implementing Solutions. 20-23 November, 2001. Queensland Department of Natural Resources and Mines, Brisbane, Australia, Townsville.

Dodge RE, Aller RC, Thomson J. 1974. Coral growth related to resuspension of bottom sediments. Nature 247: 774-577.

Dubinsky Z, Jokiel PL. 1994. Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. Pacific Science 48: 313-324.

Dubinsky Z, Stambler N. 1996. Marine pollution and coral reefs. Global Change Biology 2: 511-526.

Edinger EN, Risk MJ. 1996. Sponge borehole size as a relative measure of bioerosion and paleoproductivity. Lethaia 29: 275-286.

Edinger EN, Jompa J, Limmon GV, Widjatmoko W, Risk MJ. 1998. Reef degradation and coral biodiversity in Indonesia: Effects of land-based pollution, destructive fishing practices and changes over time. Marine Pollution Bulletin 36: 617-630.

Edinger EN, Limmon GV, Jompa J, Widjatmoko W, Heikoop JM, Risk MJ. 2000. Normal coral growth rates on dying reefs: Are coral growth rates good indicators of reef health? Marine Pollution Bulletin 5: 404-425.

Fabricius K. 1998. Reef invasion by soft corals: Which taxa and which habitats? In: Greenwood J, Hall N (Eds) Australian Coral Reef Society 75th Anniversary Conference. School of Marine Science, The University of Queensland, Brisbane, Heron Island, 77-90.

Fabricius KE, De'ath G. 2001a. Biodiversity on the Great Barrier Reef: Large-scale patterns and turbidity-related local loss of soft coral taxa. In: Wolanski E (Ed) Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef. CRC Press, London, 127 - 144.

Fabricius K, De'ath G. 2001b. Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. Coral Reefs 19: 303-309.

Fabricius KE, De'ath G. 2004. Identifying ecological change and its causes: A case study on coral reefs. Ecological Applications 14: 1448-1465.

Fabricius KE, De'ath G, McCook LJ, Turak E, Williams DMcB. 2005. Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef: Marine Pollution Bulletin 51: 384-398.

Fabricius KE, Dommisse M. 2000. Depletion of suspended particulate matter over coastal reef communities dominated by zooxanthellate soft corals. Marine Ecology Progress Series 196: 157-167.

Fabricius K, Wild C, Wolanski E, Abele D. 2003. Effects of transparent exopolymer particles (TEP) and muddy terrigenous sediments on the survival of hard coral recruits. Estuarine, Coastal and Shelf Science 57: 613-621.

Fabricius KE, Wolanski E. 2000. Rapid Smothering of Coral Reef Organisms by Muddy Marine Snow. Estuarine Coastal and Shelf Science 50: 115-120.

Falkowski PG, Dubinsky Z, Muscatine L, Porter JW. 1984. Light and the bioenergetics of a symbiotic coral. Bioscience. 34: 705-709.

Ferrier-Pages C, Gattuso JP, Dallot S, Jaubert J. 2000. Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral Stylophora pistillata. Coral Reefs 19: 103-113.

Ferrier-Pages C, Schoelzke V, Jaubert J, Muscatine L, Hoegh-Guldberg O. 2001. Response of a scleractinian coral, *Stylophora pistillata*, to iron and nitrate enrichment. Journal of Experimental Marine Biology and Ecology 259: 249-261.

Furnas MJ. 2003. Catchments and Corals: Terrestrial Runoff to the Great Barrier Reef. Australian Institute of Marine Science and CRC Reef, Townsville, Australia.

GESAMP 2001. Protecting the oceans from land-based activities. Land-based sources and activities affecting the quality and uses of the marine, coastal and associated freshwater environment. United Nations Environment Program, Nairobi.

Gilmour J. 1999. Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. Marine Biology 135: 451-462.

Golbuu Y, Victor S, Wolanski E, Richmond RH. 2003. Trapping of fine sediment in a semi-enclosed bay, Palau, Micronesia. Estuarine, Coastal and Shelf Science 57: 941-949.

Guzman HM, Holst I. 1993. Effects of chronic oil-sediment pollution on the reproduction of the Caribbean reef coral Siderastrea siderea. Marine Pollution Bulletin 26: 276-282.

Hallock P, Schlager W. 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. Palaios 1: 389-398.

Hallock P. 1988. The role of nutrient availability in bioerosion: Consequences to carbonate buildups. Palaeogeography, Palaeoclimatology, Palaeoecology 63: 275-291.

Harrington L, Fabricius K, De'ath G, Negri A. 2004. Fine-tuned recognition and selection of settlement substrata determines post-settlement survival in corals. Ecology 85: 3428-3437.

Harrington L, Fabricius K, Eaglesham G, Negri A. 2005. Synergistic effects of diuron and sedimentation on photosynthesis and survival of crustose coralline algae. Marine Pollution Bulletin 51: 415-427.

Harrison PL, Ward S. 2001. Elevated levels of nitrogen and phosphorus reduce fertilisation success of gametes from scleractinian reef corals. Marine Biology 139: 1057-1068.

Hearn CJ, Atkinson MJ, Falter JL. 2001. A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. Coral Reefs 20: 347-356.

Heyward AJ. 1988. Inhibitory effects of copper and zinc sulphates on fertilization in corals. In: Choat JH, Barnes D, Borowitzka MA, Coll JC, Davies PJ, Flood P, Hatcher GB, Hopley D (Eds) Proceedings of the Sixth International Coral Reef Symposium, Townsville, 299-303.

Hodgson G. 1990a. Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. Coral Reefs 9: 41-43.

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

Hodgson G, Walton Smith FG. 1993. Sedimentation damage to reef corals, Global aspects of coral reefs: Health, hazards and history. University of Miami, Miami, 20-25.

Hodgson G, Yau EPM. 1997. Physical and biological controls of coral communities in Hong Kong. In: Lessios HA, Macintyre IG (Eds) Proceedings of the Eighth International Coral Reef Symposium. Smithsonian Institute Press, Balboa (Panama), 459-461.

Holmes KE. 2000. Effects of eutrophication on bioeroding sponge communities with the description of new West Indian sponges, *Cliona* spp. (Porifera: Hadromerida: Clionidae). Invertebrate Biology 119: 125-138.

Holmes KE, Edinger EN, Hariyadi, Limmon GV, Risk MJ. 2000. Bioerosion of live massive corals and branching coral rubble on Indonesian coral reefs. Marine Pollution Bulletin 7: 606-617.

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

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

Hughes T, Szmant AM, Steneck R, Carpenter R, Miller S. 1999. Algal blooms on coral reefs: What are the causes? Limnology and Oceanography 6: 1583-1586.

Hughes TP, Tanner JE. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81: 2250-2263.

Hunte W, Wittenberg M. 1992. Effects of eutrophication and sedimentation on juvenile corals. 2. Settlement. Marine Biology 114: 625-631.

Hunter CL, Evans CW. 1995. Coral reefs in Kaneohe Bay, Hawaii: Two centuries of western influence and two decades of data. Bulletin of Marine Science 57: 501-515.

Hutchings PA, Peyrot-Clausade M, Osnorno A. 2005. Influence of land runoff on rates and agents of bioerosion of coral substrates. Marine Pollution Bulletin 51: 438-447.

Johannes RE, Wiebe WJ, Crossland CJ, Rimmer DW, Smith SV. 1983. Latitudinal limits of coral reef growth. Marine Ecology Progress Series 11: 105-111.

Jones RJ, Kerswell AP. 2003. Phytotoxicity of Photosystem II (PSII) herbicides to coral. Marine Ecology Progress Series 261: 149-159.

Jones RJ, Muller J, Haynes D, Schreiber U. 2003. Effects of herbicides diuron and atrazine on corals of the Great Barrier Reef, Australia. Marine Ecology Progress Series 251: 153-167.

Kendrick GA. 1991. Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: Effect of simulated scour, erosion and accretion. Journal of Experimental Marine Biology and Ecology 147: 47-63.

Kinsey DW, Davies PJ. 1979. Effects of elevated nitrogen and phosphorus on coral reef growth. Limnology and Oceanography 24: 935-940.

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

Kojis BL, Quinn NJ. 1984. Seasonal and depth variation in fecundity of Acropora palifera at two reefs in Papua New Guinea. Coral Reefs 3: 165-172.

Koop K, Booth D, Broadbent A, Brodie J, Bucher D, Capone D, Coll J, Dennison W, Erdmann M, Harrison P, Hoegh-Guldberg O, Hutchings P, Jones GB, Larkum AWD, O'Neil J, Steven A, Tentori E, Ward S, Williamson J, Yellowlees D. 2001. ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. Marine Pollution Bulletin 42: 91-120.

Lapointe BE, Barile PJ, Yentsch CS, Littler MM, Littler DS, Kakuk B. 2004. The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exumas Cays, Bahamas: a 'natural' enrichment experiment. Journal of Experimental Marine Biology and Ecology 298: 275-301.

Larcombe P, Woolfe K. 1999. Increased sediment supply to the Great Barrier Reef will not increase sediment accumulation at most coral reefs. Coral Reefs 18: 163-169.

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

Lewis JB. 1976. Experimental tests of suspension feeding in Atlantic reef corals. Marine Biology 36: 147-150.

Lewis JB. 1997. Abundance, distribution and partial mortality of the massive coral *Siderastrea siderea* on degrading coral reefs at Barbados, West Indies. Marine Pollution Bulletin 34: 622-627.

Linton D, Smith R, Alcolado P, Hanson C, Edwards P, Estrada R, Fisher T. 2002. Status of coral reefs in the northern Caribbean and Atlantic node of the GCRMN. AIMS, Townsville (Australia).

Lough JM, Barnes DJ. 1992. Comparisons of skeletal density variations in *Porites* from the central Great Barrier Reef. Journal of Experimental Marine Biology and Ecology 155: 1-25.

Lough JM, Barnes DJ. 2000. Environmental controls on growth of the massive coral Porites. Journal of Experimental Marine Biology and Ecology 245: 225-243.

Loya Y. 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. Bulletin of Marine Science 26: 450-466.

Loya Y, Rinkevich B. 1987. Effects of petroleum hydrocarbons on corals. In: Salvat B (Ed) Human impacts on coral reefs: facts and recommendations. Antenne de Tahiti Muséum E.P.H.E., Moorea, 91-102.

Loya Y. 1991. Bioerosion of coral reefs -- A chemical approach. Limnology and Oceanography 36: 377-383.

Loya Y, Lubinevsky H, Rosenfeld M, Kramarsky-Winter E. in press. Nutrient enrichment caused by in situ fish farms at Eilat, Red Sea is detrimental to coral reproduction. Marine Pollution Bulletin.

Loya Y. 2004. The Coral Reefs of Eilat – Past, Present and Future: Three Decades of Coral Community Structure Studies. In: Rosenberg E, Loya Y (Eds) Coral Reef Health and Disease. Springer, Berlin, 396 pp.

Lucas JS. 1982. Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid *Acanthaster planci* (L.). Journal of Experimental Marine Biology and Ecology 65: 173-194.

Marubini F. 1996. The physiological response of hermatypic corals to nutrient enrichment. Faculty of Science. University of Glasgow, Glasgow, 192 pp.

Marubini F, Davies PS. 1996. Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. Marine Biology 127: 319-328.

Marubini F, Atkinson MJ. 1999. Effects of lowered pH and elevated nitrate on coral calcification. Marine Ecology Progress Series 188: 117-121.

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

Matson PA, Parton WJ, Power AG, Swift MJ. 1997. Agricultural intensification and ecosystem properties. Science 277: 504-509.

McCook LJ. 1997. Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef. Marine Biology 129: 713-722.

McCook LJ. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18: 357-367.

Meyer JL, Schultz ET. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limnology and Oceanography 30: 146-156.

Monbet Y. 1992. Control of phytoplankton biomass in estuaries: a comparative analysis of microtidal and macrotidal estuaries. Estuaries 15: 563-571.

Montaggioni LF, Cuet P, Naim O, Walton Smith FG. 1993. Effect of nutrient excess on a modern fringing reef (Reunion Island, Western Indian Ocean) and its geological implications, Global aspects of coral reefs: Health, hazards and history. University of Miami, Miami, 27-33.

Morelock J, Grove K, Hernandez ML. 1983. Oceanography and patterns of shelf sediments, Mayaguez, Puerto Rico. Journal of Sedimentary Petrology 53: 371-381.

Morton B. 1994. Hong Kong's coral communities: Status, threats and management plans. Marine Pollution Bulletin 29: 74-83.

Mundy CN, Babcock RC. 1998. Role of light intensity and spectral quality in coral settlement: Implications for depth-dependent settlement? Journal of Experimental Marine Biology and Ecology 223: 235-255.

Muscatine L, Falkowski PG, Dubinsky Z, Cook PA, McCloskey LR. 1989. The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. Proceedings of the Royal Society of London, Series B 236: 311-324.

Naim O. 1993. Seasonal responses of a fringing reef community to eutrophication (Reunion Island, western Indian Ocean). Marine Ecology Progress Series 99: 137-151.

Negri A, Vollhardt C, Humphrey C, Heyward A, Jones R, Eaglesham G, Fabricius KE. 2005. Effects of the herbicide diuron on the early life history stages of coral. Marine Pollution Bulletin 51: 370-383.

Nishihira M. 1981. Interactions of Alcyonaria with hermatypic corals on an Okinawan reef flat. In: Gomez ED, Birkeland CE, Buddemeier RW, Johannes RE, Marsh JA Jr, Tsuda RT (Eds) Fourth International Coral Reef Symposium, Manila (Philippines), 722-726.

Nordemar I, Nystroem M, Dizon R. 2003. Effects of elevated seawater temperature and nitrate enrichment on the branching coral *Porites cylindrica* in the absence of particulate food. Marine Biology 142: 669-677.

Okaji K, Ayukai T, Lucas JS. 1997. Selective feeding by larvae of the crown-of-thorns starfish, *Acanthaster planci* (L.). Coral Reefs 16: 47-50.

Owen R, Knap A, Ostrander N, Carbery K. 2003. Comparative acute toxicity of herbicides to photosynthesis of coral zooxanthellae. Bulletin of Environmental Contamination and Toxicology 70: 541-548.

Pari N, Peyrot-Clausade M, Hutchings PA. 2002. Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) during 5 years of exposure. Journal of Experimental Marine Biology and Ecology 276: 109-127.

Pastorok RA, Bilyard GR. 1985. Effects of sewage pollution on coral-reef communities. Marine Ecology Progress Series 21: 175-189.

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

Purcell SW. 2000. Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. Bulletin of Marine Science 66: 199-214.

Richmond RH, Walton Smith FG. 1993. Effects of coastal runoff on coral reproduction, Global aspects of coral reefs: Health, hazards and history. University of Miami, 42-46.

Richmond RH. 1997. Reproduction and recruitment in corals: critical links in the persistence of reefs. In: Birkeland C (ed) Life and Death of Coral Reefs. Chapman & Hall, pp. 175-197.

Riegl B, Branch GM. 1995. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. Journal of Experimental Marine Biology and Ecology 186: 259-275.

Rogers CS. 1979. The effect of shading on coral reef structure and function. Journal of Experimental Marine Biology and Ecology 41: 269-288.

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

Rose CS, Risk MJ. 1985. Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman fringing reef. Pubblicazioni della Stazione Zoologica di Napoli I: Marine Ecology 6: 345-362.

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

Sammarco PW. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. Journal of Experimental Marine Biology and Ecology 45: 245-272.

Sammarco PW, Risk MJ. 1990. Large-scale patterns in internal bioerosion of Porites: Cross continental shelf trends on the Great Barrier Reef. Marine Ecology Progress Series 59: 145-156.

Sammarco PW. 1991. Geographically specific recruitment and post-settlement mortality as influences on coral communities: The cross-continental shelf transplant experiment. Limnology and Oceanography 36: 496-514.

Sato M. 1985. Mortality and growth of juvenile coral *Pocillopora damicornis* (Linnaeus). Coral Reefs 4: 27-33.

Schaffelke B. 1999a. Short-term nutrient pulses as tools to assess responses of coral reef macroalgae to enhanced nutrient availability. Marine Ecology Progress Series 182:305-310.

Schaffelke B. 1999b. Particulate organic matter as an alternative nutrient source for tropical *Sargassum* species (Fucales, Phaeophyceae). Journal of Phycology 35: 1150-1157.

Schaffelke B, Mellors J, Duke NC. 2005. Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. Marine Pollution Bulletin 51: 279-296.

Shimoda T, Ichikawa T, Matsukawa Y. 1998. Nutrient conditions and their effects on coral growth in reefs around Ryukyu Islands. Bulletin of the National Research Institute of Fisheries Science 12: 71-80.

Simkiss K. 1964. Phosphates as crystal poisons of calcification. Biological Review 39: 487-505.

Smith L, Devlin M, Haynes D. (2004). Size structure, recruitment and post-recuitment survival of nearshore corals in the Great Barrier Reef Wet Tropics. P. 38 In: Haynes D, Schaffelke B (eds) Catchment to Reef: Water Quality Issues in the Great Barrier Reef Region. CRC Reef Research Centre, Townsville, Queensland, Australia, 77 pp.

Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW. 1981. Kaneohe Bay sewerage diversion experiment: perspectives on ecosystem response to nutritional perturbation. Pacific Science 35: 279 -395.

Smith SV and 10 other authors. 2003. Humans, hydrology and the distribution of inorganic nutrient loading to the ocean. Bioscience 53: 235-245.

Snidvongs A, Kinzie RA. 1994. Effects of nitrogen and phosphorus enrichment on in vivo symbiotic zooxanthellae of *Pocillopora damicornis*. Marine Biology 118: 705-711.

Spalding MD, Ravilious C, Green EP. 2001. World Atlas of Coral Reefs. University of California Press, Berkeley, 424 pp.

Stafford-Smith MG, Ormond RFG. 1992. Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. Australian Journal of Marine and Freshwater Research 43: 683-705.

Stafford-Smith MG. 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. Marine Biology 115: 229-243.

Stambler N, Popper N, Dubinsky Z, Stimson J. 1991. Effects of nutrient enrichment and water motion on the coral *Pocillopora damicornis*. Pacific Science 45: 299-307.

Steneck R. 1997. Crustose corallines, other algal functional groups, herbivore and sediments: complex interactions along reef productivity gradients, In: Lessios HA, Macintyre IG (Eds) Proceedings of the Eighth International Coral Reef Symposium. Smithsonian Institute Press, Balboa (Panama), 695-700.

Stimson, J., Larned, S.T., 2000. Nitrogen efflux from sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. Journal of Experimental Marine Biology and Ecology 252, 159-180.

Stimson J, Larned ST, Conklin E. 2001. Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. Coral Reefs 19: 343-357.

Sutherland KP, Porter JW, Torres C. 2004. Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. Marine Ecology Progress Series 266: 273-302.

Szmant AM. 2002. Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? Estuaries 25: 743-766.

Te FT. 1992. Response to higher sediment loads by Pocillopora damicornis planulae. Coral Reefs 11: 131-134.

Te FT. 1997. Turbidity and its effects on corals: a model using the extinction coefficient (k) of photosynthetic active radiance (PAR). In: Lessios HA, Macintyre IG (Eds) Proceedings of the Eighth International Coral Reef Symposium. Smithsonian Institute Press, Balboa (Panama), 1899-1904.

Telesnicki GJ, Goldberg WM. 1995. Effects of turbidity on the photosynthesis and respiration of two south Florida reef coral species. Bulletin of Marine Science 57: 527-539.

Tilman D, and 9 other authors. 2001. Forecasting agriculturally driven global environmental change. Science 292: 281-284.

Tomascik T, Sander F. 1985. Effects of eutrophication on reef-building corals. 1. Growth rate of the reef-building coral *Montastrea annularis*. Marine Biology 87: 143-155.

Tomascik T, Sander F. 1987a. Effects of eutrophication on reef-building corals. 3. Reproduction of the reef-building coral Porites porites. Marine Biology 94: 77-94.

Tomascik T, Sander F. 1987b. Effects of eutrophication on reef-building corals. 2. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. Marine Biology 94: 53-75.

Tomascik T. 1990. Growth rates of two morphotypes of *Montastrea annularis* along a eutrophication gradient, Barbados, W.I. Marine Pollution Bulletin 21: 376-381.

Tomascik T. 1991. Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. Marine Ecology Progress Series 77: 261-269.

Tomascik T, Mah AJ, Nontji A, Moosa MK. 1997. Jakarta Bay: The way of the future? Periplus Editions, Hong Kong.

van Katwijk MM, Meier NF, van Loon R, van Howe EM, Giesen WBJT, van der Velde G. 1993. Sabaki River sediment loading and coral stress: correlation between sediments and condition of the Malindi-Watamu reefs in Kenya (Indian Ocean). Marine Biology 117: 675-683.

van Woesik R, Done TJ. 1997. Coral communities and reef growth in the southern Great Barrier Reef. Coral Reefs 16: 103-115.

van Woesik R, Tomascik T, Blake S. 1999. Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. Marine and Freshwater Research 50: 427-440.

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

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7: 737-750.

Walker DI, Ormond RFG. 1982. Coral death from sewage and phosphate pollution at Aqaba, Red Sea. Marine Pollution Bulletin 13: 21-25.

Ward S, Harrison PL. 1997. The effects of elevated nutrient levels in the settlement of coral larvae during the ENCORE experiment, Great Barrier Reef, Australia In: Lessios HA, Macintyre IG (Eds) Proceedings of the Eighth International Coral Reef Symposium. Smithsonian Institute Press, Balboa (Panama), 891-896.

Ward S, Harrison P. 2000. Changes in gametogenesis and fecundity of acroporid corals that were exposed to elevated nitrogen and phosphorus during the ENCORE experiment. Journal of Experimental Marine Biology and Ecology 246: 179-221.

Weber M, Fabricius KE, Lott C, DeBeer D. 2004. Effects of sedimentation by contrasting sediment types on the photophysiology of corals. Abstract, Tenth International Coral Reef Symposium, Okinawa, p. 28.

Wellington GM, Glynn PW. 1983. Environmental influences on skeletal banding in eastern Pacific (Panama) corals. Coral Reefs 1: 215-222.

Wesseling I, Uychiaoco AJ, Alino PM, Vermaat JE. 2001. Partial mortality in *Porites* corals: variation among Philippine reefs. International Review of Hydrobiology 86: 77-85.

West K, Van Woesik R. 2001. Spatial and temporal variance of river discharge on Okinawa (Japan): Inferring the temporal impact on adjacent coral reefs. Marine Pollution Bulletin 42: 864-872.

Wilson G, Price ARG, Huntington T, Wilson SC. 2003. Environmental status of Yemen's Gulf of Aden coast determined from rapid field assessment and satellite imagery. Aquatic Ecosystem Health and Management 6: 119-129.

Wittenberg M, Hunte W. 1992. Effects of eutrophication and sedimentation on juvenile corals. 1. Abundance, mortality and community structure. Marine Biology 116: 131-138.

Wolanski E, Marshall K, Spagnol S. 2003. Nepheloid layer dynamics in coastal waters of the Great Barrier Reef, Australia. Journal of Coastal Research 19: 748-752.

Yentsch CS, Yentsch CM, Cullen JJ, Lapointe B, Phinney DA, Yentsch SW. 2002. Sunlight and water transparency: cornerstones in coral research. Journal of Experimental Marine Biology and Ecology 268: 171-183.

Chapter 7: Changes in algal, coral and fish assemblages along water quality gradients on inshore reefs of the Wet Tropics and Princess Charlotte Bay

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7.1 Introduction

Evidence that nutrient enrichment, increased siltation and excess turbidity can lead to the local degradation of coral reefs is unequivocal (Smith 1981; Hunter and Evans 1995; Grigg 1995; Stimson and Larned 2000; Stimson *et al.* 2001; Loya *et al.* 2004; review in Fabricius, (in prep). Field studies suggest that areas downstream of well-defined point sources are characterised by (a) low or locally reduced coral biodiversity, (b) low (or failed) coral recruitment, (c) high rates of partial mortality, (d) reduced skeletal density, (e) reduced depth distribution, (f) high rates of bioerosion, and (g) a transition of hard coral dominated communities to communities dominated by non-reef building organisms, especially turfing and fleshy macroalgae (Montaggionil *et al.* 1993; West and van Woesik 2001; Schaffelke *et al.* 2005), and filter feeders (Smith 1981; Birkeland 1988).

While pollution effects on coral reefs at local scales are well understood, links at regional scales between increasing sediment and nutrient loads in rivers, and the degradation of coral reefs, have been more difficult to demonstrate (Fabricius and De'ath 2004). This is due to a lack of historic data and the confounding effects of other disturbances such as bleaching, cyclones, fishing pressure and outbreaks of the coral eating crown-of-thorns starfish (*Acanthaster planci*), and is further complicated by the naturally high variability in monsoonal river flood events. Organism responses are poorly understood, as each of the numerous inshore species has its own tolerance limit at every life stage, and interactions between the organisms add to the complexity. Though considerable knowledge has been gained from single-species exposure experiments in the laboratory, it is difficult to extrapolate from such laboratory studies to field settings and ecosystem responses. Taxonomically detailed field survey data of major assemblages along environmental gradients should therefore provide valuable information about ecosystem responses to changing water quality.

In the Great Barrier Reef (GBR), two coastal regions, including about 200 coral reefs, have been classified at high risk of exposure to terrestrial runoff (Devlin *et al.* 2003). Exposure risk was estimated based on distance and direction of the reef from each river (quantifying the probability that a plume reaches the reef), and data on river pollution. The two areas classified as high risk (Fig. 7.1) were: the inner southern reefs of the Whitsunday Islands group (central GBR, 20°0'-20° 30' S), and the Wet Tropics in the northern section of the GBR (Northern GBR, 15° 40'-17° 50' S).

In the Whitsunday Islands, ecological changes have been documented on seven reefs along a gradient of increasing concentrations of water quality and sediment parameters (especially suspended particulate matter, turbidity, silicate, and total organic matter in sediments) towards reefs located near the Proserpine and O'Connell Rivers (van Woesik *et al.* 1999).

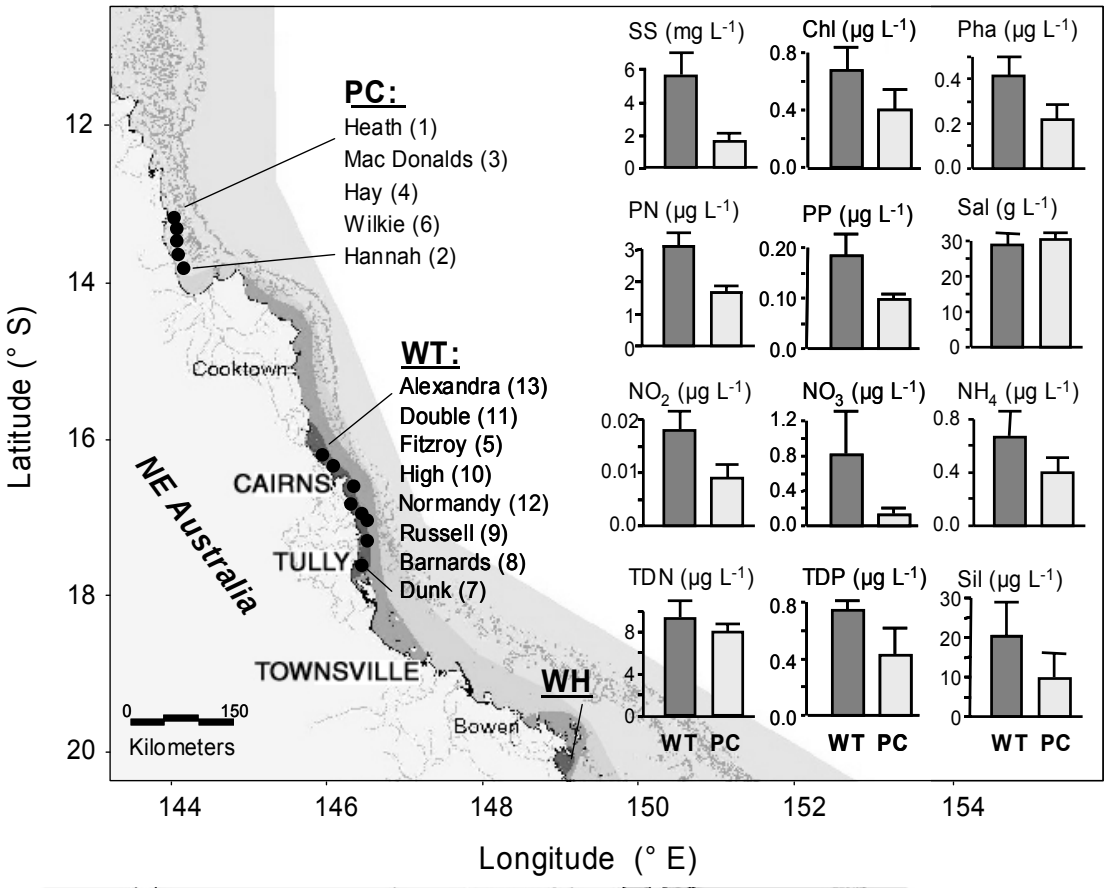


Figure 7.1. Map of the Great Barrier Reef, indicating study regions (PC = Princess Charlotte Bay, WT = Wet Tropics, WH = Whitsunday Islands), study reefs (black dots) and relative risk of exposure to river flood plumes (Devlin *et al.*, 2003): shading indicates (from darkest to lightest): 'high risk', 'moderate risk', 'low risk', and 'minimal concern' of reef being affected by terrestrial runoff. 'Risk' level is estimated using functions of distance and angle (as measure of probability that a plume reaches the reef) of each river in relation to the target reef, and the level of pollution of each river. Numbers in brackets indicated the rank order of each reef based on its water quality index (WQI; values increasing from the cleanest to least clean water; Fig. 2). The bar graphs indicate mean regional water quality concentrations ± 1 SE around the study reefs (abbreviations are listed in Methods), recorded during up to nine visits between 2000 and 2002.

Towards the river mouth, macroalgal cover increased from 0 to 74%, octocoral cover decreased from 19 to 1%, hard coral richness decreased from 15 to 5 species per transect, and the maximum depth of reef development was reduced from 12 to 4 m. Furthermore, hard coral communities changed from those dominated by *Acropora* and massive *Porites* 80 km away from the river, to reefs dominated by Faviidae, encrusting *Montipora,* encrusting *Porites* and *Turbinaria* spp. at the reefs more exposed to terrigenous influences. A mismatch between Holocene reef accretion rates and present-day reef growth at the reefs most exposed to terrigenous influences was used as evidence of recent change in response to anthropogenic activities in the river catchments.

Inshore reefs of the Wet Tropics (16 -18° S), the largest region considered at risk at exposure to terrestrial runoff, have declined in coral cover since the early 1990s, apparently due to failure to recover from a series of disturbances (Ayling and Ayling 2002; unpub. AIMS Long-Term Monitoring data). Comparatively few ecological and water quality data are available from the Far Northern GBR, the only inshore region where risk of exposure to

terrestrial runoff is considered minimal (Fig. 7.1). However, water column chlorophyll a concentrations, monitored in the GBR since 1992 as proxy measure for nutrient concentrations, show that chlorophyll levels are twice as high on the inner 20 km along the Wet Tropics Coast that receives river floods from agriculturally used catchments, as in the Far Northern region (14°S) where land use is minimal (Brodie *et al.* 1997; Devlin *et al.* 2003). Across the continental shelf, chlorophyll increases steeply towards the coast in the Wet Tropics but not in the Far North (Fabricius and De'ath 2004), indicating that nutrient availability is higher in the former region.

In this study we present field survey data on the biodiversity of algae, hard corals, octocorals and fish on naturally turbid inshore coral reefs that vary in their level of exposure to water-borne sediment, nutrient and chlorophyll concentrations, and in the degree of agricultural modification in the adjacent catchments from where flood plumes originate. We investigate the relationships between water quality and a number of ecological attributes, and discuss the evidence for water quality effects on coral reef communities on these inshore reefs.

7.2 Methods

Study Sites

The study focussed on five to eight (dependent on the organism) inshore reefs in the Wet Tropics (WT) between Tully and Port Douglas, and five reefs in the Claremont Isles, north of the Princess Charlotte Bay region (PC; Fig. 7.1). Surveys were conducted on both the windward and leeward sides of the reefs at several depth zones. The eight reefs surveyed in the Wet Tropics were (from south to north) Dunk, Barnards, Russell, Normanby, High, Fitzroy, Double and Alexandra, and the five reefs north of Princess Charlotte Bay were Hannah, Wilkie, Hay, McDonalds and Heath (Fig. 7.1). All five PC reefs were surveyed for all four groups, whereas of the eight WT reefs, Alexandra Reef was only surveyed for octocorals, Dunk and Double Island were not surveyed for fish and the Barnard Islands were not surveyed for hard corals.

All study reefs are located <20 km from north-south oriented coastlines at <20 m bathymetry. Reefs in WT have been identified as having the highest risk of exposure to agricultural runoff (Devlin *et al.* 2003), since they experience river plumes every few years from wet tropical catchments with intensive agriculture (Johnstone, Russell-Mulgrave, Tully River), and plumes from the large, dry tropical Burdekin River on a decadal basis. Reefs in PC are exposed to runoff from the dry tropical Normanby and Stewart Rivers, whose catchments are only slightly modified, being dominated by low-density cattle grazing, and having received little or no fertilizers and pesticides. Data on the disturbance history from both regions are sparse. In the last two decades some of the WT reefs experienced an outbreak of *Acanthaster planci* (early1990s), two tropical cyclones (1986 and 1990), and bleaching-related coral mortality (1998), whereas the reefs in PC have probably not experienced *A. planci* outbreaks, but have been impacted by four tropical cyclones in the last two decades, and bleaching mortality in 2002 (after the surveys reported here were completed).

Field Data

a) Water quality data: Concentrations of twelve water quality variables (particulate nitrogen and phosphorus (PN, PP), nitrate, nitrite, ammonium, total dissolved nitrogen and phosphorus (TDN, TDP), silicate (Sil), chlorophyll (Chl), phaeopigments (Phae), salinity (Sal) and suspended solids (SS)) were determined by taking surface water samples at each reef during each of nine ship trips to both regions between December 2000 and April 2002. For logistic reasons, our water sampling was limited to nine visits (Alexandra Reef only 5 times), but the regional differences we found were consistent with data from a monthly water column

chlorophyll *a* monitoring program that commenced in 1992 (Brodie *et al.* 1997), which shows that inshore chlorophyll concentrations are twice as high in the central section of the GBR including WT, compared to the remote Far Northern section including PC (Fabricius and De'ath 2004). Furthermore, in the central GBR but not in the Far North, chlorophyll concentrations increase steeply towards the coast, indicating that more nutrients are available inshore in the former area (Brodie *et al.* unpub. data).

Dissolved nitrogen, phosphorus and silicate, six 10 ml subsamples were filtered through sterile polycarbonate filters with 0.2 μm pore size, and the particle-free water frozen at –18° C for later analysis. For particulate nutrients, chlorophyll and phaeopigments, duplicate subsamples (250 ml, and 100 ml respectively) were filtered onto pre-combusted 25 mm Whatman GF/F filters (0.2 μm nominal pore size) at low vacuum (8 kPa). Filters were then wrapped into pre-combusted aluminium foil, and frozen until further analysis. Dry weight of suspended solids was determined from duplicate 1000 ml water samples filtered through pre-weighed 45 mm polycarbonate filters with 0.4 μm pore size. Surface salinity was determined from a 500 ml water sample stored in airtight bottles at room temperature. In the laboratory, the samples were analysed following standard procedures (Furnas and Mitchell 1996).

b) Abundances and Biodiversity: Four groups of taxa were surveyed using rapid ecological assessments based on standardized scuba-swims by experts: macroalgae, here defined as fleshy macroalgae, excluding crustose coralline and fine filamentous forms (McCook *et al.* 2000), hard corals (Devantier *et al.* 1998), octocorals (Fabricius and De'ath 2001), and fish (Williams 1982). Abundances of the three benthic groups were rated on a 6-point scale as 0 = 'absent', 1 = 'rare', 2 = 'uncommon', 3 = 'common', 4 = 'abundant', and 5 = 'dominant'. Abundances of some of the fish species were estimated on a log (base 5) scale (Williams, 1982), whereas less abundant fish species such as *Lethrinus* spp.*, Lutjanus* spp., *Plectropomus* spp., *Chaetodon* spp., and some pomacanthids, plectorhynchids and *Choerodon* spp., were fully enumerated.

Macroalgae surveys were conducted at three depths (slope: 18-3 m, crest: 3-1 m, and the reef flat) in early summer, late summer, and winter, in total covering 12 reefs with 218 surveys. Macroalgae were identified to genus level, except for *Rhipilia* and *Avrainvillea*, and *Galaxaura* and *Tricleocarpa*, which were aggregated. Relative abundances of Rhodophyta (red algae), Chlorophyta (green algae) and Phaeophyta (brown algae, now also called Heterokontophyta) were estimated as the sum of ratings of individual genera within these three major groups of fleshy macroalgae. Hard corals (Scleractinia) were identified to species level, and were surveyed at 2 depths (deep: 18-8 m, and shallow: 6-1 m) on 10 reefs, in a total of 48 surveys. Octocorals (Octocorallia: zooxanthellate and azooxanthellate alcyonarian soft corals and sea fans) were identified to genus level and were surveyed at 5 depths (18-13 m, 13-8 m, 8-3 m, 3-1 m, and reef flat) on 13 reefs, in a total of 147 surveys (each survey covering about 200 to 300 m^2). Cover of the main benthos groups (hard and octocorals, turf and coralline algae, macroalgae, sand and rubble, sponges etc) were also estimated during the octocoral surveys for each depth zone. Fish were surveyed between 12 m and the reef crest on 10 reefs, in a total of 34 surveys. Fish species were identified to species or species groups.

Statistical analyses

To facilitate comparison between taxonomic groups, all analyses were carried out on reef-level data (means over all survey periods, locations and depths per reef). Principal components analysis of log-transformed water quality concentrations (averaged over all visits) was used to characterize the study reefs and the relationships between the water quality variables. Concentrations of all variables except salinity were highly and positively correlated. Therefore, a water quality index (WQI) was calculated, as follows: (1) all water quality variables (except salinity) were standardised to mean zero and standard deviation

one (z-scores), and (2) the standardised values were summed over the 12 variables for each reef. Thus, a reef with a high WQI will typically have high concentrations of most of the variables that form the index, and a reef with low values has lower concentrations. Water with a high WQI value would typically appear murkier while one with a low WQI is clearer. Species abundances were fourth-root transformed (except hard corals) and reef-averaged over depths and sites. Species abundances were fourth-root transformed (except hard corals) and reef-averaged over depths and sites. Redundancy analyses (RDA, Rao 1964, Jongman *et al.* 1995) were used to relate differences in the assemblages to regional and water quality effects. Permutation tests (ter Braak 1992) were used to assess the statistical significance of the relationships.

Log-linear regression models were used to determine the regional and gradient effects on benthic cover, abundances and richness. Analyses followed the methods of Fabricius and De'ath (2004). These models were chosen because variation increased with the mean, and the implicit log transformation helped linearise the gradient effects. The models included regional effects to account for differences that may be unrelated to the water quality gradients. For each response, five models were fitted: (i) different slopes (gradient effects) within each region and different intercepts (region effects), (ii) same slope for both regions, but different intercepts (iii) single gradient common to both regions, (iv) no gradient effect but regional effects, and (v) no gradient or regional effects. The number of reefs investigated was small (10 to 13), and preliminary analyses indicated relatively weak associations between the responses and explanatory variables. Model averaging (Raftery 1995; Raftery 1988) of models based on the Bayesian Information Criterion (BIC) (Schwarz 1978) was used for all analyses of abundances and richness (Fabricius and De'ath 2004).

Based on BIC, we calculated the probability of each model (i) to (v), and the probability of a regional effect, defined as P(iv) / (P(iv) + P(v)), for all taxa seen on at least 25% of reefs. Probabilities were classified as strong to moderate ($P > 0.8$) or weak ($0.8 > P > 0.5$). Where differences existed, the direction of this difference was determined (WT>PC, or WT<PC), to calculate the percentage of taxa that had higher or lower abundances in WT. Finally, taxa that increased or decreased in abundance along the water quality gradient were identified. Only taxa that were encountered on at least 50% of the reefs were included in this assessment. For each of these taxa, the probability of the presence of a gradient effect was calculated as the sum of the probabilities of the models (i), (ii) and (iii). Probabilities were again classified as strong to moderate or weak for positive and negative relationships with water quality. All data analyses used S-Plus (Statistical Sciences 1999).

7.3 Results

Water Quality

Concentrations of many of the water quality variables differed between the Wet Tropics (WT) and Princess Charlotte Bay (PC) regions (Fig. 7.1). Mean suspended solids, chlorophyll, particulate nitrogen, particulate phosphorus and nitrate were higher in WT than in PC during the visits. Nitrate was particularly high in the WT, and negatively related to salinity. Water around most of the WT reefs had higher nutrient, sediment and chlorophyll concentrations than around PC reefs. While mean concentrations around the PC reefs were fairly homogeneous, water quality around the WT reefs varied more widely. Overall, the water quality index (WQI) was strongly associated with reefs of the WT, however Fitzroy Island and the Barnard Reefs in WT had a WQI that was similar to that of Wilkie Reef in PC (Fig. 7.2). Some WT reefs (Alexandra Reef and Double Island) were strongly associated with particulate matter (suspended solids, particulate nitrogen and phosphorus, chlorophyll and phaeopigments). Two other WT reefs (Normanby and High Islands) were strongly associated

with high concentrations of dissolved nutrients (nitrate, total dissolved nitrogen and phosphorus, and silicate) and reduced salinity.

Assemblages: Regional differences

Regional differences in cover, abundances and richness of some of the assemblages were pronounced (Table 7.1, Figs. 7.3 and 7.4). WT reefs were predominantly covered in algae and had low hard coral and octocoral cover. In WT, total algal cover was almost twice as high as PC, mostly due to differences in turfing algae, whereas cover of macroalgae and coralline algae were similar. Hard coral cover was less than a third, and octocoral cover was about half as high as in PC, whereas the cover of dead standing corals was 4.5 times higher in WT than in PC. Abundances of fish in WT were about a third of those in PC.

The taxonomic richness of some of the inshore reefs was high (Table 7.1). A total of 88 genera of fleshy macroalgae, 318 species of hard corals, 56 genera of octocorals, and 148 species of fish were distinguished in the surveys. Hard coral richness was twice as high in PC compared with WT reefs (Fig. 7.4): 44 species per site in WT (68 to 152 species per reef), compared with 89 species per site in PC (157 to 215 species per reef). Octocoral richness was also 30% lower in WT than PC (10 *vs.* 15 genera per site, 25 *vs.* 35 genera per reef). Richness of hard corals was highest on Hannah Reef, where the surveys yielded a total of 215 species, whereas the highest octocoral richness was found at Hay Reef (42 genera per reef). In contrast, the mean richness of macroalgal genera was 30% higher in WT than PC, whereas the richness of fish species was similar in both regions (Table 7.1).

A comparison of the types of taxa that contrasted in abundances provided insight into the nature of the regional differences. Among the macroalgae, abundances of Rhodophyta and Chlorophyta were 50% and 70% higher, respectively, in WT than PC (Table 7.1, Fig. 7.5). In contrast, abundances and richness of Phaeophyta were similar in both regions. Overall, nine genera had a moderate to high probability for occurring at higher abundances in WT compared with PC, of which six belonged to the division Rhodophyta, three were Chlorophyta, while none of the Phaeophyta was represented (Table 7.2). Only three taxa occurred at reduced abundances in WT compared to PC (one of each of the three main divisions; Table 7.2).

Table 7.1. Regional comparison of ecological reef attributes around inshore reefs of the Wet Tropics (WT) and Princess Charlotte Bay (PC) (Fig. 7.3). The table lists means and standard errors for each region, together with the ratio for WT/PC. Relative abundances of macroalgae are estimated as the mean sum of the relative abundance of each genus encountered per site, fish abundance is the mean sum of all fish encountered per site. Richness represents the mean number of taxa per site (genera for macroalgae and octocorals, species for hard corals and fish).

Attribute	PC	± SE	WT	± SE	Ratio WT/PC
WQI	-6.94	± 0.8	4.3	± 2.7	-0.63
Turf algae % Cover	23.6	± 1.9	50.7	± 8.1	2.15
Coralline algae % Cover	3.2	± 0.2	3.7	± 1.3	1.15
Macroalgae % Cover	12.7	± 1.7	13.3	± 5.4	1.05
Rhodophyta ($\Sigma_{(rel.\ abund.)}$)	10.0	± 0.6	14.6	± 1.4	1.46
Chlorophyta ($\Sigma_{(rel.\ abund.)}$)	4.0	± 0.1	6.7	± 0.8	1.70
Phaeophyta ($\Sigma_{(rel.\ abund.)}$)	7.9	± 0.3	7.7	± 2.0	0.97
Hard coral % Cover	28.7	± 0.6	8.2	± 2.9	0.28
Octocoral % Cover	7.9	± 0.6	4.04	± 0.7	0.51

Attribute	PC	± SE	WT	± SE	Ratio WT/PC
Rubble % Cover	15.1	± 2.3	22.5	± 4.9	1.49
Sand % Cover	23.5	± 1.8	19.1	± 4.6	0.81
Fish Abundance reef^{-1}	38710	± 4310	13330	± 5660	0.34
Macroalgae Richness	9.0	± 0.2	12.04	± 1.4	1.33
Rhodophyta	3.8	± 0.2	5.79	± 0.6	1.51
Chlorophyta	2.1	± 0.1	3.21	± 0.3	1.50
Phaeophyta	2.7	± 0.1	2.75	± 0.6	1.01
Hard coral Richness	89.3	± 2.6	43.60	± 5.0	0.49
Octocoral Richness	15.2	± 0.6	9.96	± 0.9	0.65
Zooxanthellate	8.2	± 0.3	6.47	± 0.8	0.79
Azooxanthellate	7.0	± 0.6	3.49	± 0.5	0.50
Fish Richness	51.6	± 2.2	48.54	± 6.7	0.94

For the hard corals, ninety species representing most of the major families and genera were more abundant in PC than in WT (Table 7.2, Fig. 7.6). The families Fungiidae, Faviidae and Pectiniidae, and the common genera *Acropora*, *Montipora*, *Alveopora* and *Goniopora* were all more abundant in PC than WT, whereas abundances of the genera *Porites*, *Turbinaria* and *Galaxea* showed no difference. In contrast to the 90 species that were more abundant in PC, only six species (the common *Pocillopora verrucosa* and *Porites rus*, and four uncommon to rare species) were more abundant in WT than PC.

For the octocorals, 11 genera belonging to the major families Nephtheidae and Xeniidae, and four gorgonian genera were significantly more abundant in PC than in WT, whereas the two low-encrusting or stolon-forming genera *Clavularia* and *Briareum* had higher representation in WT but were missing or rare in PC (Table 7.2).

Finally, 25 species of fish were likely to occur at higher abundance in PC than in WT. These included ten species susceptible to fishing pressure, three coral-dependent species (*Chaetodon aureofasciatus, C. lineolatus, C. plebius*), and two grazing herbivores. In contrast, 13 fish species had a high to moderate probability of occurring at higher abundance in WT than in PC. These included no coral-dependent species, only one species susceptible to fishing pressure and six grazing herbivores (Table 7.2).

The percentages of algal, coral and fish taxa that significantly differed in abundances between regions are summarized in Figure 7.6a. Among the macroalgae that strongly differed in abundance between the regions, 75% occurred predominantly in WT, whereas most of the hard coral and octocoral species were predominantly found in PC. In fish, the percentage of taxa that occurred predominantly in PC was 63%, while 37% appeared predominantly in WT.

In summary, the two regions differed in abundances and species composition of all four assemblages. Macroalgae and fish assemblages were composed of different suites of species in the two regions. In the hard corals and octocorals, most species were associated with PC reefs, and only a few species were well-represented at WT reefs; WT hard coral and octocoral assemblages were therefore composed not of a different suite of species, but of a subset of those species encountered in PC, and species that did grow in WT occurred in reduced numbers.

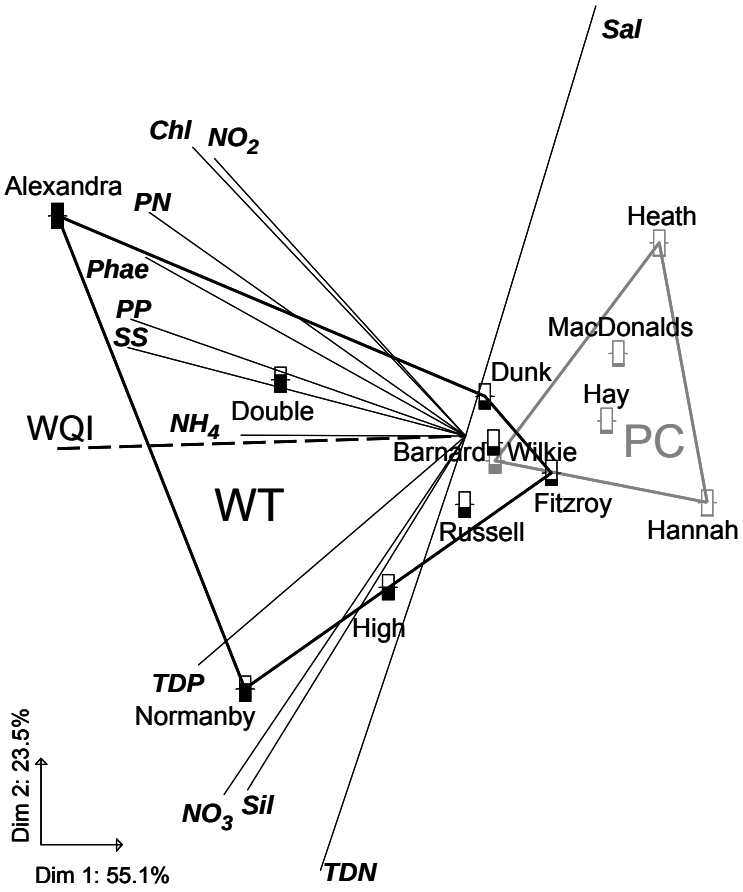


Figure 7.2. Water quality around inshore reefs in PC and WT, displayed by a principal components analysis biplot. The water quality vectors point towards the location with highest concentrations (abbreviations are listed in Methods). The vector of the water quality index (WQI, dashed line) is strongly associated with reefs of the WT. The WT and PC reefs are represented by black and grey thermometer symbols, respectively, with the fill of each symbol representing the water quality index of each reef. Concentrations of all particulate matter (suspended solids, particulate phosphorus and nitrogen, chlorophyll and phaeopigments) were highest at Alexandra Reef and lowest at Hannah Reef, whereas concentrations of silicate and lowest salinity were highest at Normanby Reef and High Island.

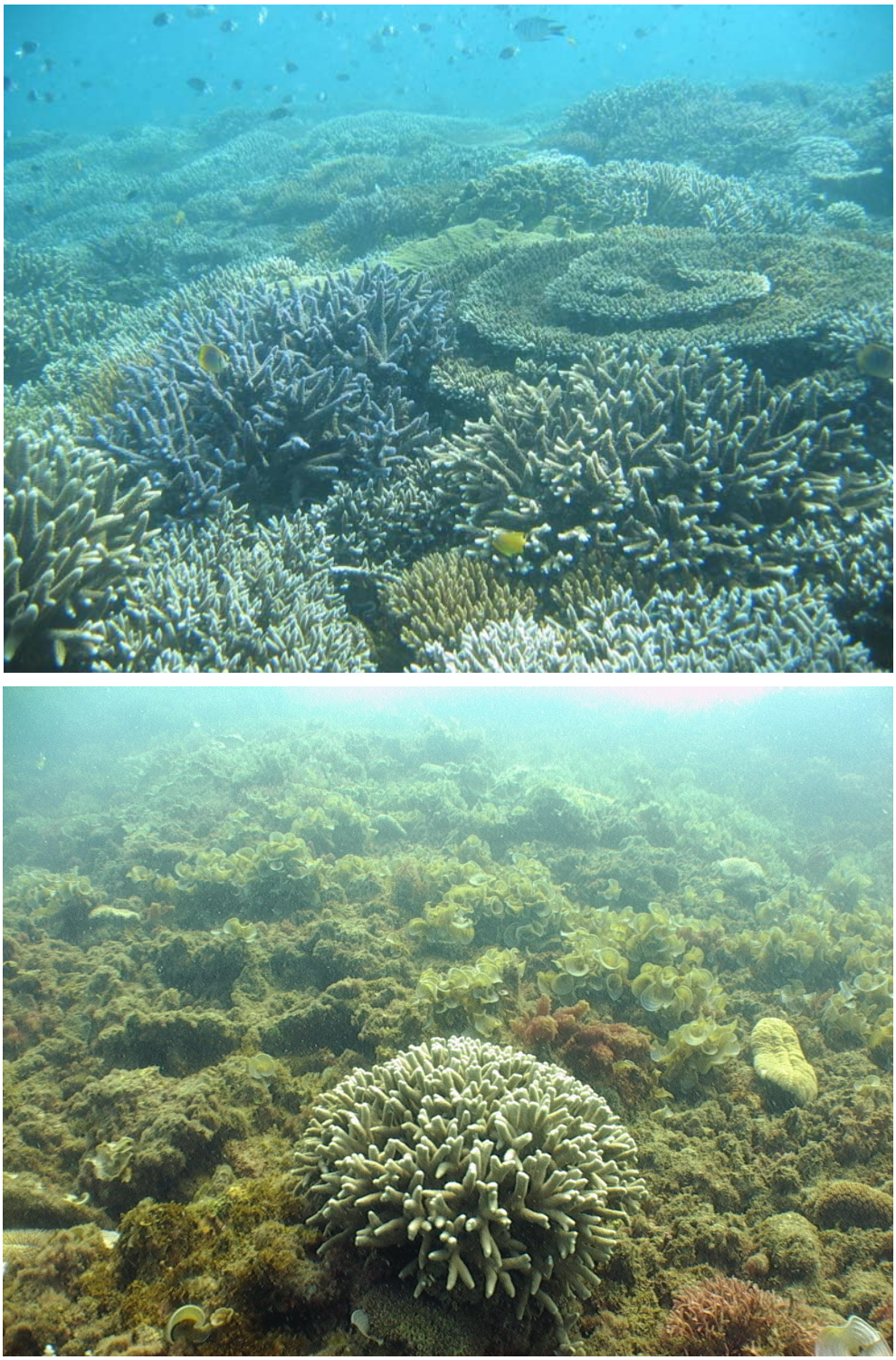


Figure 7.3. Examples of aspect of inshore reef assemblages in Princess Charlotte Bay (top) and the Wet Tropics (bottom).

Table 7.2. List of species that differ in abundance between regions (a), and change in abundances along the water quality gradient (b). Species with high probabilities (>0.95) are marked by an asterisk, all others are P >0.8. In the algae, letters behind the genus name indicate the division they belong to (R = Rhodophyta, C = Chlorophyta, P = Phaeophyta).

Algal genera	Hard Coral species	Octocoral genera	Fished fish species	Herbivorous fish species	Other fish species
a) Regional diferences: PC > WT					
Tolypiocladia (R) *	*Acropora nobilis* *	*Klyxum*	*Plectropomus leopardus*	*Naso annulatus*	*Acanthurus blochi*
Boodlea (C)	*Montipora hoffmeisteri* *	*Nephthea* *	*Cromileptes altivelis* *	*Zebrasoma veliferum* *	*Caesio cuning* *
Hydroclathrus (P)	*Palauastrea ramosa* *	*Stereonephthya* *	*Lethrinus laticaudus* *		*Pterocaesio marri*
	Galaxea astreata *	*Scleronephthya*	*Lethrinus nebulosus* *		*Scarus altipinnis*
	Merulina scabricula *	*Lemnalia*	*Lutjanus carponotatus* *		*Hipposcarus longiceps*
	Pectinia alcicornis *	*Xenia*	*Choerodon schoenlini* *		*Chaetodon aureofasciatus*
	Hydnophora rigida *	*Cespitularia* *	*Chelinus fasciatus* *		*Chaetodon lineolatus* *
	Echinopora horrida *	*Annella* *	*Cheilinus undulatus* *		*Chaetodon plebeius* *
	Echinopora pacificus *	*Iciligorgia*	*Plectorhyncus chrysotaenia* *		*Acanthochromis polyacanthus* *
	Lobophyllia dentatus *	*Alertigorgia* *	*Plectorhyncus lineatus* *		*Abudefduf sexfasciatus* *
	Oulophyllia bennettae *	*Menella* *			*Pomacentrus nagasakiensis*
	Etc. (total of 90 spp).				*Pomacanthus sextriatus*
WT > PC					
Asparagopsis (R) *	*Porites rus*	*Clavularia*	*Choerodon graphicus**	*Acanthurus triostegus* *	*Gomphosus varius*
Galaxaura-Trichleocarpa (R)*	*Montipora turtlensis* *	*Briareum*		*Naso tuberosus* *	*Thalassoma jansenii* *
Actinotrichea (R) *	*Pocillopora verrucosa*			*Naso unicornus*	*Chaetodon citrinellus* *
Portieria (R)	*Pocillopora eydouxi* *			*Scarus rubroviolaceus* *	*Chaetodon lunula*
Titanophora (R)	*Echinopora gemmacea* *			*Siganus corallinus*	*Abudefduf vaigiensis* *
Liagora/Yamadaella (R) *	*Symphyllia radians* *			*Kyphosus sp.* *	*Stegastes apicalis* *
Dictyosphaeria (C) *				*Acanthurus triostegus* *	
Neomeris (C)					
Chlorodesmis (C) *					

Algal genera	Hard Coral species	Octocoral genera	Fished fish species	Herbivorous fish species	Other fish species
b) Gradients: Decrease with WQI					
Jania (R)	*Acropora selago*	*Klyxum **	*Lethrinus lentjan **		*Scarus schlegeli*
	*Astreopora gracilis **	*Scleronephthya*	*Lutjanus carponotatus*		*Chaetodon rafflesi*
	Astreopora myriophthalma	*Astrogorgia*	*Lutjanus lemniscatus **		*Pomacentrus nagasakiensis**
	*Pectinia alcicornis **	*Menella*	*Lutjanus sebae*		
	Pavona explanulata				
	Ctenactis echinata				
	*Goniastrea australensis **				
	Goniastrea pectinata				
	Favia matthai				
	Favites halicora				
	*Favites russelli **				
	Montastrea magnistellata				
	Diploastrea heliopora				
	Herpolitha weberi				
	*Turbinaria peltata **				
Increase with WQI					
*Laurencia (R) **		*Briareum*		*Stegastes apicalis **	*Scarus ghobban **
Asparagopsis (R)					*Chromis atripectoralis*
*Neomeris (C) **					*Neopomacentrus azysron **
Halimeda (C)					

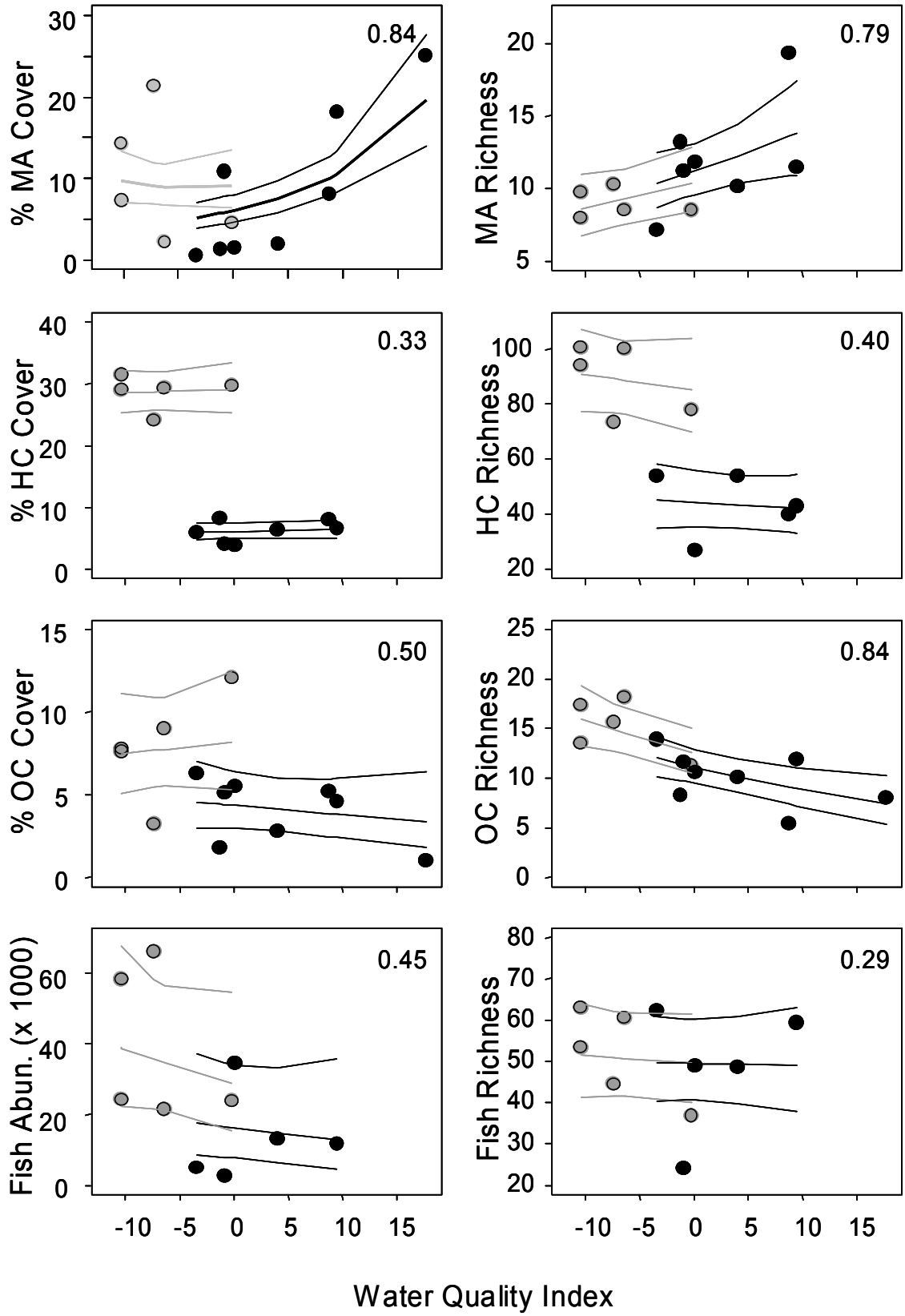


Figure 7.4. Cover, relative abundances and richness of fleshy macroalgae (MA), hard corals (HC), octocorals (OC) and fish from reefs in the two study regions, plotted against water quality (WQI). Black and grey points indicate WT and PC reefs, respectively. High WQI values represent high nutrient concentrations and low values represent relatively clean water. Solid lines are linear regression fits. The value in each panel indicates the probability for a gradient effect.

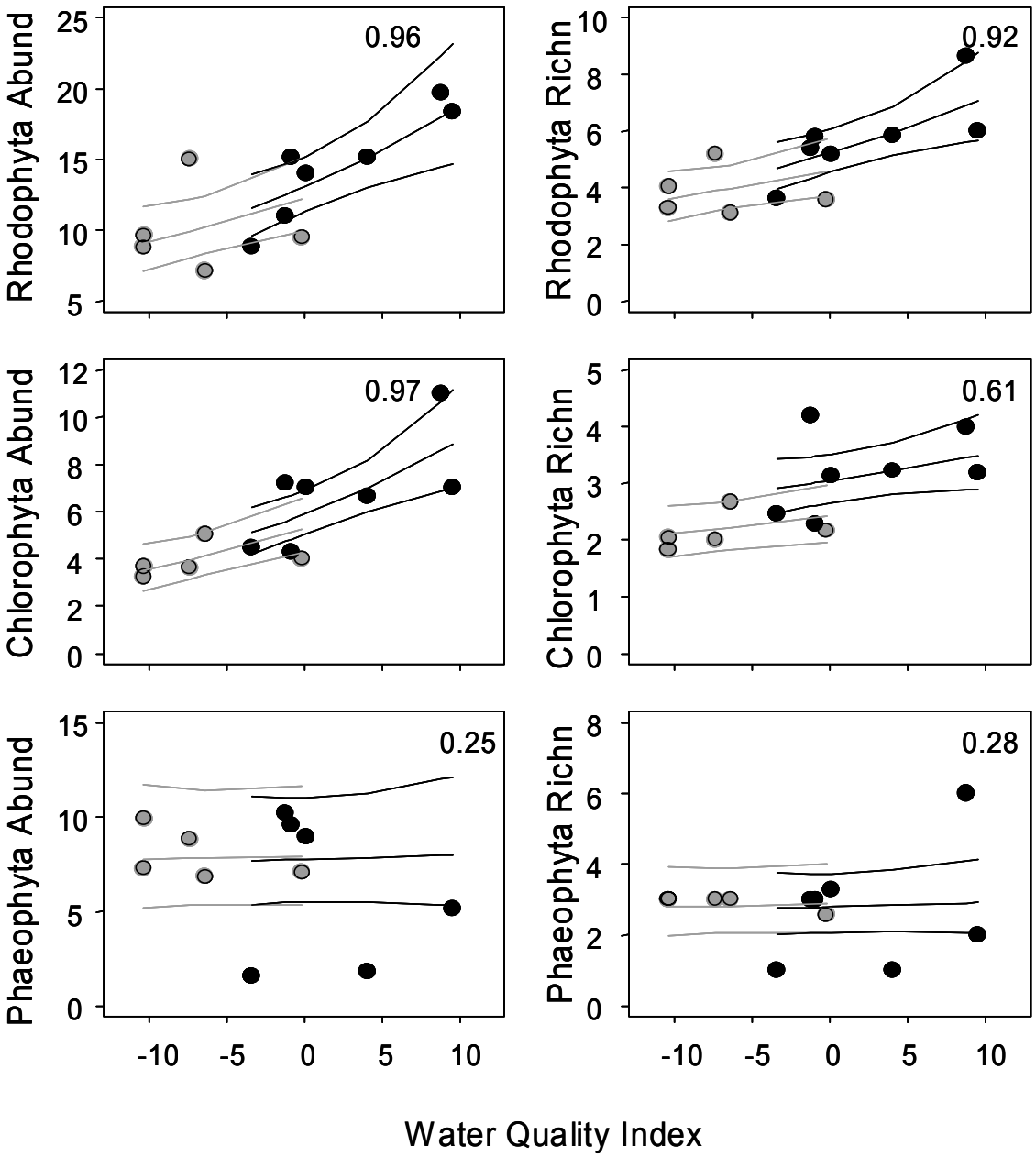


Figure 7.5. Cover, relative abundances and richness of the three main divisions of macroalgae, namely Phaeophyta, Chlorophyta, and Rhodophyta, from reefs in two regions, plotted against water quality (WQI). Black and grey points indicate WT and PC reefs, respectively. High WQI values represent high nutrient concentrations and low values represent relatively clean water. Solid lines are linear regression fits. The value in each panel indicates the probability for a gradient effect.

Assemblages: Gradients within regions

To investigate more specifically the role of water quality in shaping the reef communities, we related cover or abundances and richness of the four groups to the water quality index (WQI) scores of individual reefs. For macroalgae, total cover was highly variable, but cover tended to increase from a mean of 5% to 18% within WT with increasing WQI - i.e., increasing concentrations of particulate and dissolved nutrients, suspended solids and chlorophyll (Figure 7.4). Macroalgal richness increased from 8 to 13 genera per site. Both abundances and the generic richness of Rhodophyta, and abundances of Chlorophyta strongly increased with increasing WQI (Figure 7.5). Abundances and richness of Phaeophyta, and richness of Chlorophyta, were unrelated to WQI. Hard coral cover and richness and octocoral cover, all of which varied strongly between the regions, were unrelated to WQI (Figure 7.4). In contrast, four hard coral families (Agariciidae, Mussidae, Pocilloporidae and Faviidae) were strongly negatively related to water quality (Figure 7.6). Similarly, octocoral richness was strongly negatively related to WQI. Within WT, octocoral richness decreased by almost 50% from 12 genera per site (36 genera per reef) on the reef with the lowest WQI (best water quality) to 7 genera per site (19 genera per reef) on the reefs with highest WQI, whereas 13 to 16 genera per site (28 to 42 genera per reef) were recorded in PC. For fish, richness was similar but total relative abundances differed between regions (higher in PC than WT); however there was almost equally strong evidence that total abundances declined along the water quality gradient towards reefs with higher nutrient and sediment loads.

The percentages of algal, coral and fish taxa with positive or negative relationships to WQI are summarized in Table 7.2 and Figure 7.7b. The probabilities for gradients in abundances were weaker than probabilities for regional differences, due to the limited water quality data and small number of reefs. Nevertheless, in the macroalgae, 83% of the genera included in the analyses tended to increase in abundance with increasing WQI, compared with 17% that tended to decrease. Two to three of the macroalgae species were strongly and positively related to WQI: these were the rhodophyte *Laurencia*, the chlorophyte *Neomeris*, and to a slightly lesser extent *Asparagopsis*; all three taxa increased 5- to 6-fold along the water quality gradient. In contrast, none of the hard corals and octocorals had a high probability of increasing with increasing WQI. Instead, 13% of hard corals and 25% of octocorals showed a strong to moderate negative relationship with WQI, i.e., their abundances decreased with increasing nutrients, and overall the percentage of hard and octocoral taxa that tended to decrease with WQI was 60% and 85%, respectively. For the fish, three of the species included in the analyses increased and three decreased with WQI. Permutation tests on the abundances of all taxa in each of the four assemblages indicated that the assemblage structure of octocorals were strongly related to water quality and more weakly related to regions (Table 7.3). In contrast, for the assemblages of macroalgae, hard corals and fish, regional differences were stronger than the water quality effects.

In summary, while the water quality gradient was short and based on only limited water quality data and few reefs, the aggregated data showed clear increases in Rhodophyta and Chlorophyta along the water quality gradient, a clear decline in octocoral richness, and in the hard coral families Agariciidae, Mussidae, Pocilloporidae and Faviidae. In octocorals, gradient effects were stronger than regional differences, whereas for the other three assemblages, regional differences dominated the patterns in the assemblages.

Table 7.3. Redundancy analysis for the effects of regions (WT and PC) and water quality (WQI) on assemblages of MA = fleshy macroalgae, HC = hard corals, OC = octocorals, and fish. Sequential sums of squares were summed over the responses of each species or genus in each group to give analysis of variance tables. The pseudo-F (pF) statistic was bootstrapped and bias adjusted. Perm-P is the P-value of the permutation test used to assess the significance of the effect. For octocorals, there was a strong water quality effect and a weak region effect, whereas for the other three groups, regional differences were stronger than the water quality effect.

		DF	SS	%SS	pF	Perm P
MA	**Region**	1	14.7	18.9	2.3	0.001
	WQI	1	4.8	6.2	0.7	0.785
	Residuals	9	58.1	74.9		
HC	**Region**	1	110.0	31.0	3.6	0.003
	WQI	1	29.0	8.2	0.9	0.603
	Residuals	7	216.0	60.8		
OC	**WQI**	1	17.0	23.2	3.4	0.005
	Region	1	6.3	8.6	1.3	0.155
	Residuals	10	50.0	68.3		
Fish	**Region**	1	27.9	33.6	4.0	0.005
	WQI	1	5.9	7.1	0.8	0.653
	Residuals	7	49.1	59.2		

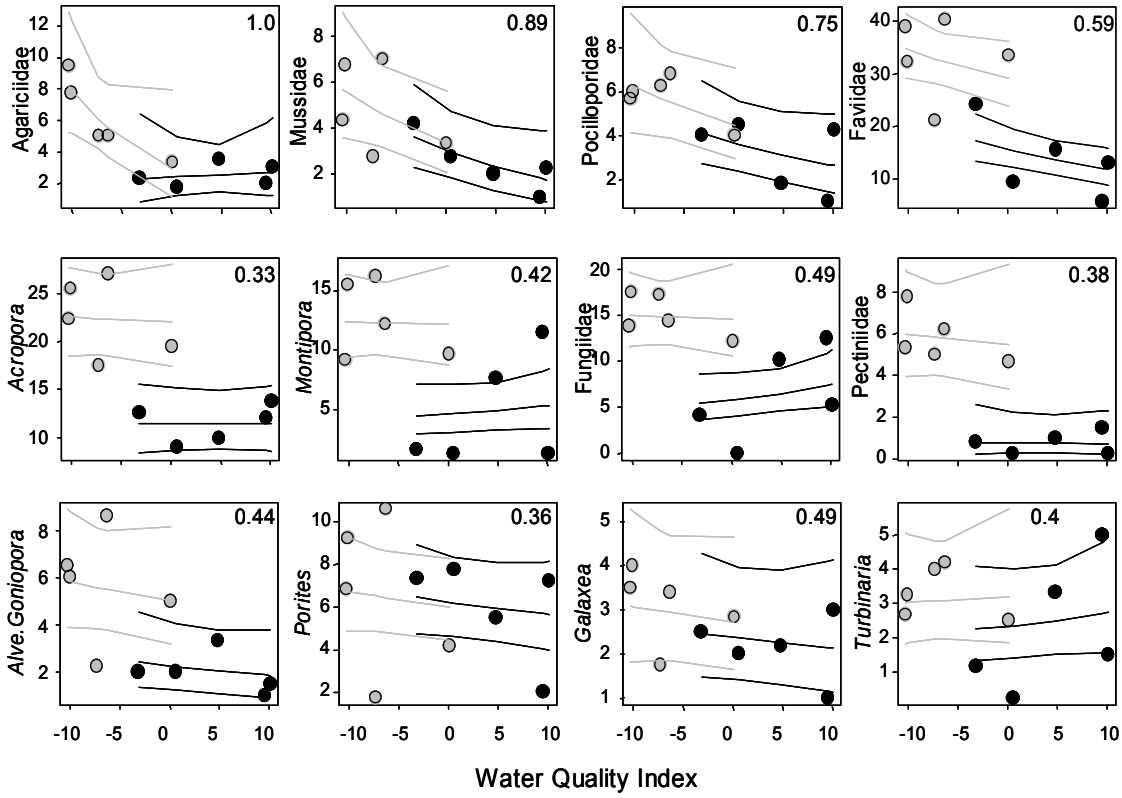


Figure 7.6. Changes in relative abundances between regions and along the WQI of the 12 main families and genera of hard corals. High WQI values represent high nutrient concentrations and low values represents relatively clean water. Black and grey points indicate WT and PC reefs, respectively. Solid lines are linear regression fits. The value in each panel indicates the probability for a gradient effect.

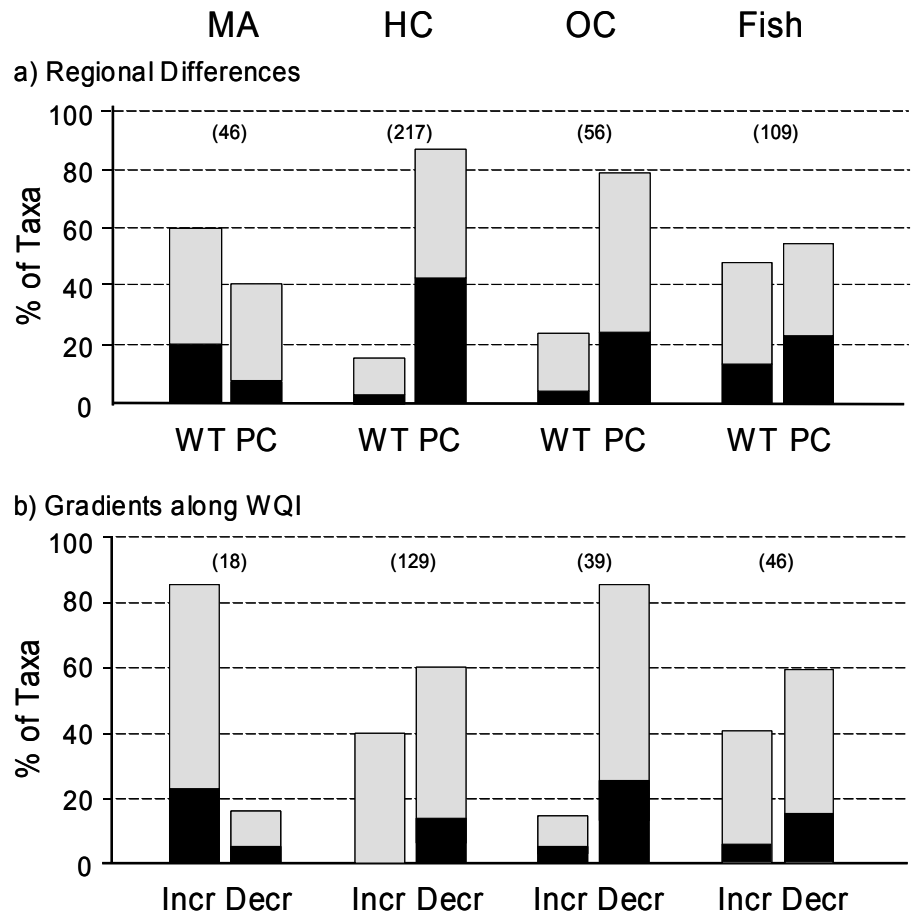


Figure 7.7. Percentage of fleshy macroalgae (MA), hard coral (HC), octocoral (OC) and fish taxa that differ in abundances between the regions (a), and that in both regions consistently positively or negatively related to the WQI gradient, hence increase or decrease in abundance with increasing nutrients (b). Analyses only included taxa that were found at least at 25% (a) and 50% (b) of reefs; taxa that followed the WQI gradient but in which the direction of change was inconsistent in the two regions were also excluded. Numbers of taxa included in the analyses are given in brackets. Probabilities are AIC probabilities for the existence of gradients in abundances along the water quality gradient; black bars indicate high to moderate probability for an association ($P > 0.8$), grey = weak ($P \leq 0.8$).

7.4 Discussion

The inshore Great Barrier Reef: water quality and geography

Turbid inshore coral reefs of the Great Barrier Reef (GBR) can support highly diverse assemblages of hard corals, octocorals, algae and fish, and high coral cover. On the 10 inshore reefs surveyed, a total of 318 species of hard corals were recorded, representing 80% of the 400 hard coral species known to occur on the GBR (Veron 2000). Similarly, 13 inshore surveys yielded 80% of the 70 documented GBR octocoral genera (Fabricius and Alderslade 2001), and 85% of the 103 fleshy macroalgae from the GBR (McCook *et al.*, 2000). Likewise, 70% of all GBR hard coral species have previously been recorded on inshore reefs of the Whitsunday Islands (Devantier *et al.* 1998). Our study therefore added evidence to the suggestion that turbid shallow inshore reefs can represent highly diverse coral reef habitats. The inshore reefs of Princess Charlotte Bay that have remained relatively undisturbed by terrestrial runoff and other anthropogenic influences were particularly rich, both in ecological and aesthetic terms. Other inshore reefs closer to human influences appear depauperate in comparison, but it has been unclear whether these differences have always existed, and to what extent they may have been related to nutrient enrichment and increased siltation from agricultural runoff.

Our water quality data indicated that mean concentrations of particulate and dissolved nutrients were generally higher on WT reefs than in PC. The existence of such regional differences is supported by two-fold differences in long-term chlorophyll *a* values recorded monthly since 1992 in both regions (Brodie *et al.* 1997, Fabricius and De'ath 2004, Brodie *et al.* in review). Water column chlorophyll concentration is widely used as a proxy for nutrient status in shallow waters. In the central GBR but not in the Far North, chlorophyll concentrations increase steeply towards the coast, indicating that the differences can not be explained just by latitude or by cross-self patterns, but that more nutrients are available in WT inshore compared with WT offshore and PC inshore and offshore (Brodie *et al.* in review). New nutrients in inshore waters are predominantly derived from river plumes (Furnas 2003). Nutrient and sediment discharges by river floods from agriculturally used catchments in the central GBR (including WT) have increased 5 to 10-fold since European settlement, whereas concentrations have remained relatively similar in the Far North (including Princess Charlotte Bay) where agriculture is minimal (McCulloch *et al.* 2003; Furnas 2003). However, since historic water quality data from the GBR are sparse, it is impossible to determine whether or not chlorophyll levels in this region have increased in response to past and present land use practices.

The shallowness and width of the northeast Australian continental shelf of the GBR plays an important role in the retention of imported material. It distinguishes the GBR system from many other Indo-Pacific coral reefs surrounded by deeper water. The median depth of the GBR seafloor is 35 m (range: intertidal to 90 m), and the shelf-width ranges from 50 km in the north to over 300 km in the south. The inshore seafloor is particularly shallow (intertidal to 20 m depth), and much of the fine sediment is therefore easily resuspended by swell. While river plumes are short-lived, biological uptake by phytoplankton and bacteria converts dissolved inorganic nutrients into particulate organic matter, the repeated resuspension of which contributes to turbidity and reduces the lower depth limit for seagrass and corals (Short *et al.* 1995; Longstaff and Dennison 1999; Anthony and Fabricius 2000; Yentsch *et al.* 2002). A large proportion of the particulate material may remain in the inshore system for prolonged periods of times (probably years to decades), undergoing cycles of deposition and resuspension while it is slowly transported northwards, prior to final deposition in a sheltered area (Larcombe *et al.* 1995), or offshore transport such as observed in the Cairns region (Wolanski *et al.* 2003a). The main issues dominating the water quality of inshore areas are therefore organic enrichment and the loss of light rather than the short-lived dissolved

inorganic nutrients. One of the problems in assessing future effects of terrestrial runoff is the unknown capacity of the system to absorb inputs of phosphates and organic materials to the GBR lagoon.

Macroalgae

Total cover of macroalgae, abundance and richness of Rhodophyta, and abundance of Chlorophyta increased along the water quality gradient from lowest to highest nutrient and particle concentrations. The doubling in relative abundances in both groups was due to small increases in a large number of genera, rather than a take-over of one or few genera. The response in Rhodophyta and Chlorophyta and the absence of a response in the Phaeophyta is intriguing. While hard coral cover was strongly negatively related to turf algal cover, it was unrelated to macroalgal cover and abundance of rhodophytes and chlorophytes. While algal abundances may have been enhanced by coral disturbance (McCook *et al.* 2001; Diaz-Pulido and McCook 2004), the data did not suggest that the coral decline lead to a release in fleshy macroalgae at a whole-reef scale. The pattern may instead represent a direct response of rhodophytes and chlorophytes to water quality, or to other unspecified habitat characteristics along the water quality gradient. Non-calcifying chlorophytes, such as *Enteromorpha* (Lotz and Schram 2000) and *Dictyosphaeria* (Smith 1981) were identified in previous studies of severe eutrophication as potential indicators for nutrient enrichment, and various studies have proposed the use of rhodophytes as indicators of eutrophication (Lapointe 1987; Horrocks *et al.* 1995). The rhodophyte *Asparagopsis taxiformis*, one of the taxa strongly correlated with the water quality gradient, is commonly found in disturbed sites, from eutrophic inshore reefs (Diaz-Pulido and McCook 2002) to pristine offshore sites (Hatcher 1984). The lack of response in the phaeophytes is consistent with previous results showing that *Sargassum* thrives and is nutrient-replete on offshore reefs (McCook 1996), but the interpretation of these patterns is complex. For example, the growth of *Sargassum* is enhanced by small additions and depressed at slightly higher additions of dissolved inorganic nutrients, but growth is also enhanced by the adhesion of particulate matter to the leaf surfaces in controlled laboratory studies (Schaffelke and Klumpp 1998; Schaffelke 1999). Similarly, slow-release fertilizer application suppressed brown frondose macroalgae in a field study in the Caribbean, while enhancing the green filamentous macroalgae *Enteromorpha prolifera* and other green turf algae and having no effect on red algae (McClanahan *et al.* 2002).

Net growth rates in macroalgae can be limited by one or a combination of factors, including nutrients, herbivory, light, flow and wave action, and limitations can depend on species, habitat types and region. In particular, herbivory is known to obscure the responses of algae to nutrients and sediments (McCook 2001; Miller *et al.* 1999; McCook *et al.* 2001; Jompa and McCook 2002; Smith *et al.* 2001). However, in our study, macroalgal abundance increased with increasing nutrients within the WT reefs, despite the relatively high abundance of herbivores on the WT reefs. This suggests that growth rates of some algae outstripped consumption by herbivores, perhaps due to nutrient enhanced growth or reduced fish grazing as a result of increased sediment trapping by the algae.

Hard Corals

For hard corals, richness was only half as high in WT as in PC. This was due to low abundances in the sensitive taxa *Acropora* and *Montipora,* some of the Pocilloporidae, and some of the more persistent Pectiniidae and Fungiidae. In contrast, differences were weaker in the genera *Porites*, *Galaxea* and *Turbinaria*, which are known to be among the most persistent and sediment- and nutrient-tolerant coral genera (Done 1982, Stafford-Smith and Ormond 1992; Birkeland 2000; Philipp and Fabricius 2003). Coral cover has declined due to bleaching, *A. planci* and a cyclone on Russell and Normanby Reefs in WT since 1990 (Ayling and Ayling 2002), and these hard coral specific disturbances will have strongly contributed to

the low abundances of the more sensitive taxa in WT. On these reefs, coral cover did not recover but either remained level or continued to decline in the years when no obvious disturbances were recorded. A similar ~1% per year decline in coral cover from an average of 22% in 1986 to ~8% in 2002 was recorded on eight WT inshore reefs in the WT region (AIMS Long-term Monitoring Program, unpub. manta tow data), three of which were part of our investigation (Barnard, Normanby, and Fitzroy Reef). These two data sets indicate that storms, bleaching and *A. planci* were the direct causes for the observed decline in coral cover, explaining the low abundances of genera such as *Montipora* and *Acropora.* However, our data of a number of species gradually decreasing along the water quality gradient suggest that water quality conditions may have added to the effects of other disturbances and latitude.

Along the water quality gradient, decreases were observed in the moderately resilient, long-lived and relatively bleaching-insensitive families Mussidae, Agariciidae and Faviidae, and the pioneer family Pocilloporidae. In contrast, no changes along the water quality gradient were recorded in the most sensitive genera and families (as these taxa were largely missing in WT), and in the toughest genera and families. A latitudinal decline in hard coral richness is well established, but the 50% difference in richness between the regions cannot be entirely explained by latitude: hard coral richness decreases by only 25% along the whole length of the GBR, and richness of inshore reefs increases both south and north of WT (Devantier *et al.* unpub. data). Many of the species that were found in higher abundances in PC than in WT in this study, also occur in the Whitsunday Islands at the cleaner sites but not at sites with high chlorophyll levels closer to the river mouth (e.g. *Hydnophora rigida, Palauastrea ramose, Acropora nobilis, Echinopora horrida*, and many others; van Woesik *et al.* 1999, Devantier *et al.* 1998). The low abundances or absence of many of these taxa in WT is therefore not due to latitudinal effects and only partly due to the specific disturbance history of the WT, but likely to be at least partly related to water quality conditions. It is important to note that the assemblages on our study reefs did not undergo species replacement from low to high nutrient conditions. Instead, reefs in the most nutrient-rich environments supported a subset of species of the least nutrient-enriched environments, with about 50% of species missing and no additional species entering the assemblage.

Early life stages of hard corals are particularly sensitive to changes in water quality, and coral settlement and juvenile survival are inhibited by sedimentation especially when sediments are organically enriched (Babcock and Smith 2002, Fabricius *et al.* 2003). Hard coral recruitment rates are three times higher on PC than WT inshore reefs, for unknown reasons (Fabricius *et al.* unpub. data). It is possible that the main effect of organic enrichment on hard coral assemblages is impairment of recruitment. Thus, while the present-day WT inshore hard coral assemblages reflect a history of repeated disturbances, water quality may affect hard coral assemblages by slowing their recovery rates, or by increasing their vulnerability to disturbances. In the absence of further severe disturbances, these reefs may eventually return to being occupied by highly diverse hard coral assemblages.

Octocorals

Octocoral richness declined by 60% along the water quality gradient. Octocoral richness declines with latitude by ~30% along the length of the GBR (Fabricius and De'ath 2001). Hence as with hard corals, latitude alone is insufficient to explain the difference between the two regions. Soft coral abundance has been found to be significantly negatively correlated with turbidity, suspended particulate matter, silicate and total organic sediment contents (van Woesik *et al.* 1999). Furthermore, richness of zooxanthellate octocorals has been found to declines along a gradient of increasing chlorophyll across the continental shelf off the Wet Tropics (Fabricius and De'ath 2004), and declines by one genus for each meter of visibility lost in otherwise comparable GBR habitats (Fabricius and De'ath 2001). An investigation of the types of taxa missing in WT further confirms that water quality affects octocoral richness.

The two taxa found in higher abundances in WT than PC (*Briareum* and *Clavularia*) generally occur in highest abundances in turbid waters throughout the GBR, whereas genera within the families Nephtheidae and Xeniidae (that had higher representation in PC than in WT) are generally found in moderately clear water (Dinesen 1983, Fabricius and Alderslade 2001). Evidence is therefore increasing that octocorals respond more strongly and more specifically to water quality than do hard corals.

Fish

For fish, total relative abundances were three times higher in PC than WT, however there was also evidence that total abundances declined with decreasing water quality. Importantly, fish assemblages were composed of different suites of species in the two regions. This contrasted with the hard corals in which WT assemblages were composed of subsets of PC species rather than different suites of species. The most striking differences in the fish assemblages were the greater abundance of species vulnerable to fishing in PC and the greater abundances of grazing herbivores in WT. The greater fishing pressure in WT compared to PC (Mapstone *et al.* 2004, Williams 2002), and the observation that any fished species in WT were generally at or below the minimum legal size for capture (in contrast to their large sizes in PC) strongly indicates that the difference in species vulnerable to fishing between the regions is a result of relative fishing pressures. The second major difference was the greater abundance of the common grazing herbivores in WT, with six species that comprised the majority of grazers being more abundant in the more turbid waters of WT than PC. Only two common grazing species were more abundant in PC than WT. The roles of modified habitat complexity and altered food availability for coral- and algae-feeding guilds deserve more attention. The finding of increased herbivore abundances in WT is intriguing as there is no evidence that herbivore abundances are food regulated, and it also contrasts with the conclusion of Wolanski *et al.* (2003b), that the abundance of herbivorous fish in the GBR is predicted by water clarity.

Overall, the species richness of fish on the WT and PC inshore reefs were similar, and intermediate between that of another well-studied inshore reef of the central GBR south of WT (Pandora Reef) and three mid-shelf reefs of the Central GBR off Townsville (Williams 1982). Acanthurids and labrids were notably richer on the WT reefs than PC but, surprisingly, the largely coral-dependent butterflyfishes (Chaetodontidae) were equally rich (but some were less abundant) in the WT and PC, despite differences in coral cover. Among the WT reefs, fish diversity was particularly low on South Barnard Island, which was characterized by a rocky substratum and low dead or live coral cover. The relatively high diversity of fish on other WT reefs may be related to the close proximity to the diverse communities on adjacent mid-shelf reefs that may serve as a source of recruits (similar mid-shelf reefs in the region to the north of PC have relatively low diversity; Williams unpub. data).

Assessing ecological responses in inshore reef communities

Detailed surveys at relatively fine taxonomic resolution, when cautiously interpreted in the context of available biophysical environmental data and biological knowledge of key species, can provide important information on the health and status of inshore coral reefs. A cross-comparison of the results indicates that of the four taxonomic groups investigated, octocorals were the assemblage most strongly related to water quality. Octocoral abundances are particularly tightly linked to physical environmental conditions (Fabricius and De'ath 1997; Karlson *et al.* 1996), possibly because no major predator exists for octocorals (*A. planci* do not eat octocorals; De'ath and Moran 1998), whereas abundances of the other three groups are partly controlled by predation: most macroalgae are affected by fish grazing, hard corals by *A. planci*, and some of the larger fish by human fishing pressure. Our data also show strong response in a number of rhodophytes and chlorophytes to water quality, which deserves closer investigation. Among the hard corals, water quality effects were most

noticeable in the families Mussidae, Agariciidae and Faviidae, which are moderately resilient, long-lived, relatively bleaching-insensitive and not among the most preferred food for *A. planci*. In contrast, the most sensitive genera and families were largely missing in WT, and the toughest genera and families did not change in abundance along the water quality gradient. Changes in abundances of moderately sensitive groups such as the Mussidae, Agariciidae and Faviidae, are therefore most suitable as indicators for environmental stress. For fish, there appeared to be a relationship between total abundances and water quality, and some of the species decreased whereas others increased in abundance with water quality.

Causes for differences in assemblages are naturally difficult to determine definitively in ecological studies, especially if historic data are sparse. A framework based on epidemiological criteria can help synthesize and weigh available evidence to assess the likelihood of a causal association (Fabricius and De'ath 2004). In our study, both the regional differences in water quality and assemblages, and the existence of ecological gradients along the water quality gradients, added evidence that many of the responses were related to the differences in water quality. The changes along the water quality gradient that were consistent in direction with other studies (decreasing corals and increasing algae), the monotonic responses, and the large and ecologically relevant effect sizes, all added evidence that the inshore reef assemblages are strongly shaped by present-day water quality conditions. The implementation of management plans to halt or reverse a decline in water quality, through improved upstream land-use practices and waste water treatment, is vital to ensure the long-term health of inshore reefs of the GBR (The State of Queensland and Commonwealth of Australia, 2003).

7.5 References

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

Ayling AM, Ayling AL. 2002. The dynamics of Cairns Section Fringing Reefs: 2001. Final Report. GBRMPA, Townsville.

Babcock RC, Smith L. 2002. Effects of sedimentation on coral settlement and survivorship, Proceedings of the Ninth International Coral Reef Symposium, Bali, Indonesia, pp. 245-248.

Birkeland C. 1988. Geographic comparisons of coral-reef community processes. In: Choat, J.H. *et al.* (Eds.), Proceedings of the Sixth International Coral Reef Symposium, Townsville (Australia), pp. 211-220.

Birkeland C. 2000. Changes over 23 years in a coral community at a sewer outfall in a fast-current area of Palau. Abstract, Ninth International Coral Reef Symposium, Bali, Indonesia, pp. 271.

Brodie J, Furnas MJ, Steven ADL, Trott LA, Pantus F, Wright M. 1997. Monitoring Chlorophyll in the Great Barrier Reef Lagoon: Trends and Variability, 8th International Coral Reef Symposium, Panama, pp. 797-802.

De'ath G, Moran PJ. 1998. Factors affecting the behaviour of crown-of-thorns starfish (*Acanthaster planci* L.) on the Great Barrier Reef: 2: Feeding preferences. Journal of Experimental Marine Biology and Ecology 220: 107-126.

Devantier LM, De'ath G, Done TJ, Turak E. 1998. Ecological assessment of a complex natural system: A case study from the Great Barrier Reef. Ecological Applications 8: 480-496.

Devlin M, Brodie J, Waterhouse J, Mitchell A, Audas D, Haynes D. 2003. Exposure of Great Barrier Reef inner-shelf reefs to river-borne contaminants. Second National Conference on Aquatic Environments: Sustaining Our Aquatic Environments – Implementing Solutions. 20-23 November, 2001. Queensland Department of Natural Resources and Mines, Brisbane, Australia.

Diaz-Pulido G, McCook LJ. 2002. The fate of bleached corals: Patterns and dynamics of algal recruitment. Marine Ecology Progress Series 232: 115-128.

Diaz-Pulido G, McCook LJ. 2004. Effects of live coral, epilithic algal communities and substrate type on algal recruitment. Coral Reefs 23: 225-233.

Dinesen ZD. 1983. Patterns in the distribution of soft corals across the central Great Barrier Reef. Coral Reefs 1: 229-236.

Done TJ. 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1: 95-107.

Fabricius KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50: 125-146.

Fabricius K, Alderslade P. 2001. Soft Corals and Sea Fans: A comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science, Townsville, 264 pp.

Fabricius K, De'ath G. 1997. The effects of flow, depth and slope on cover of soft coral taxa and growth forms on Davies Reef, Great Barrier Reef. In: Lessios H (Ed) Proceedings of the Eighth International Coral Reef Symposium. Smithsonian Tropical Research Institute, Balboa, Panama, pp. 1071-1076.

Fabricius KE, De'ath G. 2001. Biodiversity on the Great Barrier Reef: Large-scale patterns and turbidity-related local loss of soft coral taxa. In: Wolanski E (Ed) Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef. CRC Press, London, pp. 127 - 144.

Fabricius KE, De'ath G. 2004. Identifying ecological change and its causes: A case study on coral reefs. Ecological Applications 14: 1448-1465.

Fabricius K, Wild C, Wolanski E, Abele D. 2003. Effects of transparent exopolymer particles (TEP) and muddy terrigenous sediments on the survival of hard coral recruits. Estuarine, Coastal and Shelf Science 57: 613-621.

Furnas MJ. 2003. Catchments and Corals: Terrestrial Runoff to the Great Barrier Reef. Australian Institute of Marine Science, CRC Reef. Townsville, Australia.

Furnas MJ, Mitchell AW. 1996. Nutrient inputs into the central Great Barrier Reef (Australia) from subsurface intrusions of Coral Sea waters: A two-dimensional displacement model. Continental Shelf Research 16: 1127-1148.

Grigg RW. 1995. Coral reefs in an urban embayment in Hawaii: A complex case history controlled by natural and anthropogenic stress. Coral Reefs 14: 253-266.

Hatcher BG. 1984. A maritime accident provides evidence for alternate stable states in benthic communities on coral reefs. Coral Reefs 3: 199-204.

Horrocks JL, Stewart GR, Dennison WC. 1995. Tissue nutrient content of *Gracilaria* spp. (Rhodophyta) and water quality along an estuarine gradient. Marine and Freshwater Research 46: 975-983.

Lapointe BE. 1987. Phosphorous- and nitrogen-limited photosynthesis and growth of *Gracilaria tikvahiae*. Marine Biology 93: 561-568.

Hunter CL, Evans CW. 1995. Coral reefs in Kaneohe Bay, Hawaii: Two centuries of western influence and two decades of data. Bulletin of Marine Science 57: 501-515.

Jompa J, McCook LJ. 2002. The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). Limnology and Oceanography 47: 527-534.

Jongman RHG, Ter Braak CJF, van Tongeren OFR. (Eds) 1995. Data analysis in community and landscape ecology. Cambridge University Press, 299 pp.

Karlson RH, Hughes TP, Karlson SR. 1996. Density-dependent dynamics of soft coral aggregations: The significance of clonal growth and form. Ecology 77: 1592-1599.

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

Longstaff BJ, Dennison WC. 1999. Seagrass survival during pulsed turbidity events: the effects of light deprivation on the seagrasses *Halodule pinifolia* and *Halophila ovalis*. Aquatic Botany 65: 105-121.

Lotz H, Schram W. 2000. Ecopysiological traits explain species dominance patterns in marcroalgal blooms. Journal of Phycology 36: 287-295.

Loya Y, Lubinevsky H, Rosenfeld M, Kramarsky-Winter E. 2004. Nutrient enrichment caused by in situ fish farms at Eilat, Red Sea is detrimental to coral reproduction. Marine Pollution Bulletin (in press).

Mapstone BD, Davies CR, Little LR, Punt AE, Smith ADM, Pantus F, Lou DC, Williams AJ, Ayling AM, Russ GR, McDonald AD, *et al.* 2004. The effects of line fishing on the Great Barrier Reef and evaluations of alternative potential management strategies. CRC Reef Research Centre Technical Report No 52, Townsville, Australia.

McClanahan TR, Cokos BA, Sala E. 2002. Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize. Marine Pollution Bulletin 44: 441-451.

McCook LJ. 1996. Effects of herbivores and water quality on the distribution of *Sargassum* on the central Great Barrier Reef: cross-shelf transplants. Marine Ecology Progress Series 139: 179-192.

McCook LJ. 2001. Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. Coral Reefs 19: 419-425.

McCook LJ, De'ath G, Price IR, Diaz-Pulido G, Jompa J. 2000. Macroalgal resources of the Great Barrier Reef: Taxonomy, distributions and abundances on coral reefs. Report to the Great Barrier Reef Marine Park Authority.

McCook LJ, Jompa J, Diaz-Pulido G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19: 400-417.

McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D. 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421: 727-730.

Miller MW, Hay ME, Miller SL, Malone D, Sotka EE, Szmant AM. 1999. Effects of nutrients versus herbivores on reef algae: A new method for manipulating nutrients on coral reefs. Limnology and Oceanography 44: 1847-1861.

Montaggionil LF, Cuet P, Naim O, Walton Smith FG. 1993. Effect of nutrient excess on a modern fringing reef (Reunion Island, Western Indian Ocean) and its geological implications, Global aspects of coral reefs: Health, hazards and history. University of Miami, Miami, pp. 27-33.

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

Raftery AE. 1988. Approximate Bayes factors for generalized linear models. Department of Statistics, University of Washington.

Raftery AE. 1995. Bayesian model selection in social research (with Discussion). In: Marsden PV (Ed) Sociological Methodology. Blackwells, Cambridge, Mass., pp. 111-196.

Rao C. 1964. The use and interpretation of principal components analysis in applied research. Sankhyã A 26: 329-358.

Schaffelke B. 1999. Particulate organic matter as an alternative nutrient source for tropical *Sargassum* species (Fucales, Phaeophyceae). Journal of Phycology 35: 1150-1157.

Schaffelke B, Klumpp DW. 1998. Nutrient-limited growth of the coral reef macroalga *Sargassum baccularia* and experimental growth enhancement by nutrient addition in continuous flow culture. Marine Ecology Progress Series 164: 199-211.

Schaffelke B, Mellors J, Duke NC. 2005. Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. Marine Pollution Bulletin 51: 279-296.

Schwarz G. 1978. Estimating the Dimension of a Model. Annals of Statistics 6: 461-464.

Short FT, Burdick DM, Kaldy JE III. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. Limnology and Oceanography 40: 740-749.

Smith SV. 1981. Responses of Kaneohe Bay, Hawaii, to relaxation of sewage stress. In: Neilson BJ, Cronon LE (Eds) International Conference on the Effects of Nutrient Enrichment in Estuaries, 29 May 1979, Williamsburg, VA (USA), pp. 391-412.

Smith JE, Smith CM, Hunter CL. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19: 332-342.

Stafford-Smith MG, Ormond RFG. 1992. Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. Australian Journal of Marine and Freshwater Research 43: 683-705.

Statistical Sciences 1999. S-PLUS, Version 2000 for Windows. a division of Mathsoft Inc., Seattle.

Stimson J, Larned ST. 2000. Nitrogen efflux from sediments of a subtropical bay and the potential contribution to macroalgal nutrient requirements. Journal of Experimental Marine Biology and Ecology 252: 159-180.

Stimson J, Larned ST, Conklin E. 2001. Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalga *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii. Coral Reefs 19: 343-357.

ter Braak CJF. 1992. Permutation versus bootstrap significance tests in mulitple regression and anova. In: Jöckel K, Rothe G, Sendler W (Eds) Bootstrapping and related techniques. Springer Verlag, Berlin, pp. 79-86.

The State of Queensland and Commonwealth of Australia. 2003. Reef Water Quality Protection Plan; for catchments adjacent to the Great Barrier Reef World Heritage Area. Queensland Department of Premier and Cabinet, Brisbane.

van Woesik R, Tomascik T, Blake S. 1999. Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. Marine and Freshwater Research 50: 427-440.

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

West K, van Woesik R. 2001. Spatial and temporal variance of river discharge on Okinawa (Japan): Inferring the temporal impact on adjacent coral reefs. Marine Pollution Bulletin 42: 864-872.

Williams DMcB. 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. Coral Reefs 1: 35-43.

Williams LE (Ed) 2002. Queensland's fisheries resources. Current condition and recent trends: 1998-2000. Queensland Department of Primary Industries, Brisbane, pp. 180.

Wolanski E, Marshall K, Spagnol S. 2003a. Nepheloid layer dynamics in coastal waters of the Great Barrier Reef, Australia. Journal of Coastal Research 19: 748-752.

Wolanski E, Richmond R, McCook L, Sweatman H. 2003b. Mud, marine snow and coral reefs. American Scientist 91: 44-51.

Yentsch CS, Yentsch CM, Cullen JJ, Lapointe B, Phinney DA, Yentsch SW. 2002. Sunlight and water transparency: cornerstones in coral research. Journal of Experimental Marine Biology and Ecology 268: 171- 183.

Chapter 8: Changes in benthic structures and coral recruitment along a water quality gradient in the Whitsunday Islands, central Great Barrier Reef

Katharina Fabricius and Glenn De'ath

8.1 Introduction

Exposure to terrestrial runoff leading to organic enrichment, elevated levels of sedimentation and reduced light can seriously degrade coral reefs (review in Chapter 6). Measures are needed that reliably indicate changes in exposure to terrestrial runoff, and that are valid for specific regions as well as across regions. Reefs exposed to terrestrial runoff commonly have low coral cover and biodiversity, low coral recruitment, increased partial mortality and bioerosion, reduced skeletal density, and a transition of hard coral dominance to dominance by macroalgae (Montaggionil *et al.* 1993; West and van Woesik 2001; Schaffelke *et al.* 2005). These responses are likely candidate measures to assess changes in water quality conditions.

Two regions of the GBR, namely the inner southern reefs of the Whitsunday Islands group and the Wet Tropics, that contain about 200 coral reefs, have been classified at high risk of exposure to terrestrial runoff, based on distance and direction of the reef from individual rivers, and data on river pollution (Devlin *et al.* 2003). Chapter 7 presented data on changes in community structure and abundance of potential indicator measures for the Wet Tropics and Princess Charlotte Bay. Similar records exist from the Whitsunday Islands (van Woesik *et al.* 1999), where ecological changes have been documented on seven reefs along a gradient that shows increasing concentrations of water quality and sediment parameters (especially suspended particulate matter, turbidity, silicate, and total organic matter in sediments) with decreasing distance from the Proserpine and O'Connell Rivers (van Woesik *et al.* 1999). Towards the river mouths, macroalgal cover increased from 0 to 74%, octocoral cover decreased from 19 to 1%, hard coral richness decreased from 15 to 5 species per transect, and the maximum depth of reef development was reduced from 12 to 4 m. Furthermore, hard coral communities changed from those dominated by *Acropora* and massive *Porites* 80 km away from the river, to reefs dominated by Faviidae, encrusting *Montipora*, encrusting *Porites* and *Turbinaria* spp. at the reefs more exposed to terrigenous influences. A mismatch between Holocene reef accretion rates and present-day reef growth at the reefs most exposed to terrigenous influences was used as evidence of recent change in response to anthropogenic activities in the river catchments.

In this study we investigated the relationships between water quality and a number of ecological attributes on cover and biodiversity of hard corals, octocorals and macroalgae on the Whitsunday Islands reefs along our water quality gradient (Chapter 2). We focused on specific measures that allowed comparison with our results from the Wet Tropics (Chapter 7), and discuss the evidence for water quality effects on coral reef communities on these inshore reefs.

A number of studies have also shown that coral recruits are more sensitive to changing water quality than adult corals (Table 8.1). For example, sedimentation mortality thresholds for coral recruits are an order of magnitude lower than those for larger colonies (tens rather than hundreds of mg cm^{-2} (Fabricius *et al.* 2003). Failing coral settlement and recruitment is therefore often considered the primary cause of reef deterioration related to terrestrial runoff. Indeed, where reef degradation has been associated with poor water quality, disturbances other than eutrophication were often the proximate causes of coral mortality, and runoff effects only became obvious when hard corals failed to re-establish. Coral recruitment is therefore commonly used as a proxy measure of the ability of reefs to recover from disturbance.

Table 8.1. Summary of reported effects of water quality on coral reproduction and early life stages in corals (from Fabricius 2005).

Agent	Response	Source
≥1 μM NH_4 and/or ≥1 μM PO_4	Reduced egg fertilisation rates in *Acropora,* increased rate of abnormally formed embryos.	(Harrison and Ward 2001)
NH_4 (11 to 36 μM m^{-3}) and/or PO_4 (2 - 5 μM m^{-3})	Reduced spat densities on tiles in NH_4 enriched, but not in PO_4 enriched treatments; smaller and fewer eggs per polyp, reduced egg fertilization, increased proportion of irregular embryos.	(Ward and Harrison 2000)
20 μM NH_4 for 4 months	Failed planulation in *Pocillopora damicornis*. Reduced egg size, but no difference in fecundity and fertilisation in *Montipora* with zooxanthellate eggs.	(Cox and Ward 2002)
Increased nutrients from floating fish farms	Reduced coral planulation.	(Loya *et al.* 2004)
Eutrophication gradient in Barbados	Reduced gametogenesis, larval development, larval settlement, recruit and juvenile density and diversity, increased juvenile mortality.	(Tomascik and Sander 1987) (Tomascik 1991) (Hunte and Wittenberg 1992; Wittenberg and Hunte 1992)
Excess pollutants, nutrients, sediment dredging in Hong Kong	Low coral recruitment, few zooxanthellate octocorals, disappearance of giant clams (*Tridacna* spp.), high bioerosion.	(Morton 1994) (Hodgson and Yau 1997)
Excess sedimentation from logging in Philippines	Declining coral cover, declining biodiversity due to disappearance of sediment-sensitive species over 12 months, inhibition of coral settlement.	(Hodgson 1990a; Hodgson 1990b) (Hodgson and Walton Smith 1993)
Suspended sediment (50 and 100 mg l^{-1})	Reduced fertilisation, uninhibited post-fertilisation embryonic development, reduced larval survival and larval settlement.	(Gilmour 1999)
Turbidity by SPM (0, 10, 100, 1000 mg l^{-1})	Unaltered settlement rates, but increased rates of reversed metamorphosis after settlement ("polyp bail-out") at 100 and 1000 mg L^{-1}.	(Te 1992)
Turbidity, sedimentation	Reduced fecundity.	(Kojis and Quinn 1984)
Shading	Reduced fecundity.	(Carlon 2002)
Shading	Species-specific effects on settlement and metamorphosis.	(Babcock and Mundy 1996; Mundy and Babcock 1998)
Sedimentation	Reduced larval settlement on upper surfaces, especially when sediments are trapped by thick turf algae.	(Babcock and Davies 1991) (Te 1992) (Babcock and Mundy 1996) (Babcock and Smith 2002); (Birrell *et al.* 2005)
Sedimentation (1 to 11.7 mg cm^{-2} d^{-1})	Reduced recruit survival.	(Babcock and Smith 2002)
Muddy marine sediments (14 mg cm^{-2}), with and without enrichment with marine snow	After 48 h, reduced recruit survival in sediments enriched with marine snow.	(Fabricius *et al.* 2003)

Agent	Response	Source
Sedimentation	Increased juvenile mortality (abrasion, smothering, competition with algae).	(Birkeland 1977) (Sato 1985) (Sammarco 1991) (Wittenberg and Hunte 1992)
Eutrophication, sedimentation	Increased mean colony sizes (interpreted as sign of low recruitment rates).	(Cortes and Risk 1985); (Tomascik and Sander 1985)
Terrestrial runoff, heavy sedimentation (>10 mg cm^{-2} d^{-1} and >10 mg l^{-1})	Reduced coral recruitment.	(Pastorok and Bilyard 1985); (Rogers 1990) (Richmond 1997)
Water from creek runoff (28 ppt salinity)	Reduced fertilisation (-86%), reduced larval development (up to -50%).	(Richmond and Walton Smith 1993)
Gradient in exposure to terrestrial runoff	Reduced recruit and juvenile density.	(Smith *et al.* 2004)

Chapter 6 reviewed how the four main water quality variables (dissolved inorganic nutrients, particulate organic matter (POM), light loss from turbidity and sedimentation) affect the six main pre- and post-settlement processes, namely (1) gamete production, (2) egg fertilisation, (3) embryo development and larval survival, (4) larval settlement and metamorphosis, (5) recruit survival, and (6) juvenile growth and survival. Each of the four water quality parameters affect different stages of coral recruitment, and each of the effects is negative: for example, dissolved inorganic nutrients inhibit fecundity, fertilization, embryo and larval development, and possibly larval settlement; suspended particulate matter reduces pre-settlement survival; shading alters larval settlement, and sedimentation inhibits settlement and increases post-settlement mortality.

In this study, we quantified how benthic cover and diversity, and coral juvenile densities and diversity changed on the same sites along the water quality gradient in the Whitsunday Islands, to save as a baseline for a comparison with our equivalent data from the Wet Tropics. The comparative analyses are not yet completed and will be presented in a publication elsewhere.

8.2 Methods

Surveys were conducted on 10 reefs. Listed from inner-most coastal location to outer-most reef, these were, Repulse, Lindeman, Long, Dent, Haslewood, Hook, Whitsundays, Deloraine and Border Islands, and Bait Reef. At the windward and a leeward side of each reef, two replicate randomly placed belt transects were surveyed parallel to the reef slope, at 2 and 8 m depths for the benthos, and at 2, 5, 8, and - if available - 12 m depths, following a measuring tape. At nine of the 20 sites, the reef did not extend to 12 m depth and hence the 12 m transects were not established.

Benthos cover and composition were characterised along 20 m long transects at 2 and 8 m depths using an underwater video camera. A ~30 cm wide strip was recorded along the length of each transect. To quantify benthos composition from the video footage, five points on 40 stop frames per transect (200 points per transect) were analysed and the benthos underneath each point was identified following (Christie *et al.* 1996). Benthic organisms were identified to the lowest taxonomic resolution possible; usually genus or family. For analyses, most of the rare taxa were pooled into higher taxa: most hard and soft corals were analysed at the level of family, while macroalgae were pooled into the three main phyla, Rhodophyta, Phaeophyta and Chlorophyta.

To determine juvenile densities, detailed searches were conducted in a 30-cm wide belt transect along the first 10 m of the transect tapes. Searches were conducted on upper and lower surfaces, within nooks and crevices and underneath algal carpets by one observer (KF) to maximize consistency. A total of 127 transects were surveyed, yielding 2538 juveniles. Each scleractinian and octocoral juvenile was recorded to highest taxonomic level possible; to genus level where possible for these small colonies, but to family level in some groups such as Faviidae and Plexauridae). For simplicity, juveniles were defined as colonies with a maximum colony diameter ≤5 cm, excluding remnants. The minimum size of reproductive maturity in corals is often around 3-5 cm (e.g. faviids including *Echinopora lamellosa* (Fan and Dai 1995)), *Goniastrea aspera* (Babcock 1984), *G. australensis* (Kojis and Quinn 1981), and *Stylophora pistillata* (Rinkevich 1996); however minimum size of maturity varies between species and habitats, and certain colonies spawn for the first time at >10 cm in size (e.g. (Fan and Dai 1995). Furthermore, in colonial organisms that can undergo fission from partial mortality, individual size and age are not necessarily directly related, however sexual maturity tends to be related to colony size and colonies can lose their reproductive maturity when reduced to a small size.

At all stations, water sampling was conducted as outlined in Chapter 2, and the water quality index derived from these analyses (a sum of all z-transformed light and water quality variables per site) used to characterise the water quality condition of all sites.

Generalised linear models, using poisson distributions, were used to display the relationships between benthic data and the water quality index. A principal components analysis was used to display patterns in the juvenile assemblages, with the environmental variables, distance across the shelf and water quality index, superimposed over the biplot (see Chaper 2). The species data were averaged over duplicate transects and z-transformed for the PCA as differences in abundances rather than absolute abundances were considered relevant in this context.

8.3 Results

a) Benthic composition

Benthos cover visibly changed along the water quality gradient (Figs. 8.1, 8.2 and 8.3). Hard coral cover declined five-fold (from ~50% to ~10%) along the gradient from clear to turbid sites, while octocoral cover declined from ~25% to 3% (Fig. 8.2). Cover with crustose coralline algae was low throughout the Whitsunday Islands; mostly zero in the most turbid conditions, but higher at the clearest-water mid-shelf reef. The taxonomic richness of hard corals and octocorals declined towards the most turbid sites to about a third of those of the cleaner-water sites (from 11.5 to 4 hard coral taxa, and from 6.5 to 1.5 octocoral taxa per transect).

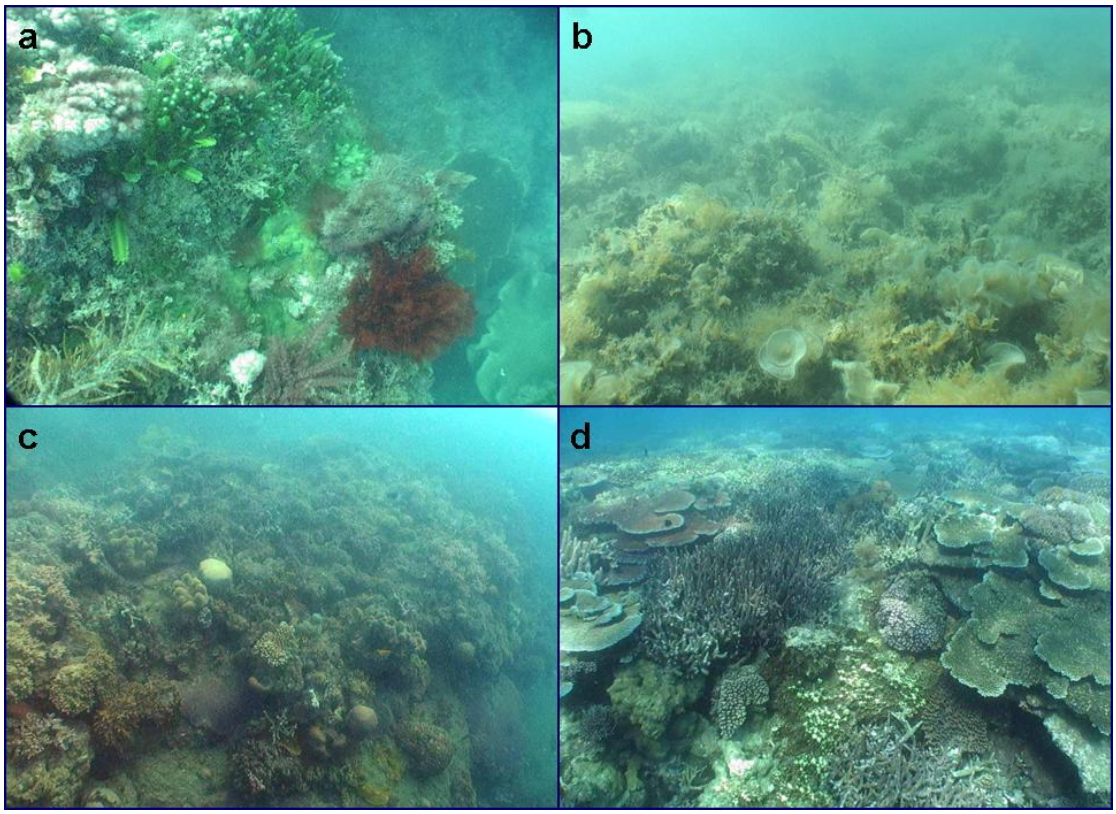


Figure 8.1. Photographs of shallow-water coral reefs sites along the water quality gradient in the Whitsunday Islands. (a) A green and red macroalgal dominated coral community at Repulse Island; (b) the brown macroalgal dominated coral reefs of Long Island, (c), octocoral dominated communities on Hook Island, and (d) *Acropora*-dominated communities on Border Island.

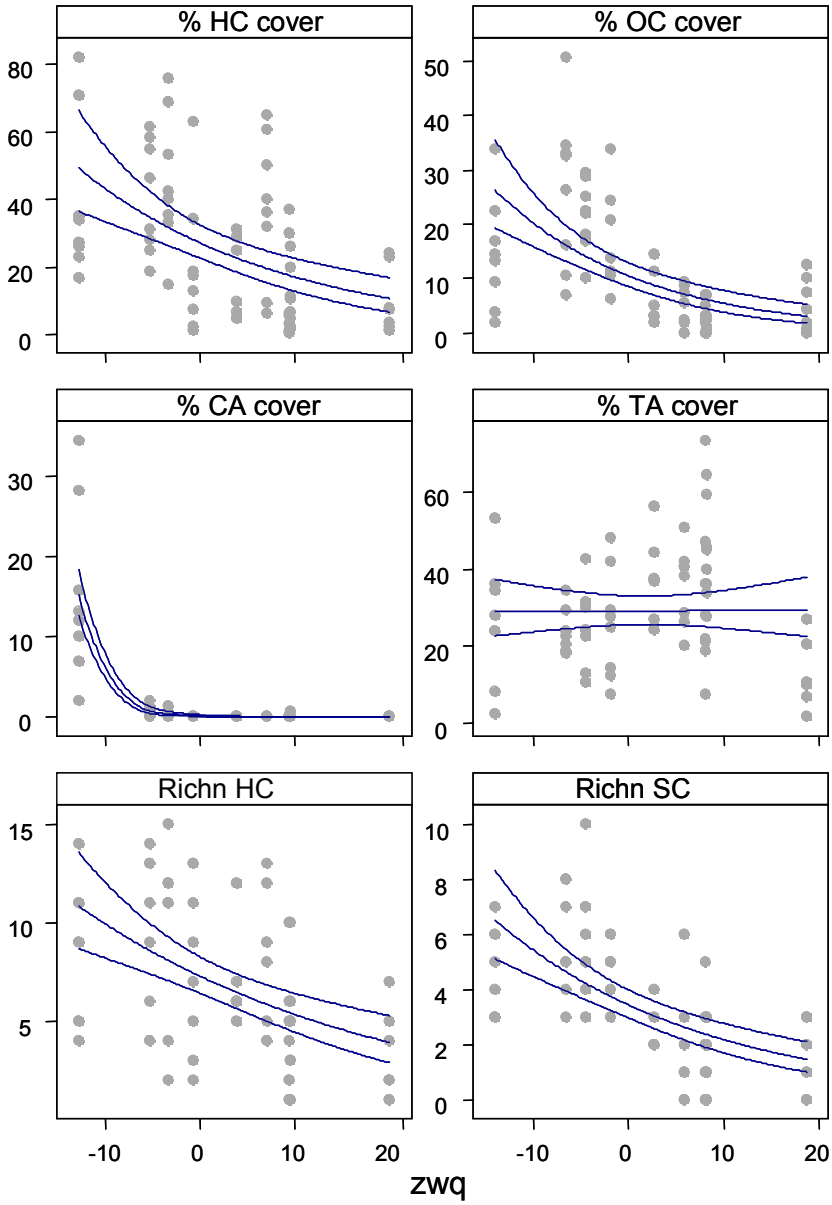


Figure 8.2. Changes in benthic cover (hard corals = HC, octocorals = OC, crustose coralline algae = CA, turf algae = TA), and taxonomic richness of hard corals and octocorals, at 2 and 8 m depths along the water quality gradient in the Whitsunday Islands. Low values of the water quality index (zwq) represent clean water; high values represent turbid high-nutrient water conditions.

In contrast, total macroalgal cover, especially of brown macroalgae (Phaeophyta) strongly increased along the water quality gradient, from near-absence in clear-water reefs to >50% of all substratum on the most turbid reefs (Fig. 8.3). Red macroalgae (Rhodophyta) also increased from zero to an average of 7%, with two of the most turbid sites being occupied by 20-25% red macroalgae. Green macroalgae (Cyanophyta) had overall low abundances, except for two offshore sites with high abundances of the calcifying green alga *Halimeda*, and two inshore sites with non-calcifying green algae (Fig. 8.3).

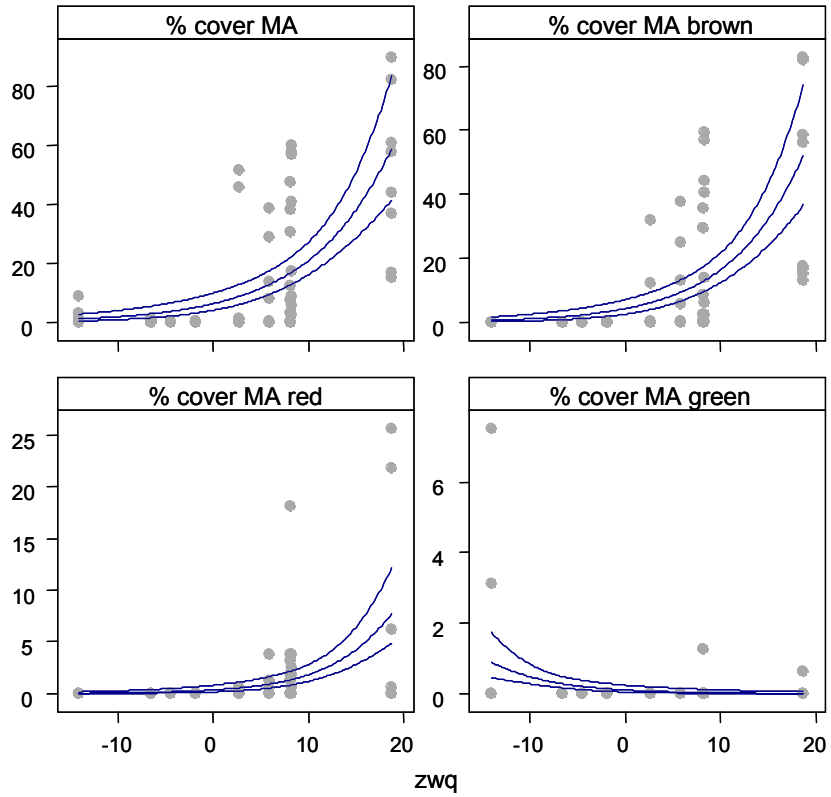


Figure 8.3. Changes in total macroalgal cover (MA), red, green and brown macroalgae at 3 and 8 m depths along the water quality gradient in the Whitsunday Islands. Low values of the water quality index (zwq) represent clean water; high values represent turbid high-nutrient water conditions. Note the different scales on the y-axis.

b) Coral recruitment

Overall, the mean density of hard coral and octocoral juveniles across the 10 reefs averaged 2.9 m^{-2} (± 0.2 SE; n = 10 reefs) for hard corals, and 3.4 ± 0.4 m^{-2} for octocorals. Juvenile densities were similar at all depths for hard corals, whereas for octocorals, densities increased three-fold from 1.7 ± 0.5 m^{-2} at 2 m depth, to 6.4 ± 2.4 m^{-2} at 12 m depth; (Table 8.2). The taxonomic richness increased with depth by ~25% in hard corals and 40% in octocorals (Table 8.2).

Table 8.2. Relationship between total hard coral and octocoral juvenile densities and taxonomic richness, and water depth (in metres).

	Slope	Std. Error	t value	Pr(>|t|)
HC juv m^{-2}	0.0735	0.0619	1.188	0.237
OC juv m^{-2}	0.4449	0.1634	2.722	0.0074
HC richness (groups $transect^{-1}$)	0.1783	0.0638	2.793	0.0061
OC richness (groups $transect^{-1}$)	0.1872	0.0518	3.612	0.00044

At all depths, the density and taxonomic richness in hard coral and octocoral juveniles declined significantly along the water quality gradient (Fig. 8.4). Juvenile densities on reefs in the most turbid waters were around a half to a fifth of those in cleaner water. Similarly, the taxonomic richness in hard coral juveniles in the most turbid waters was around half to a sixth of that in cleaner water. In octocorals, richness in the most turbid waters was about a quarter of that in cleaner waters. Water quality effects were more pronounced at greater depths than in shallow water.

Hard coral and octocoral juveniles showed clear spatial structures in their assemblages (Fig. 8.5). Only a few species (the hard coral *Turbinaria*, and the zooxanthellae-free octocorals *Subergorgia*, *Astrogorgia* and other Plexauridae, and *Dendronephthya*) were associated with reefs with the most turbid water. At intermediate distance across the shelf and intermediate levels of turbidity, communities were dominated by the thick-tissued hard coral families Pectiniidae, Faviidae, and Mussiidae, and the thick-tissued octocoral family Alcyoniidae (*Sinularia*, *Klyxum*, *Sarcophyton* and *Lobophytum*). The outer Whitsunday Islands reefs were occupied by an assemblage composed of a diverse range of hard coral and octocoral juveniles, none of which were specific for this environment. The Whitsunday midshelf reefs were clearly separated from the Whitsunday Islands communities, and characterised by a high representation of *Acropora, Porites* and *Pocillopora*, and a highly diverse assemblage of octocoral juveniles, including the clear-water taxa *Lemnalia*, *Xenia*, *Isis, Capnella* and *Efflatounaria* that were only rarely or not at all encountered within the Whitsunday Islands.

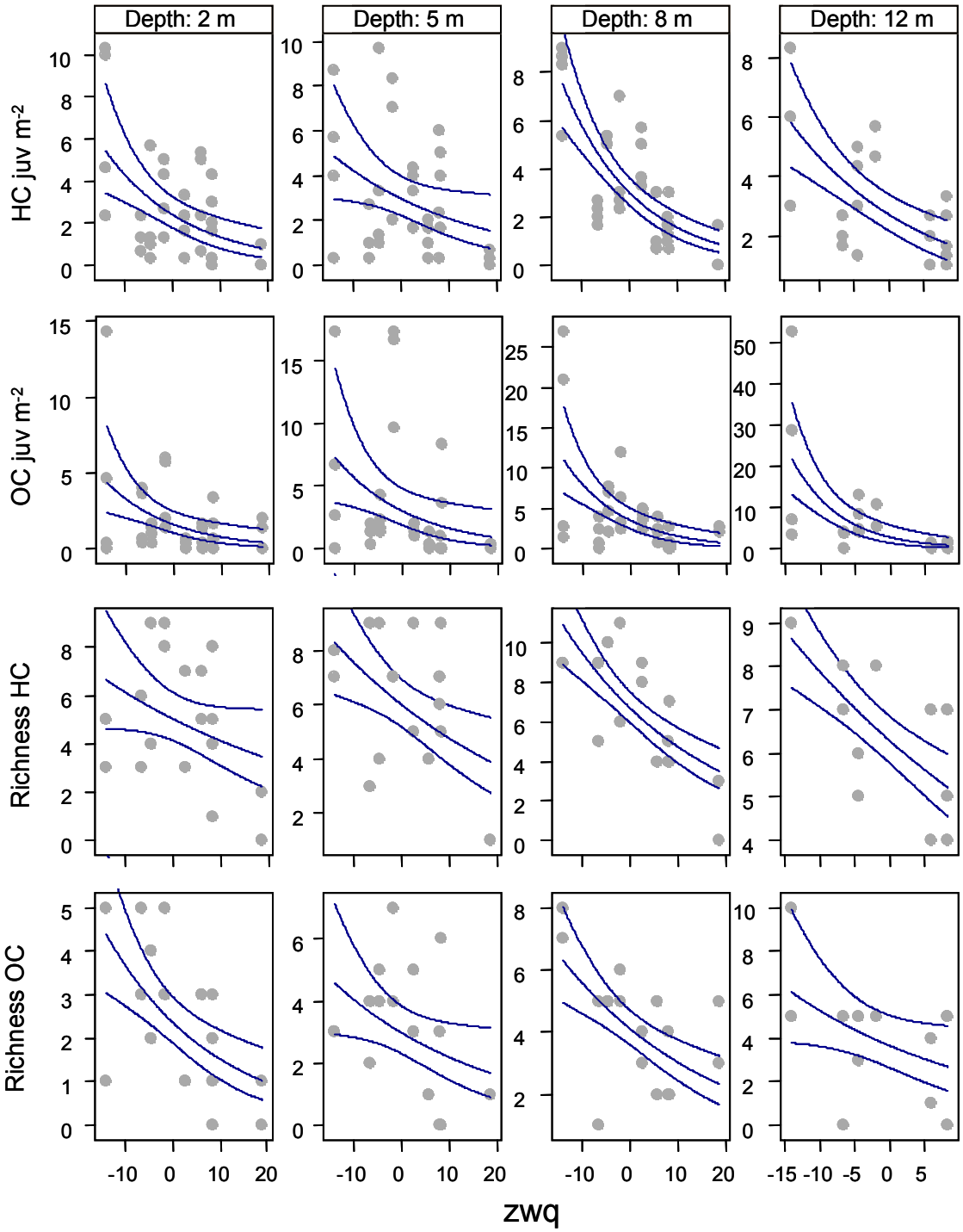


Figure 8.4. Changes in the density and taxonomic richness of juvenile hard corals (HC) and octocorals (OC) at the four depths along the water quality gradient in the Whitsunday Islands. Density is expressed as the number of juvenile colonies per square metre; richness is expressed as the number of taxa per 10 m long (3 m^2 area) transect. Low values of the water quality index (zwq) represents clean water, high values represent turbid high-nutrient water conditions.

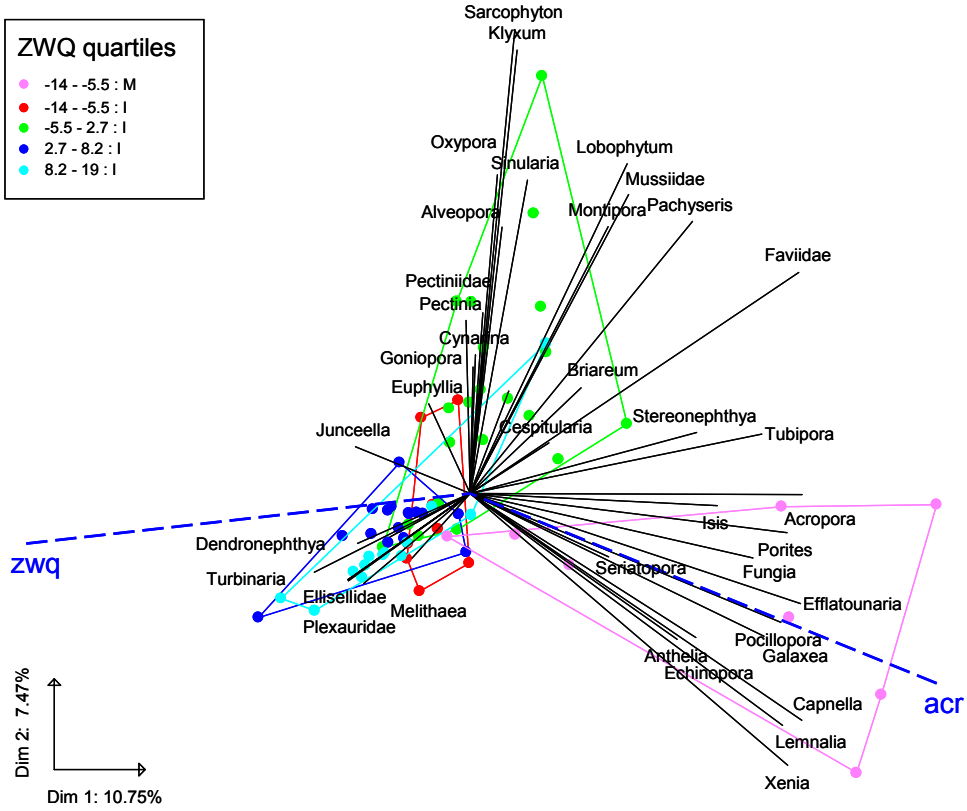


Figure 8.5. Taxonomic composition of hard coral and octocoral juveniles along the water quality gradient of the Whitsunday Islands. Coloured symbols indicate water quality conditions on the inshore islands (I) and midshelf reefs (M), with high zwq values indicating turbid and high-nutrient waters, and negative values indicating clear water conditions. The species vectors indicate the locations with highest representation of each taxon. Species data are averaged over duplicate transects per depth and site, and z-transformed.

8.4 Discussion

Spatial heterogeneity in the coral reef communities of the Whitsunday Islands was strong, and dominated by steep gradients in benthic cover, community composition and juvenile densities along the water quality gradient. Towards the coast, hard coral and octocoral cover declined to low levels, crustose coralline algae was absent in most places, while macroalgal cover was >50%. Brown and red macroalgae grew prolifically in the most turbid conditions where nutrient levels were highest, whereas the distribution patterns of the green macroalgae were more complex and differed between taxonomic groups.

The preliminary community analyses are only descriptive in nature and do not allow separation of the several confounding factors that are correlated with the water quality gradient. As discussed before, the water quality gradient is strongly related to cross-shelf position, so environmental changes include distance to the coast and to the two main river mouths as well as a number of other factors (e.g. bathymetry, currents and frequency of flood plume exposure). The data also do not serve to test whether or not reef condition has changed over time in response to changing discharge patterns from intensifying agriculture (Rohde *et al.* 2006). Instead, they describe spatial patterns that may help to predict how communities will change over time if water quality conditions should improve or deteriorate.

Biodiversity can decline over time through two contrasting pathways – either through selective mortality of the most sensitive species, or the failure of the most sensitive species to recruit into an area, even though the adult colonies persists in altered environmental conditions. A comparison of abundances and species composition of adult and juvenile life stages will be an essential next step towards distinguishing between these two processes. Analyses will now be conducted to compare the Whitsunday Islands patterns in community composition, the abundances of key coral taxa and juvenile density and species composition, with the patterns recorded in the Wet Tropics and Princess Charlotte Bay (Chapter 7, and Fig. 8.6). Such analyses are essential to identify those community measures that are most reliably associated with certain water quality conditions in several regions, and the processes leading to reduced biodiversity.

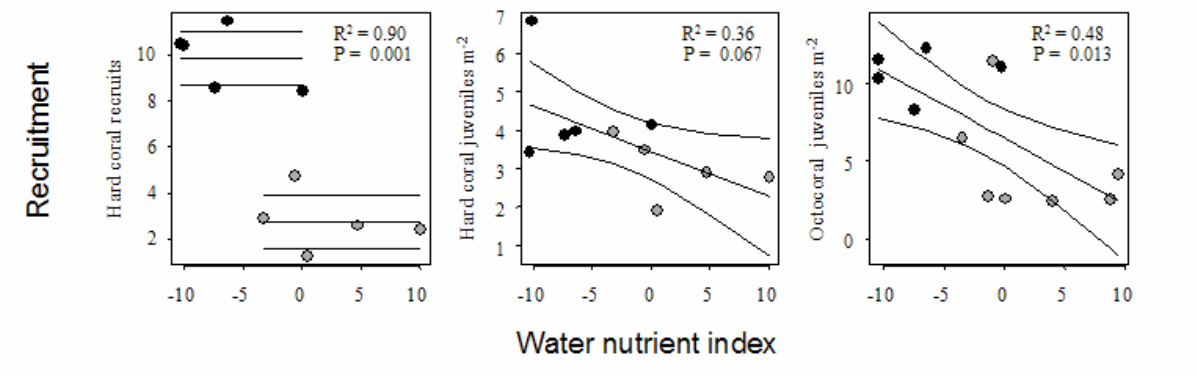


Figure 8.6. Densities of hard coral recruits on settlement tiles (left panel), and of hard coral and octocoral juveniles (middle and right panel) on 10-12 reefs along the water quality gradient in the Wet Tropics (grey dots) and Princess Charlotte Bay (black dots) [water quality gradient: see Chapter 7; recruitment data: unpub. data].

The specific cause for declining recruitment rates along the water quality gradient remained unresolved in this correlative set of observational data. As shown in the Introduction (Table 8.1), several specific environmental factors could lead to reduced coral recruitment densities and reef community diversity on the turbid inshore reefs. For example, sedimentation strongly inhibits coral settlement and recruit and juvenile survival; few coral larvae settle on sediment-covered surfaces, and survival on such surfaces is minimal. Light also strongly affects coral recruitment, as coral larvae use light quantity and quality to choose their settlement site. At low light levels, corals tend to settle on upper surfaces, where they face a high risk of being killed by sedimentation (Birkeland *et al.* 1981). Light reduction from turbidity in combination with sedimentation therefore result in failed recruitment rates at darker depth, and consequently compressed depth zonations in reef communities.

Biotic factors can also lead to low recruitment rates. For example, coral larvae are specialised to settle on certain crustose coralline algae that are essentially absent on the most turbid inshore reefs (Harrington *et al.* 2004). Dense carpets of macroalgae following coral mortality can also inhibit coral settlement and reduce juvenile survival. The mechanisms responsible for the algal- coral juveniles interactions are still poorly understood, but some recent studies have started investigating the role of chemically modulated coral-algal interactions and the role of sediment trapping by algae (e.g. (Birrell *et al.* 2005; Kuffner *et al.* 2006). Lower structural complexity after coral mortality also reduces shelter for grazing herbivores that limit algae cover. This, in turn reduces the ability of coral recruits to settle and survive and eventually replace the macroalgae (McCook 1999; McCook *et al.* 2001). Therefore, both increased nutrient levels and lowered predation can result in a transition from

coral dominance to a lasting macroalgal dominance, as has been observed in the Caribbean and many other places, a phenomenon referred to as 'phase shift' (Done 1992).

The nature of the cross-shelf gradient suggests that the factors of reduced light, higher sedimentation, higher macroalgal cover and reduced structural complexity will all lead to the same outcome: rates of larval settlement and juvenile survival will be lowest in the most turbid reefs with lowest light and highest level of sedimentation and most macroalgae. In the Whitsunday Islands, the difference in coral recruitment and biodiversity was three to four-fold between turbid reefs and environments with cleaner water. The implications of these differences for the ability of reefs to recover from disturbance are obviously strong.

The threshold level for adult coastal corals to survive sediment exposure varies widely among species, which may partly explain the reduced taxonomic diversity, and reduced abundances of more sensitive and thin-tissued taxa, such *Acropora* and octocorals of the family *Xeniidae*, in turbid and silty environments. The threshold level also varies by about an order of magnitude between adult and juvenile corals. Experimental studies that applied 60-200 mg cm^{-2} of sediments to adult corals have commonly reported physiologically impaired performance or death of underlying tissue ((Rogers 1990); (Stafford-Smith 1993); (Philipp and Fabricius 2003); (Weber *et al.* 2006). In comparison, clay sediment deposition rates of 2-12 mg cm^{-2} d^{-1} reduced larval settling and survival in *Acropora* in the field (Babcock and Smith 2002), and sedimentation rates of 3-7 mg cm^{-2} d^{-1} decreased the number of *Acropora* larvae settling on upper plate surfaces in tanks (Babcock and Davies 1991). (Fabricius *et al.* 2003), showed that *Acropora* recruits were able to survive sedimentation levels of 14 mg cm^{-2} for two days if the sediment had low concentrations of organic material, while the same amount enriched with organic carbon induced mortality.

8.5 Conclusions

The strength and consistency of response in (1) the abundances of brown and red macroalgae, (2) the taxonomic richness of octocorals, and (3) the density and taxonomic richness of both hard coral and octocoral juveniles, all indicate that such basic summary community measures represent reliable, robust and relevant measures of ecosystem status in coral reefs reflecting prolonged exposure to water quality and other environmental conditions.

For macroalgae, quite basic background data are still missing that would help to understand the contrasting responses in the three main phyla of macroalgae; research on key macroalgal species should cover physiology (nutrient and light requirements, temperature), biology (life history, seasonality, senescense) and ecology (predation) that may be related to the development of dominance over corals.

Sensitive and specific responses to changing water quality by octocorals has been shown previously for the GBR (Fabricius and De'ath 2001), Hong Kong (Fabricius and McCorry 2006) and Palau (Fabricius *et al.* in press). Octocorals are less susceptible to major disturbance than are hard corals, and families with quite contrasting environmental niches are included in this heterogeneous group, which may partly explain that octocoral community composition quite closely reflects environmental conditions. Work to identify indicator species from within the coral and octocoral communities has commenced and will help to further fine-tune such indicator systems for the inshore reefs of the GBR. The main groups of octocorals can be distinguished to genus level after relatively little training in the field, and to genus or family level from video tapes, and once the most relevant indicator genera are listed, these taxa could become essential components for future inshore reef monitoring programs.

For coral recruitment, responses to poor water quality are consistent and unambiguous (Chapter 6), and the implications of reduced recruitment rates for the ability of reefs to

recover from disturbance are strong. Some measure of coral recruitment rates should therefore be a standard element of any inshore coral reef monitoring programs. Further research should identify the most cost effective and informative methods to monitor coral recruitment rates.

8.6 References

Babcock R. 1984. Reproduction and distribution of two species of Goniastrea (Scleractinia) from the Great Barrier Reef Province. Coral Reefs 2: 187-195

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

Babcock R, Mundy C. 1996. Coral recruitment: Consequences of settlement choice for early growth and survivorship in two scleractinians. Journal of Experimental Marine Biology and Ecology 206: 179-201

Babcock R, Smith L. 2002. Effects of sedimentation on coral settlement and survivorship Proceedings of the Ninth International Coral Reef Symposium, Bali, Indonesia. Pp 245-248.

Birkeland C. 1977. The importance of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proceedings of the 3rd International Coral Reef Symposium. Pp 15-21.

Birkeland C, Rowley D, Randall RH. 1981. Coral recruitment patterns at Guam

Birrell CL, McCook LJ, Willis BL. 2005. Effects of algal turfs and sediment on coral settlement. Marine Pollution Bulletin [Mar. Pollut. Bull.]. 51: 408-414

Carlon DB. 2002. Production and supply of larvae as determinants of zonation in a brooding tropical coral. Journal of Experimental Marine Biology and Ecology 268: 33-46

Christie C, Bass D, Neale S, Osborne K, Oxley W. 1996. Surveys of sessile benthic communities using the video technique. Long term monitoring of the Great Barrier Reef, standard operational procedure No 2. Australian Institute of Marine Science (http://www.aims.gov.au/reef-monitoring), Townsville

Cortes JN, Risk MJ. 1985. A reef under siltation stress: Cahuita, Costa Rica. Bulletin of Marine Science 36: 339-356

Cox EF, Ward S. 2002. Impact of elevated ammonium on reproduction in two Hawaiian scleractinian corals with different life history patterns. Marine Pollution Bulletin 44: 1230-1235

Devlin M, Brodie J, Waterhouse J, Mitchell A, Audas D, Haynes D. 2003. Exposure of Great Barrier Reef inner-shelf reefs to river-borne contaminants 2nd National Conference on Aquatic Environments: Sustaining Our Aquatic Environments – Implementing Solutions. 20-23 November, 2001. Queensland Department of Natural Resources and Mines, Brisbane, Australia, Townsville.

Done TJ. 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247: 121-132

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

Fabricius K, Wild C, Wolanski E, Abele D. 2003. Effects of transparent exopolymer particles (TEP) and muddy terrigenous sediments on the survival of hard coral recruits. Estuarine, Coastal and Shelf Science 57: 613-621

Fabricius KE. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50: 125-146

Fabricius KE, Alderslade P, Williams GC, Colin PL, Golbuu Y. in press. Octocorallia in Palau, Micronesia: Effects of biogeography and coastal influences on alpha biodiversity. In: H Y (ed) Coral Reefs of Palau. JICA, Japan

Fabricius KE, De'ath G. 2001. Biodiversity on the Great Barrier Reef: Large-scale patterns and turbidity-related local loss of soft coral taxa. In: Wolanski E (ed) Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef. CRC Press, London, pp 127 - 144

Fan TY, Dai CF. 1995. Reproductive ecology of the scleractinian coral Echinopora lamellosa in northern and southern Taiwan. Marine Biology 123: 565-572

Gilmour J. 1999. Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. Marine Biology 135: 451-462

Harrington L, Fabricius K, De'ath G, Negri A. 2004. Fine-tuned recognition and selection of settlement substrata determines post-settlement survival in corals. Ecology 85: 3428-3437

Harrison PL, Ward S. 2001. Elevated levels of nitrogen and phosphorus reduce fertilisation success of gametes from scleractinian reef corals. Marine Biology 139: 1057-1068

Hodgson G. 1990a. Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis*. Coral Reefs 9: 41-43

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

Hodgson G, Walton Smith FG. 1993. Sedimentation damage to reef corals Global aspects of coral reefs: Health, hazards and history. University of Miami, Miami. Pp 20-25.

Hodgson G, Yau EPM. 1997. Physical and biological controls of coral communities in Hong Kong. In: Lessios (ed) Eighth International Coral Reef Symposium. Smithsonian Institute Press, USA, Panama. Pp 459-461.

Hunte W, Wittenberg M. 1992. Effects of eutrophication and sedimentation on juvenile corals. 2. Settlement. Marine Biology 114: 625-631

Kojis BL, Quinn NJ. 1981. Reproductive strategies in four species of Porites (Scleractinia)

Kojis BL, Quinn NJ. 1984. Seasonal and depth variation in fecundity of Acropora palifera at two reefs in Papua New Guinea. Coral Reefs 3: 165-172

Kuffner I, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, KS B. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Marine Ecology Progress Series 323: 107-117

Loya Y, Lubinevsky H, Rosenfeld M, Kramarsky-Winter E. 2004. Nutrient enrichment caused by in situ fish farms at Eilat, Red Sea is detrimental to coral reproduction. Marine Pollution Bulletin (in press)

McCook LJ. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18: 357-367

McCook LJ, Jompa J, Diaz-Pulido G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19: 400-417

Montaggionil LF, Cuet P, Naim O, Walton Smith FG. 1993. Effect of nutrient excess on a modern fringing reef (Reunion Island, Western Indian Ocean) and its geological implications Global aspects of coral reefs: Health, hazards and history. University of Miami, Miami. Pp 27-33.

Morton B. 1994. Hong Kong's coral communities: Status, threats and management plans. Marine Pollution Bulletin 29: 74-83

Mundy CN, Babcock RC. 1998. Role of light intensity and spectral quality in coral settlement: Implications for depth-dependent settlement? Journal of Experimental Marine Biology and Ecology 223: 235-255

Pastorok RA, Bilyard GR. 1985. Effects of sewage pollution on coral-reef communities. Marine Ecology Progress Series 21: 175-189

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

Richmond RH. 1997. Reproduction and recruitment in corals: critical links in the persistence of reefs. Chapman & Hall

Richmond RH, Walton Smith FG. 1993. Effects of coastal runoff on coral reproduction Global aspects of coral reefs: Health, hazards and history. University of Miami. Pp 42-46.

Rinkevich B. 1996. Do reproduction and regeneration in damaged corals compete for energy allocation? Marine Ecology Progress Series 143: 297-302

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

Rohde K, Masters B, Brodie J, Faithful J, Noble R, Carroll C. 2006. Fresh and Marine Water Quality in the Mackay Whitsunday Region 2004/2005. Mackay Whitsunday Natural Resource Management Group, Mackay, Australia

Sammarco PW. 1991. Geographically specific recruitment and post-settlement mortality as influences on coral communities: The cross-continental shelf transplant experiment. Limnology and Oceanography 36: 496-514

Sato M. 1985. Mortality and growth of juvenile coral *Pocillopora damicornis* (Linnaeus). Coral Reefs 4: 27-33

Schaffelke B, Mellors J, Duke NC. 2005. Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. Marine Pollution Bulletin 51: 279-296

Smith L, Devlin M, Haynes D. 2004. Size structure, recruitment and post-recuitment survival of nearshore corals in the Great Barrier Reef Wet Tropics. In: Haynes D, Schaffelke B (eds) Catchment to Reef: Water Quality Issues in the Great Barrier Reef Region. CRC Reef Research Centre, Townsville, Queensland, Australia., Townsville. 77 pp.

Stafford-Smith MG. 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. Marine Biology 115: 229-243

Te FT. 1992. Response to higher sediment loads by *Pocillopora damicornis* planulae. Coral reefs 11: 131-134

Tomascik T. 1991. Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. Marine Ecology Progress Series 77: 261-269

Tomascik T, Sander F. 1985. Effects of eutrophication on reef-building corals. 1. Growth rate of the reef-building coral *Montastrea annularis*. Marine Biology 87: 143-155

Tomascik T, Sander F. 1987. Effects of eutrophication on reef-building corals. 3. Reproduction of the reef-building coral *Porites porites*. Marine Biology 94: 77-94

van Woesik R, Tomascik T, Blake S. 1999. Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. Marine and Freshwater Research 50: 427-440

Ward S, Harrison P. 2000. Changes in gametogenesis and fecundity of acroporid corals that were exposed to elevated nitrogen and phosphorus during the ENCORE experiment. Journal of Experimental Marine Biology and Ecology 246: 179-221

Weber M, Lott C, Fabricius K. 2006. Different levels of sedimentation stress in a scleractinian coral exposed to terrestrial and marine sediments with contrasting physical, geochemical and organic properties. Journal of Experimental Marine Biology and Ecology 336: 18-32

West K, van Woesik R. 2001. Spatial and temporal variance of river discharge on Okinawa (Japan): Inferring the temporal impact on adjacent coral reefs. Marine Pollution Bulletin 42: 864-872

Wittenberg M, Hunte W. 1992. Effects of eutrophication and sedimentation on juvenile corals. 1. Abundance, mortality and community structure. Marine Biology 116: 131-138

Chapter 9: Seasonal variation in biomass and tissue nutrients of intertidal seagrasses (*Halophila ovalis* and *Halodule uninervis*) in relation to sediment nutrient contents in North Queensland

Jane Mellors, Katharina Fabricius and Glenn De'ath

Summary

This study assessed temporal changes in seagrass biomass and tissue nutrients in relation to pore water and adsorbed nutrients in sediments, at five sites, bi-monthly over a period of 23 months. Two of the sites were occupied by the species *Halophila ovalis*, the other three sites were occupied by *Halodule uninervis*. The data represent the most detailed time series of sediment and seagrass properties in these two structurally small species of seagrasses available to date.

Changes over time were complex, and appeared to be dominated by disturbances and recovery from disturbances, obscuring any seasonal patterns in this <2 years data set. Spatial patterns remained stronger than temporal patterns, despite some pronounced changes both in sediments and seagrass properties over time. The individual patterns observed across these meadows may suggest that they are all in different stages of recovery, and therefore the time frame of this study was not long enough to evaluate a meadow in full recovery displaying seasonal dynamics. Examination of individual locations demonstrating meadow stability, to tease out the subtleties of seasonal change would be desirable but was beyond the scope of this study.

Once Location had accounted for the majority of variance within the data set, porewater ammonium NH_4^+ was the best predictor of biomass and tissue nitrogen N. Porewater NH_4^+ was positively related to plant tissue N, and negatively related to biomass. This may indicate that as NH_4^+ increases, plant tissue N also increases, but that the acquisition of NH_4^+ within the seagrass plant is not being translated into an increase in biomass – on the contrary, some factor is limiting growth where NH_4^+ is high. Light is likely to be the factor limiting seagrasses along this highly turbid coastline, with seasonal terrestrial freshwater, nutrient and sediment inputs and wind generated sediment resuspension.

Most seagrass biomass was stored underground but the correlation between above- and below-ground biomass was high, suggesting that total biomass provides almost as much information as separate assessments of leaves, rhizomes and roots. Changes in seagrass biomass were much greater than changes in tissue nutrient concentration. Tissue nutrients were only slightly elevated at times of low biomass, suggesting that only a small proportion of the seagrass nutrients is being stored in the remaining biomass when biomass declines. As a result, differences in biomass strongly determined the amount of nutrients available within seagrasses per unit area.

Tissue nutrient N may be used as an indicator of water quality, although it has to be emphasised that tissue nutrient contents do not signify ecological health of a seagrass meadow. A combination of variables is required to report on the health of a meadow: the presence of a species, its nutrient requirements for growth, the nutrient and light history of the location, and the age or stage of development of the meadow as dictated by its disturbance regime.

There is a need for a better understanding of seagrass responses with respect to the interaction between light and nutrients in relation to meadow development. Experimentation on the interaction between light, nutrients and temperature in controlled systems is required. Coupling this with varying degrees of exposure would enable us to better model intertidal plant responses. There is also a need to categorise seagrass meadows according to sediment type and sediment nutrient state, and have the ability to classify seagrass meadows by development stage. To be able to classify development stage/age of meadows, a diagnostic tool is required. Internode length of rhizomes looks promising (Mellors 2003; McMahon 2005), however this needs to be tested on species other than *Halophila ovalis* and on a larger number of meadows.

This study highlights the uniqueness of location with respect to seagrass meadow dynamics and behaviour. Supporting programs such as Seagrass-Watch and the Reef Water Quality Protection Plan (RWQPP) Seagrass Monitoring program will increase the number of meadows being examined across a broader geographical scale and varied disturbance regimes. These programs are limited in their approach though, as they focus on intertidal meadows of structurally small seagrass. There is a need to extend our knowledge of seagrass meadows to include intertidal meadows of structurally large seagrasses (possibly reef top meadows) and shallow sub-tidal area meadows; areas that have logistical challenges.

Based on the evidence presented in this study, we suggest that structurally small seagrasses in this region are not primarily nutrient limited, but are limited by one or more of the other factors that affect their growth. We also suggest that in this region, the disturbance regime of a location, that is, the localised aspects of exposure to predominate winds, tidal exposure, turbidity and hence light availability, and to a lesser degree the frequency and intensity of herbivory, particularly dugong grazing (Preen 1995), dictates abundance and temporal signal of these intertidal seagrass meadows. There is a need to encompass the variability inherent in the different seagrass meadows within each habitat type that occurs within the Great Barrier Reef World Heritage Area (GBRWHA). For each meadow/habitat type it is important to recognise the different species, their relative form and function, and the disturbance history/stage of development of these meadows. This type of approach will foster community and managerial understanding that not all seagrass meadows are the same, and that differences exist between meadows because of their geographical setting, species composition and abundance, sediment mineralogy, stage of meadow development and past nutrient history.

9.1 Introduction

Fluctuations in biomass and productivity observed in temperate seagrasses follow seasonal changes in solar energy and temperature, with a strong increase in spring, a peak in the summer and a subsequent decline in autumn (Hemminga and Duarte 2000). In Australia, temperate and subtropical seagrasses also follow this pattern of biomass change (temperate: Bulthuis and Woelkerling 1981; Kirkman *et al.* 1982; Larkum *et al.* 1984; Walker and McComb 1988; Hillman *et al.* 1989; subtropical: Young and Kirkman 1975; Walker and McComb 1988). Very little has been published on measurements of temporal changes in abundance of inshore seagrasses in tropical Australia, with the exception of a few studies (Mellors *et al.* 1993; McKenzie 1994; Lanyon and Marsh 1995). These studies only provided information on temporal changes of biomass in Australian tropical seagrasses. The authors attributed differences in light availability and temperature as the primary drivers for this seasonality. Lanyon and Marsh (1995) also suggested rainfall as a driver, supporting a previous hypothesis of Bridges *et al.* (1982) and Coles *et al.* (1989) that seasonal rainfall may be an important factor influencing seagrass productivity in meadows that are directly influenced by terrestrial run-off or river discharge (Carruthers *et al.* 2002). While this may infer an increase in nutrient delivery to these meadows, no-one has studied temporal changes of seagrass meadows in relation to sediment nutrients in this region.

Sediments provide the primary source of nutrients for seagrass growth (Iizumi and Hattori 1982; Short 1983; Short and McRoy 1984; Brix and Lyngby 1985; Boon 1986; Short 1987; Moriarty and Boon 1989; Fourqurean *et al.* 1992; Udy and Dennison 1996). Determining the nutrient status of a rhizosphere (the volume of sediment in which seagrass rhizomes and roots reside), therefore requires sampling the porewater (the water contained within the spaces between sediment grain particles) for dissolved nutrients, and the sediments for adsorbed exchangeable nutrients. The adsorbed nutrients are held on the electrically charged surfaces of the sediment. The remainder of the nutrient pool is dissolved in the porewater and is in dynamic equilibrium with nutrients held electrostatically. Plant uptake or water movement depletes nutrients in the porewaters. The nutrients attached to sediment particles then move into the porewaters as a result of this nutrient depletion in the porewaters (Baker and Eldershaw 1993). This rate of exchange should vary temporally according to plant requirements.

With the exception of Lanyon and Marsh (1995), temporal studies within north Queensland have focused on meadows of structurally large species. Within the GBRWHA, the majority of coastal seagrass meadows are comprised of the structurally smaller species: *Halophila* and the narrow leaved form of *Halodule* (Lee Long *et al.* 1993). Our understanding of seagrass meadows within this region remains far from extensive (Carruthers *et al.* 2002). Many generic concepts of seagrass ecology and habitat function from temperate regions (Duarte 1999; Walker *et al.* 1999) involving structurally large seagrasses are being inappropriately transcribed to tropical seagrass systems dominated by structurally small seagrass species.

This study examined temporal variation in biomass and plant tissue nutrients of the structurally small seagrass *Halophila ovalis* and *Halodule uninervis* (narrow leaf) in relation to sediment nutrients, within five intertidal meadows every two months over 23 months. Sampling was restricted to relatively homogenous seagrass-covered areas to ensure maximum comparability between sites. Three elements of the seagrass environment were sampled routinely throughout this study: (1) sediment structure, those parameters that pertain to sediment grain size (2) the sediment nutrient environment, and (3) the seagrasses themselves, i.e. biomass, shoot density and plant tissue nutrients (see Table 9.1).

Table 9.1. Sediment and seagrass variables measured in five locations during twelve visits between August 1993 and June 1995, and abbreviations used.

a) Sediment variables			
Sediment structure		**Sediment nutrients**	
Water content	avgH	Bicarbonate extracted phosphate	Bicarb
Porosity	avgPorosity	Bray extracted phosphate	Bray
Particle size density	avgPSD	Extracted ammonium	KCl
		Dissolved inorganic ammonium	pwNH4
		Dissolved inorganic nitrate + nitrite	pwNO23
		Dissolve inorganic phosphate	pwPO4
b) Seagrass variables			
Plant abundance		**Plant tissue nutrients**	
Leaf biomass	drylvs.m2	% leaf N	n.leaf.m2
Rhizome biomass	dryrhz.m2	% leaf P	p.leaf.m2
Root biomass	dryrts.m2	% rhizome N	n.rhz.m2
Total biomass	Totaldw.m2	% rhizome P	p.rhz.m2
Leaf density	leaves.m2	% root N	n.root.m2
		% root P	p.root.m2

9.2 Study sites and methods

Field sampling

The study area was within the central part of the Great Barrier Reef Lagoon between Mission Beach and Magnetic Island. Five seagrass meadows were selected for this study; two meadows were within the Wet tropics region and the remaining three locations were around Magnetic Island (Dry Tropics). Sampling occurred within the monospecific stands of the dominant seagrass species within each location every two months, from August 1993 until June 1995; a total of 12 visits, 162 samples. For the purposes of this study, each location was characterised by a dominant species of seagrass as summarised in Table 9.2.

Table 9.2. The location of five intertidal seagrass meadows investigated in this study. Longitudes and latitudes (WGS 84), predominant seagrass species with average percent cover, as determined by a visual estimate within 0.25 m^2 quadrats at each location.

Location	Longitude[1]	Latitude[1]	Predominant species (% cover)
Lugger Bay, South Mission Beach	146.10°E	17.92°S	*Halodule uninervis* (10-20%)
Meunga Creek, Cardwell	146.02°E	18.30°S	*Halodule uninervis* (40%)
Bolger Bay, Magnetic Island, Townsville	146.80°E	19.16°S	*Halophila ovalis*[2] (<5%)
Picnic Bay, Magnetic Island, Townsville	146.85°E	19.18°S	*Halophila ovalis* (50-70%)
Geoffrey Bay, Magnetic Island, Townsville	146.86°E	19.16°S	*Halodule uninervis* (20-30%)

[1] Longitudes and latitudes from Morrissette 1992.
[2] In 1992 Bolger Bay recorded 70% cover.

Changes in the biomass and nutrient content of the seagrass, and sediment porewater and adsorbed nutrients were sampled as schematically presented in Fig. 9.1. Eighteen, 0.25 m^2 quadrats were placed haphazardly in each meadow. Three of these quadrats were chosen randomly and excavated for the analysis of seagrass biomass and plant nutrient parameters. Two sampling techniques were used to sample the different nutrient pools, the porewater and the adsorbed nutrients (Fig. 9.2). Duplicate porewater samples for the analysis of dissolved inorganic nutrients were taken within each of the 18 quadrats, and averaged. Sediment core samples for the analysis of adsorbed inorganic nutrients were taken from the three quadrats from which the seagrass biomass and plant nutrient parameters were determined, as well as five others, from June 1994 making a total of eight samples for adsorbed nutrient determination. Due to constraints of the first Analytical Laboratory used, adsorbed nutrient samples were not analysed before June 1994. Another three sediment cores were taken in the vicinity of the quadrats for analysis of sediment particle sizes, density and porosity. Whilst sampling occurred within the same seagrass meadow every field trip, the placement of the quadrats differed between trips.

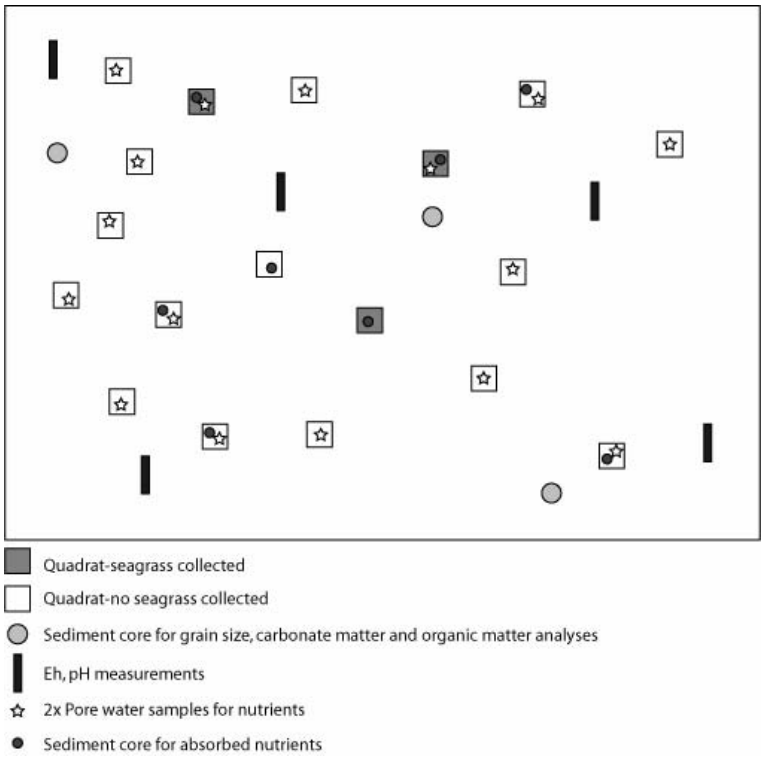


Figure 9.1: Schematic diagram of sampling design for samples taken after June 1994 (not to scale). Location of each quadrat was assigned haphazardly.

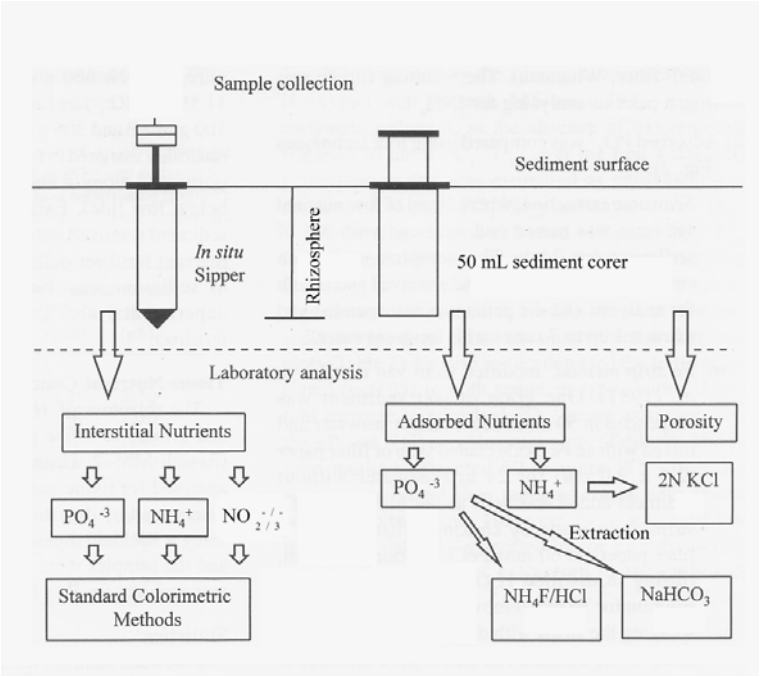


Figure 9.2. Schematic diagram of the sampling equipment used for the relevant parts of the nutrient pool and the nutrients determined and extracted from the porewater nutrient pool and the adsorbed nutrient pool (modified from Udy and Dennison 1996).

Porewater Sediment Nutrients

The sediment nutrient pool is comprised of porewater nutrients and adsorbed/exchangeable nutrients. Sediment porewater was collected *in situ* using sediment sippers (modified from Murray *et al.* 1992; Udy and Dennison 1996). The *in situ* sipper was a two-stage vacuum filtration device (Fig 9.3). It was made of an external perforated PVC pipe with an inner 10 μm mesh screen. The top of the sipper was connected to a 0.45 μm micro-pore filter held in place within a filter holder. The top of the filter holder was connected to a 50 mL central aperture syringe, via a 3 cm length of catheter tubing. The sipper was placed in the sediment and a vacuum created by pulling up the syringe plunger. This vacuum caused the porewater to be pulled through the first stage of filtration (sipper) and then through the micropore filter into the syringe. The sample was then transferred to sterilised 10 mL vials, sealed and placed on dry ice to minimise chemical transformation and microbial activity. Sippers were made to two different lengths corresponding to the measured depth of the species' rhizosphere: 2.5 cm for *Halophila ovalis*, and 10 cm for *Halodule uninervis*. Sipper samples were assumed to be a depth integrated sample of the rhizosphere.

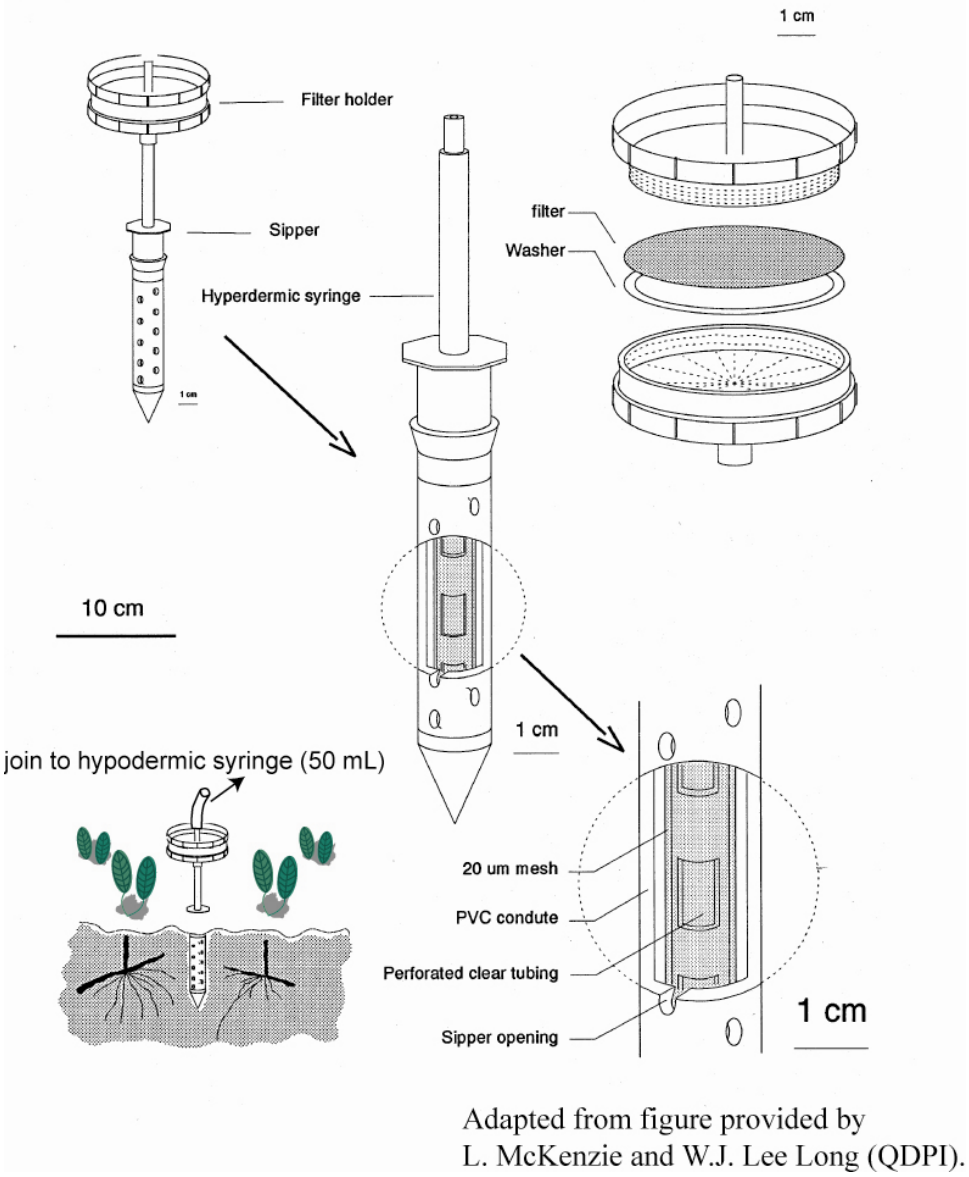


Figure 9.3 Illustration of the *in situ* sediment sipper, depicting its two stage filtration system, and placement in the rhizosphere for the collection of porewater (modified from Murray *et al.* 1992; Udy and Dennison 1996).

Adsorbed sediment nutrients

To collect sediment samples for the analysis of exchangeable inorganic nutrients, hypodermic syringes (50 mL) with their ends removed were pushed into the sediment to the lower depth limit of the rhizosphere. Once extracted from the sediment, the syringes were stoppered and placed on ice in the field. They were then stored refrigerated until further analysis. This collection method was also used for acquiring samples for the analyses of sediment grain size, particle size density and porosity.

Particle size density

Particle size density (PSD) is a measure of the mass of a sediment sample in a given volume of particles. The density of the particles is a result of the chemical composition and structure of the minerals in the sediment. Hence measurement of PSD can be deduced by comparing the sample's PSD with the known densities of other minerals. It is a measure required to calculate porosity.

Triplicate samples of water-saturated sediment cores were collected at the time of nutrient sampling. Cores were collected in 'cut-off' 50 mL syringes and rubber stoppered, as described above, taking care not to compress the core. The volume of each core was measured from the syringe gradations. The intact syringe was weighed (g), dried in an oven (80°C, 48 h) and then reweighed to determine weight loss. Particle size density (P_s) was calculated using the following equation.

Equation 1:

$$P_s = (\text{Dry sample wt})/(\text{Volume} - ((\text{Wet sample wt} - \text{Dry sample wt})/d_w))$$

Where d_w = specific gravity of water = 1.025

Porosity

Porosity (as determined by Equation 2) results from the sediment particles not occupying all the possible space. It is therefore the measure of the volume of void space to the total volume of sediment and is dependent on grain size (Folk 1974, Freidman 1978). The void spaces or pores accommodate fluids, generally water. This fluid is known as porewater and is the site for dissolved nutrients. Typically porosity decreases as particle size increases. This is true for sediments that are well sorted.

Equation 2:

$$\phi \text{ (porosity)} = (H/1.025)/(H/1.025 + (1-H)/p_s))$$

Where H = proportion of water - (wet weight - dry weight)/ wet weight
and P_s = particle size density

Whilst analyses of porewater and adsorbed nutrients in isolation of each other can be achieved using their own units (µmol $L_{porewater}^{-1}$ and µmol $kg_{sediment}^{-1}$ respectively), any comparison of these two nutrient pools requires a conversion of these units to µmol $L_{sediment}^{-1}$. This conversion is accomplished using the measure of porosity and particle size density (P_s) as per equations 3 and 4. The conversion of nutrient levels to µmol $L_{sediment}^{-1}$, overcomes the differences in physical sediment characteristics between locations.

Equation 3:

$$\text{Porewater nutrients } (\mu\text{mol } L_{sediment}^{-1}) = \mu\text{mol } L^{-1} \times \phi$$

Equation 4:

$$\text{Adsorbed nutrients } (\mu\text{mol } L_{sediment}^{-1}) = \mu\text{mol } kg^{-1} \times p_s \times (1- \phi)$$

Seagrass

Seagrass samples were collected from 0.25 m^2 quadrats (0.5 m x 0.5 m) due to the relative density of seagrass present, following the recommendations of Duarte and Kirkman (2001). Seagrass samples were rinsed initially in seawater then in tap water.

Laboratory analyses of samples

Chemical determination of dissolved inorganic nutrients

Porewater samples were analysed for dissolved inorganic nutrients, ammonium (NH_4^+), nitrite + nitrate (NO_2^- + NO_3^-), and phosphate (PO_4^{3-}) using a Skalar segmented flow auto-analyser (provided by AIMS water quality laboratory, results precise to four decimal places for PO_4^{3-}, two decimal places for NH_4^+, using standard water quality techniques (Strickland and Parsons 1972; Ryle *et al.* 1981). Ammonium is the dominant freely available source of fixed N available to seagrasses, and is usually the preferred source (Moriarty and Boon 1989), however NO_2^- + NO_3^- are also known to play a role in some systems and were hence included in the analyses (Hemminga *et al.* 1991).

The chemical analyses for the extracted nutrients were performed by the Institute of Resource Management, Indooroopilly Qld. PO_4^{3-} analyses were based on the method of Murphy and Riley (in Rayment and Higginson 1993). Levels of potassium chloride KCl extracted N were determined using methods outlined in Strickland and Parsons (1972).

Nutrient extraction of adsorbed exchangeable sediment nutrients

Sediment samples were analysed for extractable inorganic NH_4^+, and PO_4^{3-}. Cores were homogenised to provide a depth-integrated sample. Adsorbed exchangeable NH_4^+ was extracted using PO_4^{3-} (Rayment and Higginson 1993).

Two techniques were used to extract PO_4^{3-} the Bray method (Bray and Kurtz 1945, Rayment and Higginson 1993) hereafter referred to as 'Bray' and the Olsen/Colwell/Bicarbonate method (Mengel and Kirkby 1987; Rayment and Higginson 1993), hereafter referred to as 'bicarbonate' (provided by the Institute of Resource Management, Indooroopilly Qld; results precise to three decimal places). The Bray technique tends to extract PO_4^{3-} incompletely in an alkaline environment owing to the presence of calcium carbonate $CaCO_3$ (Pailles and Moody 1995). The bicarbonate method is not affected by pH and is more appropriate for alkaline soils pH>7.8 (Baker and Eldershaw 1993). Both techniques were used in an attempt to determine which is the better measure of biologically available PO_4^{3-}

Seagrass

Biomass

In the laboratory, leaves, rhizomes and roots were separated. Epiphytic algae were physically removed from each component of the plant. Samples were oven dried at 60°C, to a constant weight (balance used was precise to four decimal places).

Plant tissue nutrients

Dried biomass samples of leaves, rhizomes and roots were separately homogenised by milling to a fine powder. Nitrogen and PO_4^{3-} were extracted using a standardised selenium Kjeldahl digest and the concentrations determined with an automatic analyser using standard techniques (Strickland and Parsons 1972, Institute of Resource Management, Indooroopilly Qld). The nutrient state of a meadow was characterised as g $N_{seagrass}$ m^{-2} and g $P_{seagrass}$ m^{-2} as calculated by equation 5:

Equation 5:

$$\% \text{ plant tissue nutrient} \times \text{biomass (g DW } m^{-2}) = \text{g Nutrient}_{seagrass}\ m^{-2}$$

Statistical analyses

Sediment and seagrass data were square-root transformed prior to analyses to stabilise variances. Loess smoothers were used to display changes in values over time. A principal components analysis was used to graphically investigate spatial patterns in the sediment properties. ANOVAs were also used to assess spatial and temporal patterns in seagrass tissue nutrients.

Boosted regression trees (De'ath, in press) were used to determine the amount of variance predicted in each of the seagrass response variables due to each of the sediment and environmental variables, and to determine which of the environmental variables explained most of the variation. Linear models without higher-level interactions were also used to assess the relationship between environmental and seagrass variables, after comparison against polynomial models showed that the latter did not provide better data fits. Redundancy analyses were used to graphically display the relationship between seagrass and sediment variables, and to determine the proportion of variation in seagrasses explained by the environmental variables.

9.3 Results

Spatial and temporal patterns in sediment properties

Concentrations of dissolved inorganic nutrients (NH_4^+, PO_4^{3-} and nitrogen oxides) strongly contrasted between locations. For example, sediments at Meunga Creek had the highest levels of the N-related nutrients (especially NH_4^+), porosity and water content, but low levels of PO_4^{3-} (Fig. 9.4). In contrast, Geoffrey Bay had highest levels of porewater $PO_4^{3-}$and particle size density, but low concentrations of N. Porewater NH_4^+ was about 3-4 times higher than NO_2^- + NO_3^-combined. Bray and Bicarb PO_4^{3-} values contrasted strongly at Geoffrey Bay, but were within similar ranges at the other locations. Porewater NH_4^+ was about an order of magnitude lower than adsorbed NH_4^+, and similarly, porewater PO_4^{3-} was about an order of magnitude lower than adsorbed PO_4^{3+}.

Sediment properties varied over time at Meunga Creek and Bolger Bay, and changed far less at Lugger, Picnic and Geoffrey Bay. The temporal variation in porewater and particulate nutrients and physical properties displayed some systematic but apparently non-seasonal variation (Fig. 9.5a - c). Some of the temporal patterns were consistent between locations; in

particular, porewater NH_4^+ more than doubled at all locations within the first eight months after sampling commenced, after which the trends started varying between locations. Porewater nutrients were more variable than adsorbed nutrients. Concentrations of NO_2- + NO_3- were an order of magnitude lower than those of NH_4^+.

The principal components analysis showed that spatial patterns in sediment properties were stronger than temporal changes (Fig. 9.6). Sediment properties at Lugger, Picnic and Geoffrey Bay changed very little over time and between replicate samples, whereas Meunga Creek and Bolger Bay were far more variable over time and between replicates. The muddy sediments of Meunga Creek and Bolger Bay were characterised by low particle size density (PSD) and high porosity reflecting sediment types that have a high clay and organic content. These locations also recorded high levels of adsorbed Bray-PO_4^{3-} and high levels of porewater NH_4^+, reflecting the ability of sediments with high clay content to sequester nutrients.

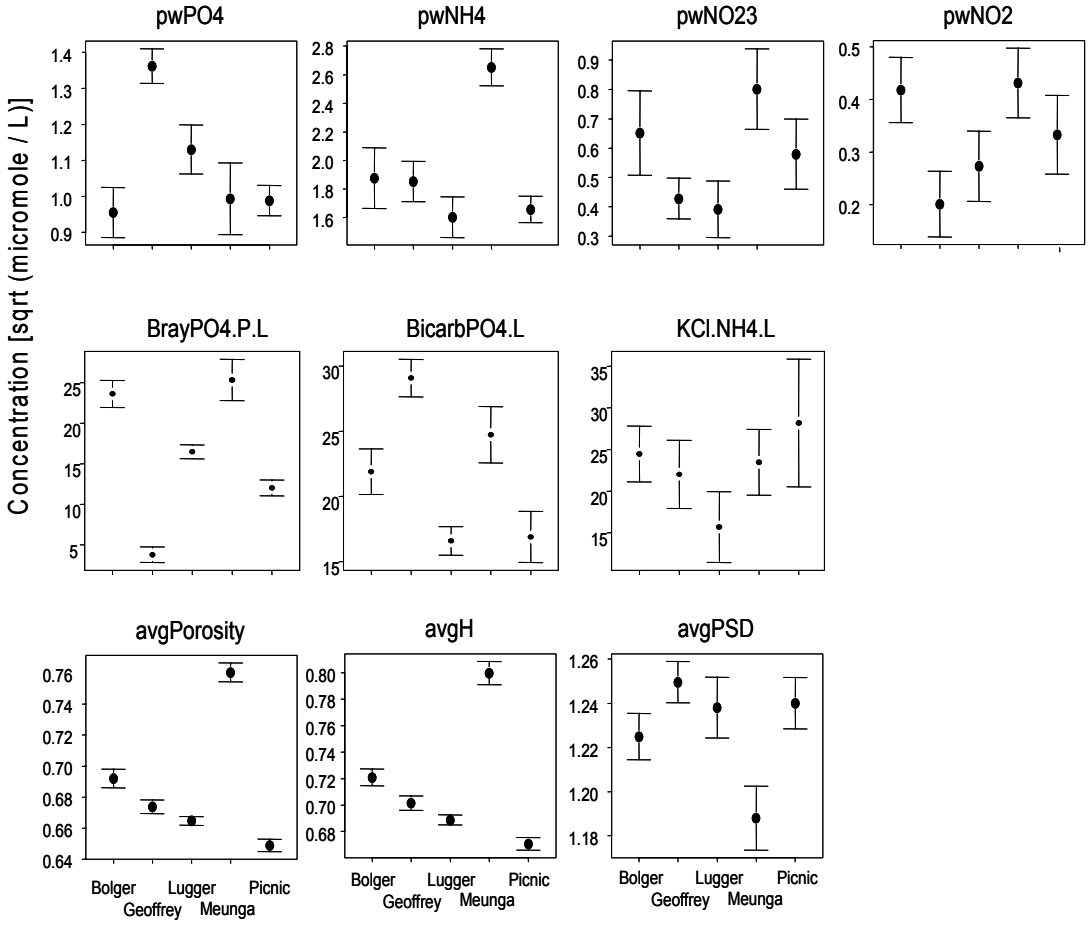


Figure 9.4. Mean concentrations, ± 1 SE, of sediment properties across sites. For abbreviations, see Table 9.1

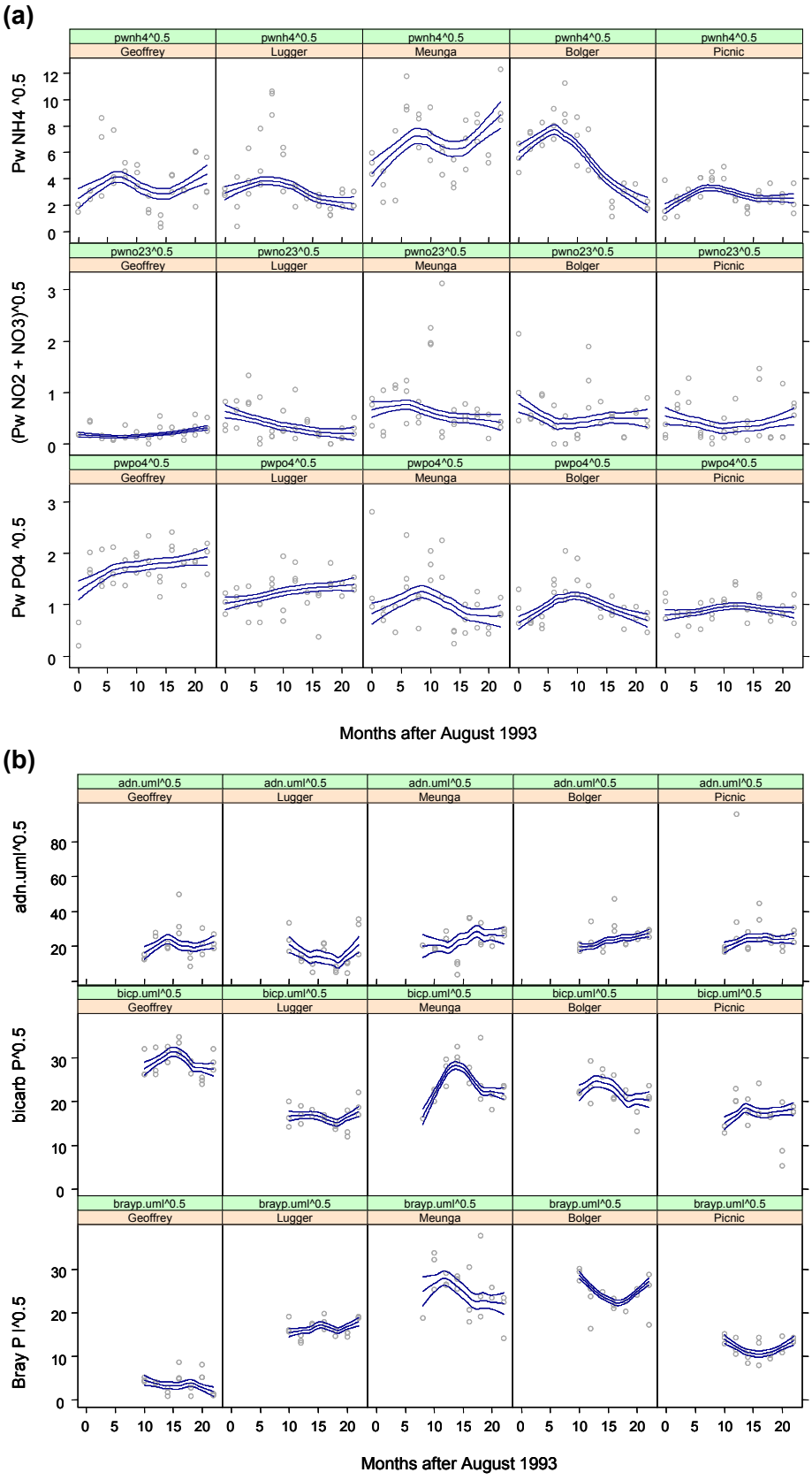


Figure 9.5. Temporal variation in sediment variables at the five locations. The central line represents the y-x relationship based on loess smoothers, upper and lower lines are 1 SE. (a) porewater nutrients, (b) adsorbed nutrients, (c) physical sediment properties (see following page).

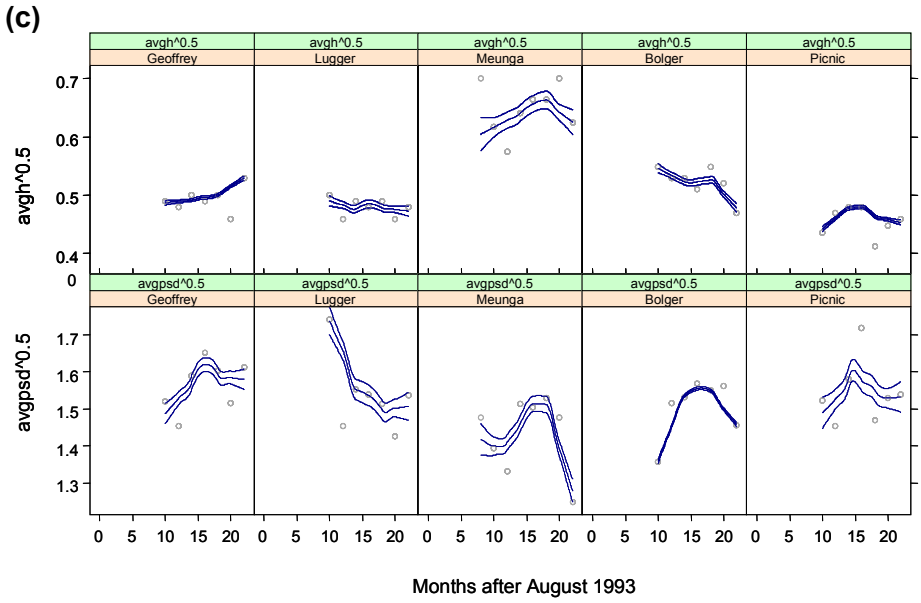


Figure 9.5. (continued).

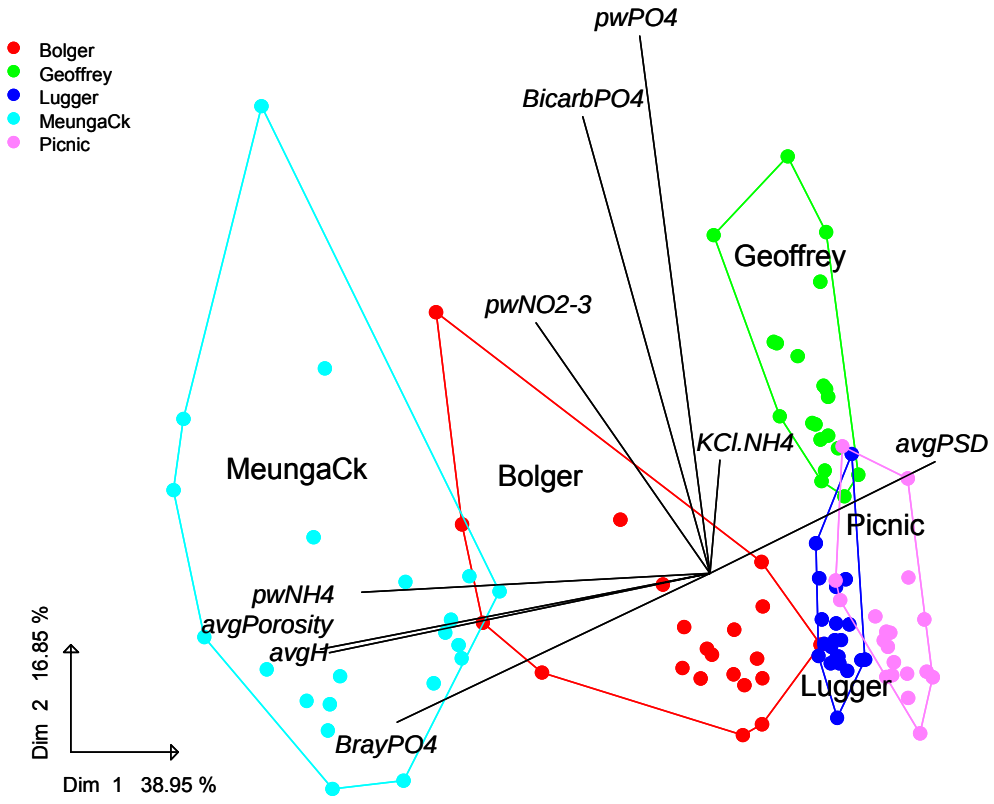


Figure 9.6. Principal components analysis of all sediment properties from the five locations and all sampling times. The points represent individual samples (N = 102 samples). The plot shows that spatial patterns in sediment properties are stronger than temporal changes, although Meunga Creek and Bolger Bay underwent some strong changes over time.

Seagrass properties

Seagrass biomass

For *H. uninervis*, total dry weight (DW) averaged 16.95 g m^{-2}, of which 58.8% was comprised of rhizomes, 18.2% roots and 22.4% leaves. For *H. ovalis*, total DW averaged 12.1 g m^{-2}, of which 43.5% was rhizomes, 23.9% roots and 33.0% leaves (Table 9.3). Maximum values of total DW were as high as 56 and 42 g m^{-2} in *H. uninervis* and *H. ovalis*, respectively. For both of these species, rhizomes contribute the most towards total biomass.

Table 9.3. Proportion of biomass across leaves, roots and rhizomes. Means of untransformed data.

	drylvs.m2	dryrts.m2	dryrhz.m2
H. uninervis	22.4%	18.2%	58.7%
H. ovalis	33.0%	23.9%	43.5%

Seagrass dry weight of leaves, roots and rhizomes changed considerably across the locations, between species and over time as evidenced by the highly significant interaction term as summarised in Table 9.4 and Figure 9.7. The greatest driver of biomass variance was Location coupled with inter-annual variation, which was greater than intra annual variation; consequently no significant seasonal pattern was evident. No species - specific pattern was evident either. All Plant components followed similar trends through time (Fig 9.7).

Table 9.4. ANOVA outputs for differences in the six measures of seagrass biomass (DW of leaves, roots and rhizomes, and total DW) across species and locations (*H. ovalis* in Picnic Bay and Bolger Bay, *H. uninervis* in Meunga Creek, Geoffrey Bay and Lugger Bay), and time. See also Fig 9.7. Data are square-root transformed. Time was fitted as a smooth term (3 df).

	Df	DW rhizomes		DW roots		DW leaves		Total DW	
		F	P	F	P	F	P	F	P
Species	1	49.11	<0.001	2.106	0.1488	0.1878	0.6654	26.2023	<0.0001
Time	3	13.76	<0.001	22.56	<0.001	16.89	<0.0001	22.7954	<0.0001
Spec : Locat	3	27.88	<0.001	42.13	<0.001	43.04	<0.0001	39.0098	<0.0001
Spec : Time	3	0.8175	0.4915	0.2821	0.8383	0.6929	0.5577	0.8467	0.4703
Spec : Locat : Time	9	5.005	<0.001	6.826	<0.001	4.768	<0.0001	7.1303	<0.0001
Residuals	153								

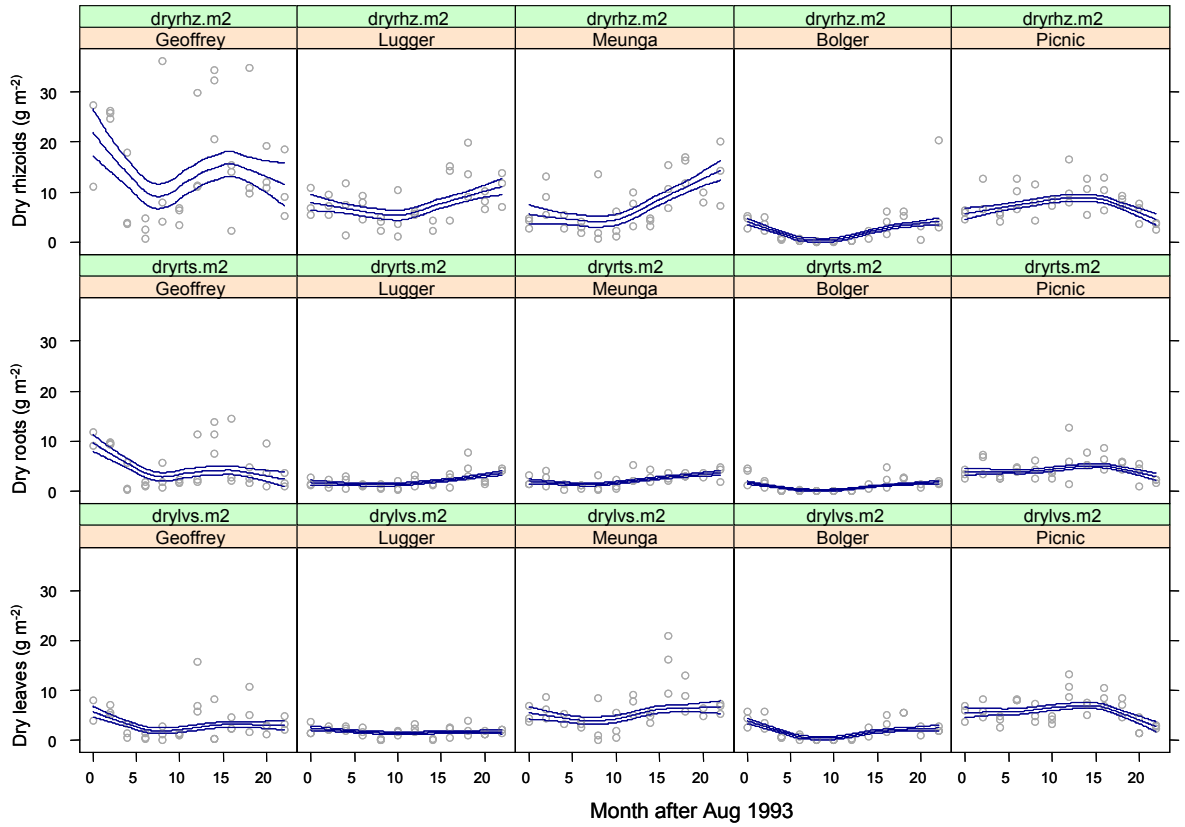


Figure 9.7. Changes in seagrass biomass (dry weight of rhizomes, roots and leaves) over time.

Seagrass biomass at Lugger Bay and Meunga Creek (Wet tropics, *H. uninervis* meadows) and Bolger Bay showed a similar pattern in biomass over years, with a decrease in biomass between August 1993 and August 1994 then an increase until sampling finished in June 1995 (Fig 9.7). The amplitude of change was much smaller at Bolger Bay.

Biomass at Picnic Bay displayed an opposite pattern to this. At this site, biomass increased from August 1993 to November 1994 then decreased until June 1995 when sampling ceased (Fig 9.7). Seagrass biomass at Geoffrey Bay displayed a combination of these patterns, with biomass decreasing from August 1993 to June 1994, increasing until December 1994 then decreasing again until sampling ceased in June 1995. The sample variability at this site was large, rendering this pattern statistically non-significant.

Seagrass tissue nutrients

Differences in the six measures of seagrass tissue nutrients (%P in leaves, roots and rhizomes, and %N in leaves, roots and rhizomes) across the two species (Table 9.5a), their locations and time are summarised in Table 9.5b and Figures 9.8a and 9.8b. Most of the tissue N in both species was bound in the leaves, whereas tissue P was distributed more evenly across the three plant parts.

Table 9.5a. Mean tissue nutrient data (percent of dry weight). Data are untransformed.

	Leaf.N (%)	Leaf.P (%)	Root.N (%)	Root.P (%)	Rhiz.N (%)	Rhiz.P (%)
H. uninervis	3.964	0.277	1.460	0.269	1.026	0.193
H. ovalis	3.046	0.367	0.888	0.175	1.079	0.240

Tissue N had multiple responses depending on the component of the plant that was being analysed. Leaf N varied over time (Table 9.5b). Rhizome N varied according to species and time while significant differences in root N were driven by differences in species. For both leaf P and rhizome P the interaction between species and time was significant but differences in root P were best explained by differences between species.

Temporal changes again varied strongly between locations with inter-annual changes overwhelming any intra-annual (seasonal) variation in tissue nutrients. Lugger Bay and Bolger Bay both showed to be maintaining their levels of leaf N until around June 1994 when leaf N decreased at both sites. At Meunga Creek, leaf N appeared to be increasing until June 1994 and then also declined. Leaf N at Geoffrey Bay also declined after June 1994 however it showed an increase after November 1994. Leaf N at Picnic Bay did not vary for the duration of this study and recorded the lowest levels for all locations (Fig 9.8a).

Differences in leaf P across locations appeared related to species as all sites characterised by *Halodule uninervis* showed a similar pattern and at levels relative to each other. Bolger Bay and Picnic Bay (*Halophila ovalis* meadows) varied in levels of tissue leaf P. Bolger Bay plants had higher levels of tissue P than that recorded for plants at Picnic Bay and the levels through time were dissimilar (Fig 9.7b).

Table 9.5b. ANOVA outputs for differences in the six measures of seagrass tissue nutrients (%N and %P in leaves, roots and rhizoids) across species and locations (*H. ovalis* in Picnic Bay and Bolger Bay, *H. uninervis* in Meunga Creek, Geoffrey Bay and Lugger Bay), and time. See Fig 9.6. Data are square-root transformed. Time was fitted as a smooth term (4 df).

	Df	**Leaf N**		**Leaf P**	
		F	**P**	**F**	**P**
Species	1	5.4	0.087	7.32	0.07
Species : Locat	3	7.66	0.00057	4.93	0.0065
Time	4	4.18	0.00799	2.12	0.1017
Spec : Time	4	0.24	0.91403	9.66	<0.0001
Species : Locat : Time	12	1.33	0.25352	0.9	0.561
Residuals	31				
	Df	**Root N**		**Root P**	
		F	**P**	**F**	**P**
Species	1	54.34	0.006	3.98	0.139
Species : Locat	3	0.49	0.695	5.91	0.0027
Time	4	2.2	0.093	4.51	0.0057
Spec : Time	4	0.76	0.558	1.05	0.399
Species : Locat : Time	12	0.35	0.97	0.97	0.4971
Residuals	30				
	Df	**rhiz.n**		**rhiz.p**	
		F	**P**	**F**	**P**
Species	1	0.02	0.9612	2.39	0.34
Species : Locat	3	9.13	0.00016	15.99	<0.0001
Time	4	3.03	0.03168	3.53	0.0171
Spec : Time	4	2.89	0.03786	5.91	0.0011
Species : Locat : Time	12	0.71	0.73189	1.67	0.1216
Residuals	32				

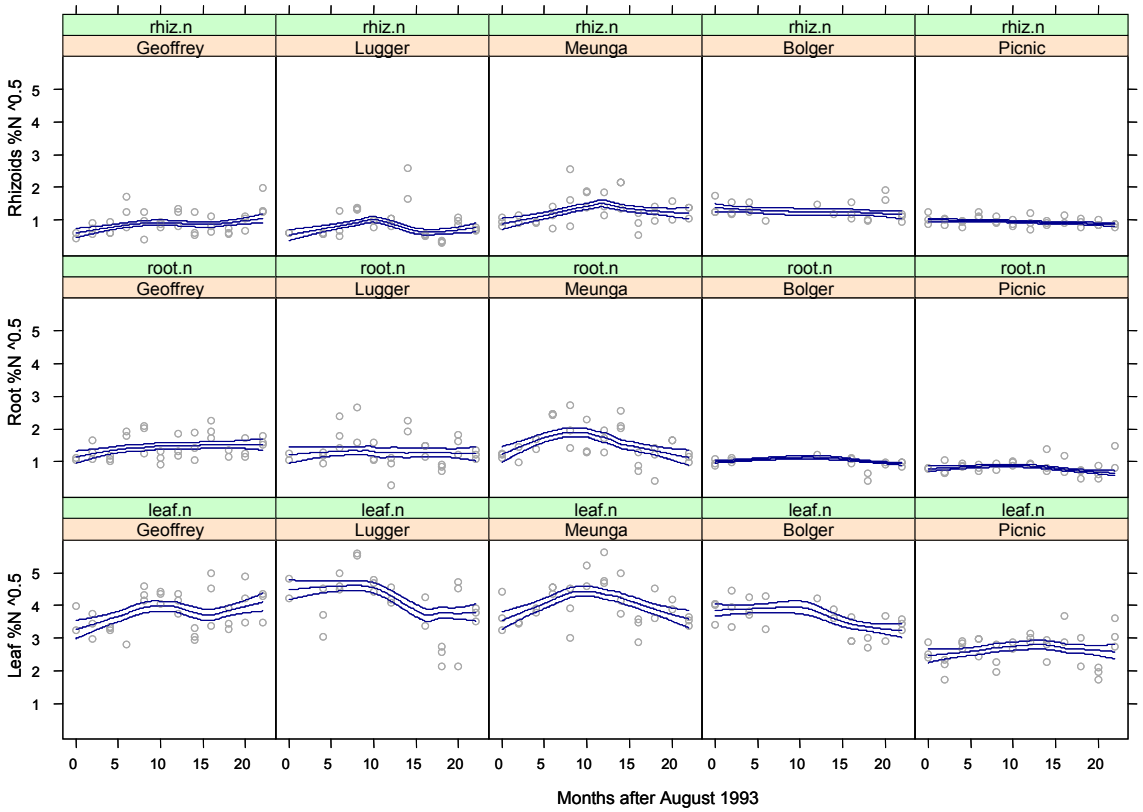


Figure 9.8a. Changes over time in mean seagrass tissue N rhizomes, roots and leaves at the five locations over the 12 visits. Data are square-root transformed. For abbreviations see Figure 9.5a.

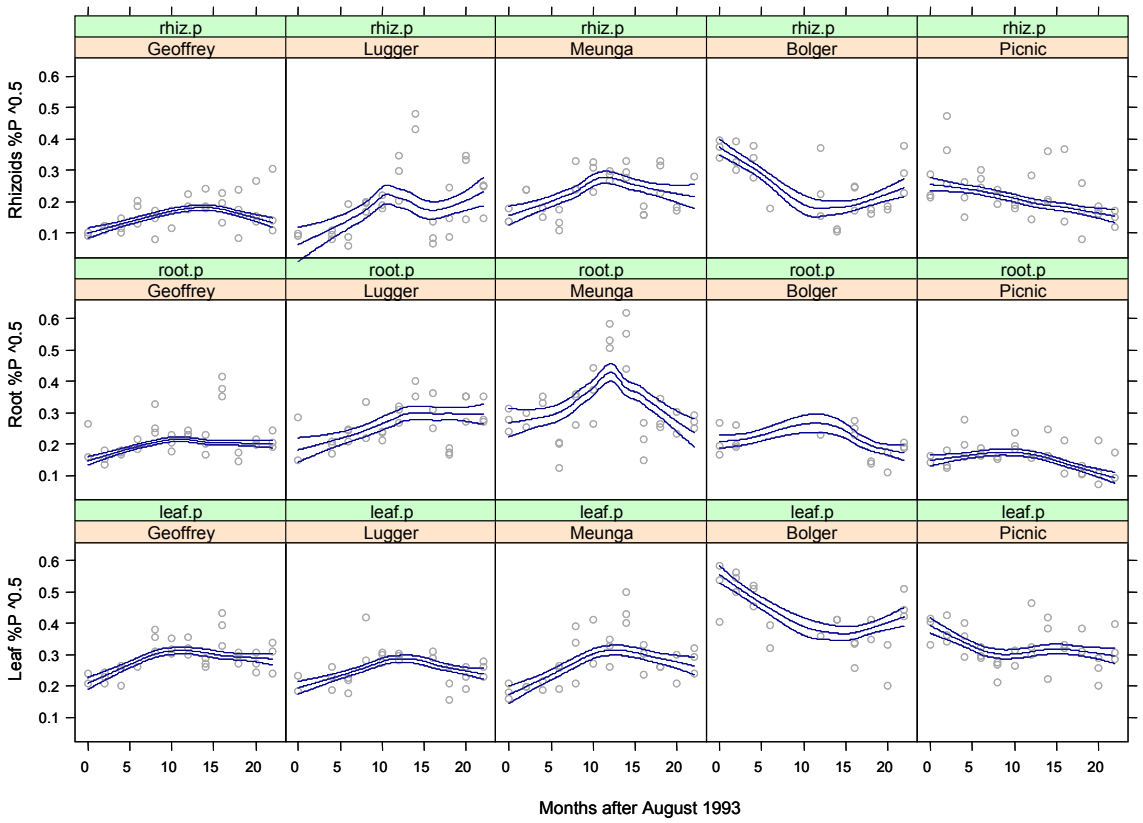


Figure 9.8b. Changes over time in mean seagrass tissue P in rhizomes, roots and leaves at the five locations over the 12 visits. Data are square-root transformed. For abbreviations see Table 9.1.

Relationships between seagrass and sediment properties

Boosted regression tree analyses were used to identify the relative contributions of porewater and adsorbed sediment nutrients, PSD and water content, sampling time (month after Aug 93), and location (including species), in explaining variation in seagrass properties. Best predicted were the leaf N concentration (leaf %N; 41% of predicted variance), and the biomass variables root DW m^{-2}, total DW m^{-2} and rhizomes DW m^{-2}(33%, 31% and 30% of predicted variance, respectively) (Table 9.6).

Most of the variation in seagrass properties was explained by Location. Interestingly, sampling time explained very little of the variation in any of the variables. Water content was important in predicting several of the tissue nutrients. Amongst the nutrients, porewater NH_4^+ was by far the most important predictive variable both for biomass data, and for the variation in leaf, root and rhizome N. Adsorbed NH_4^+ predicted a proportion of two of the biomass variables (leaves DW and total DW), but was unrelated to any of the other seagrass variables. Porewater PO_4^{3-} was related to some variation in leaf and root tissue nutrients. Adsorbed PO^{3-} (both the Bray and the Bicarbonate methods) explained some variation in root %P, while $PO_4^{3-}{}_{Bray}$ explained some variation in rhizome %N.

Table 9.6. Percentage of variance in seagrass properties predicted by sediment properties and location, and percentage of the total percentage of variance predicted by each of the explanatory variables. For example, 21% of variance in the dry weight of leaves m^{-2} is predicted by the whole model, 47% of which (47% of 21% = 9.9%) are attributable to location effects (including differences between the 2 species), and 18% of the 21% (= 3.78%) are explained by adsorbed N. Preliminary analyses had shown that PW NO_2+NO_3 and pore size density explained very little of the variances in seagrass properties, these variable were therefore omitted. Low values are also omitted for clarity.

	Total % Var pred.	Locatn	Smpl time	Sedim water cont.	PW NH_4^+ [uml]	Ads N [uml]	PW PO_4^{3-} [uml]	Bicarb P [uml]	Bray P [uml]
Dryweight leaves m^{-2}	21	47				18			
Dryweight roots m^{-2}	33	33			42				
Dryweight rhizomes m^{-2}	30	43	7.9		28				
Total DW m^{-2}	31	37			29	10.6			
Leaves m^{-2}	0.6								
Leaves (%N)	41	52			21		10.6		
Leaves (%P)	21	40		38			7.4		
Roots (%N)	29	42			12.9		11.4		
Roots (%P)	10.4	47		10.6				13	23
Rhizoids (%N)	8.9			28	18				21
Rhizoids (%P)	9.2	21		62					
SG all N m^{-2}	0.7								
SG all P m^{-2}	1.2								

Porewater NH_4^+ was the best predictor for seagrass biomass and tissue nutrients, with seagrass biomass being negatively related to porewater NH_4^+ and tissue nutrients being positively related to porewater NH_4^+ at some of the sites (Fig. 9.9). Higher concentrations of porewater NH_4^+ were also related to lower amounts of total N bound in seagrass meadows per unit area (measured as the sum of (biomass x %N) for roots plus rhizomes plus leaves) at Geoffrey, Lugger and Bolger Bay.

Linear models without higher-level interactions were used to test these relationships (Table 9.7). The table confirmed that many of the seagrass properties significantly varied between locations, between species, and also with porewater NH_4^+.

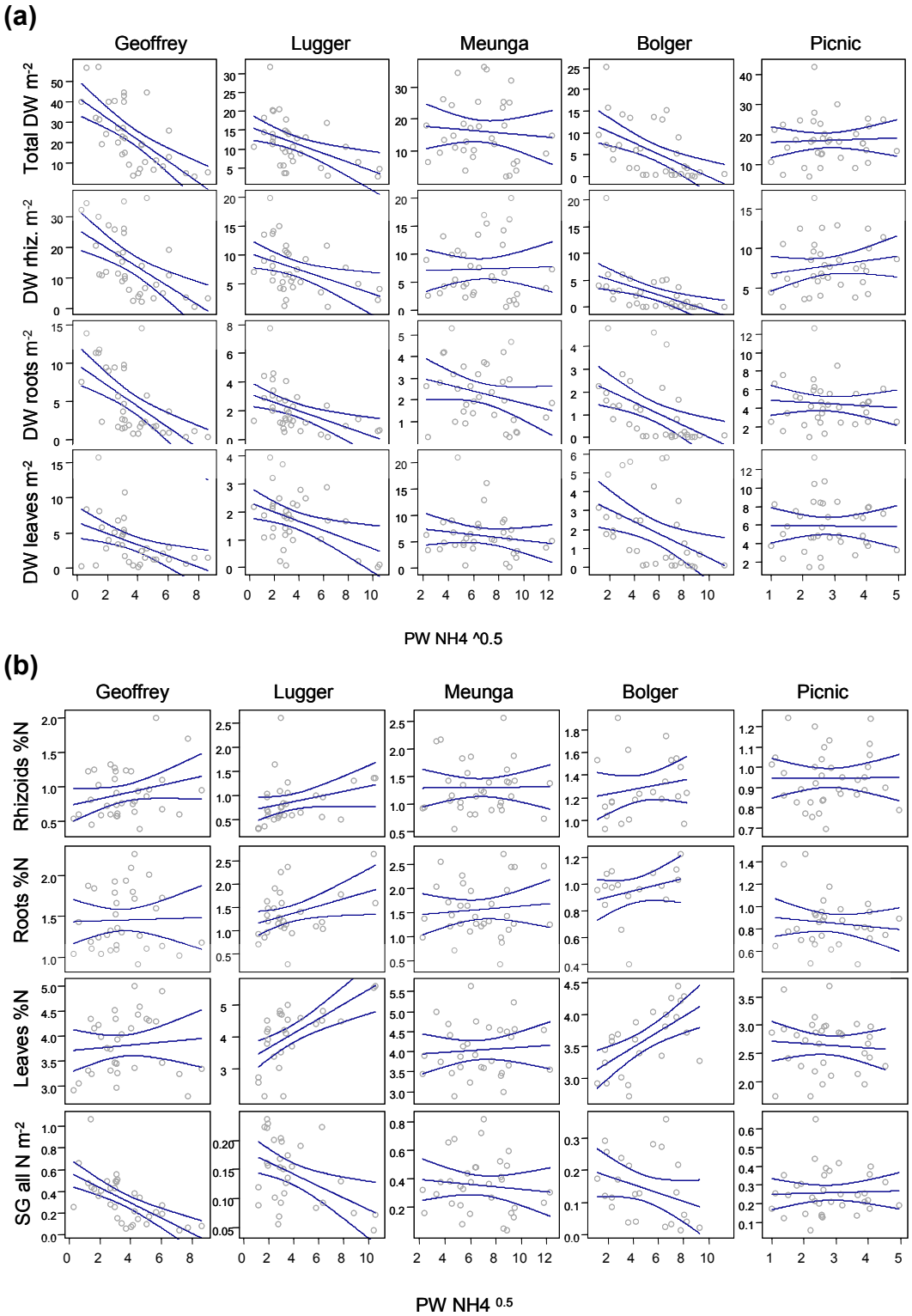


Figure 9.9. Relationship between seagrass biomass and tissue N variables against porewater NH4. Higher concentrations of porewater NH_4^+ were related to lower total amounts of N bound in seagrass per unit area at Geoffrey, Lugger and Bolger Bay but not the other sites (SG all N m^{-2} = sum of (biomass x %N) for roots plus rhizoids plus leaves).

Table 9.7. p-values for ANOVAs testing the effects of porewater NH_4 and location on all responses (linear models on square-root transformed data).

	pwnh4	spec	locat.x	pwnh4:spec	pwnh4:locat.x
Df	1	1	**3**	1	3
drylvs.m2	**0.0001**	0.9894	**<0.0001**	0.5928	0.2232
dryrts.m2	**<0.0001**	**0.0215**	**<0.0001**	0.861	0.0001
dryrhz.m2	**<0.0001**	**<0.0001**	**<0.0001**	0.7655	0
totaldw.m2	**<0.0001**	**<0.0001**	**<0.0001**	0.7946	0.0001
leaves.m2	**0.0001**	0.0635	**0.0275**	0.6104	0.1514
leaf.n	**<0.0001**	**<0.0001**	**<0.0001**	0.9181	0.0063
leaf.p	0.2094	**<0.0001**	**0.0002**	0.6456	0.0387
root.n	**<0.0001**	**<0.0001**	0.5447	0.6728	0.4455
root.p	**0.0009**	**<0.0001**	**<0.0001**	0.1521	0.0544
rhiz.n	**<0.0001**	**0.0058**	**0.0002**	0.4938	0.3772
rhiz.p	0.4139	**0.0002**	**0.0076**	0.1677	0.5836
n.leaf.m2	0.5186	**0.2215**	**<0.0001**	0.2949	0.3293
p.leaf.m2	**0.0409**	**0.002**	**<0.0001**	0.4913	0.4403
n.root.m2	**<0.0001**	**0.001**	**<0.0001**	0.1124	0.0001
p.root.m2	**<0.0001**	**0.0091**	**0.0004**	0.0645	0.0473
n.rhiz.m2	**0.0022**	**0.0001**	**<0.0001**	0.9122	0.0002
p.rhiz.m2	**<0.0001**	**0.0019**	**0.0013**	0.3459	0.009
sg.n.m2	**0.0003**	**0.0006**	**<0.0001**	0.5335	0.0157
sg.p.m2	**<0.0001**	**0.0744**	**<0.0001**	0.423	0.0967
sg.alln.m2	**0.0078**	**0.0013**	**<0.0001**	0.4809	0.0008
sg.allp.m2	**<0.0001**	**0.0596**	**<0.0001**	0.4231	0.0066

Finally, redundancy analyses were used to display the relationships between all sediment and all seagrass variables for each of the species (Fig. 9.10). The analyses confirmed previous findings.

In *Halophila ovalis*, all tissue nutrient measures were high in Bolger Bay (Fig 9.10a), where levels of porewater NH_4^+, adsorbed PO_4^{3-}, and water content were high. All dry weight measures were high in Picnic Bay, where porewater NH_4^+, adsorbed PO_4^{3-}, and water content were low, but porewater PO_4^{3-} and adsorbed NH_4^+ were high. For *H. ovalis,* the sediment variables plus time explained almost 60% of the variance in the seagrass data; this variance was reduced to 51% when Month was excluded as a factor, indicating that temporal variation did contribute to explaining some of the differences in the data.

In *Halodule uninervis*, dry weight was high but tissue nutrients were low in Geoffrey Bay, and sediments in this bay were characterised by low levels in all nutrients except for adsorbed NH_4^+ and PO_4^{3-} (bicarbonate method) (Fig. 9.10b). In contrast, tissue nutrients were high but biomass was low at Meunga Creek, and sediments in this bay were characterised by high levels in most nutrients. Lugger Bay had low values in seagrass biomass and tissue nutrients, and its sediments were also low in all values except porewater nutrients. Within locations, seagrass properties were quite variable over time and between replicates, except in Lugger Bay, where all values were low. For *H. uninervis,* the sediment variables plus time explained 39.1% of the variance in the seagrass data; this variance remained almost unaltered (38.0%) when Month was excluded as a factor, indicating that temporal variation did not contribute to explaining differences in the data.

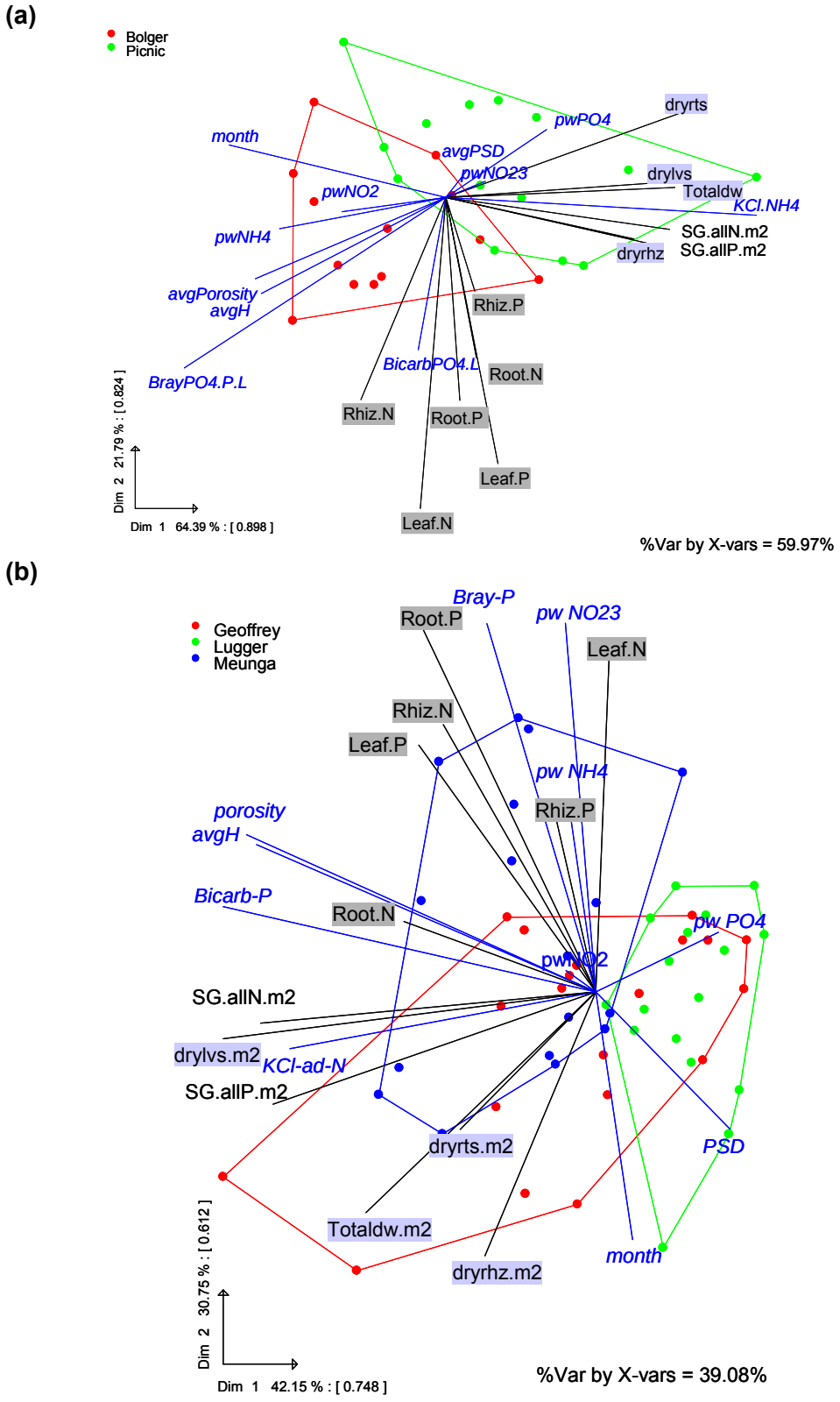


Figure 9.10. Redundancy analysis displaying the relationship between all sediment and all seagrass variables for each of the species: a) *Halophila ovalis,* b) *Halodule uninervis*. The biomass variables are printed in a blue field, the tissue nutrients in a grey field. Total standing crop of seagrass nutrients per m^2 (dry weight times tissue nutrients for leaves, roots and rhizomes combined) are given as SG.allN.m2, and SG.allN.m2, respectively. Explanatory variables are the sediment properties for each of the 33and 62 samples, respectively, and time. Data are z-transformed.

9.4 Discussion

From a global perspective, we recorded relatively low porewater nutrient concentrations in the six meadows sampled (cf Mellors et al 2005). In addition, we observed comparatively high levels of adsorbed N combined with low levels of adsorbed PO_4^{3-} (cf. Udy and Dennison 1997a, b; Udy *et al.* 1999). Biomass measures were low for all species, but tissue nutrient content was high for *Halodule uninervis* and *Halophila ovalis* (cf Mellors et al 2005). These observations, combined with the low suspended and particulate nutrients recorded along this coastline (Furnas and Mitchell 1995), suggest that the nutrients in the coastal shallow seagrass environments of this region are bound up in the sediments and biome rather than free in the water column.

This study reconfirmed that seagrass species invest a greater proportion of their biomass into their below ground components, however the magnitude of this investment appears greater in these species (Table 9.3). This is consistent with plants that need to secure their place within a highly variable environment (Purves *et al.* 2001). It also reconfirmed that leaves are the site of maximum tissue nutrient storage particularly for N (Table 9.5a; Touchette and Burkholder 2000). Despite these generic conclusions, variability between the meadows was predominantly driven by location.

The importance of location indicates the significance of local site history. The geographic setting of a location dictates its sediment regime, while the frequency of disturbance and availability of light dictates the structure of the meadow. The factors that affect the sediment regime and light availability at each location are: a) distance from major rivers, b) protection from south-easterly trades winds, c) frequency and magnitude of resuspension, and d) sediment particle sorting. Differences in sediment mineralogy and grain size, in turn, influence the nutrient regime at specific locations. For example, across the five locations studied, locations with muddy wetter sediments tended to have high levels of porewater NH_4^+ and $PO_4^{3-}{}_{Bray}$ than locations with coarser sediments (Fig. 9.6).

Intra-annual temporal structuring of the seagrass meadows was not apparent from this study for either seagrass biomass (Table 9.4, Fig. 9.7) or tissue nutrients (Table 9.5b, Figs. 9.8a and 9.8b). This is contrary to studies of seagrass meadows within this region that found distinct seasonal patterns with maximum abundance usually occurring in spring/summer and minima in winter (Mellors *et al.* 1993; McKenzie 1994). Rather, temporal variance was at the inter-annual time scale with suggestions that even longer time frames are involved. This suggests that the meadows of structurally small species studied in this investigation were all in different stages of development and had not yet reached a steady state. In that case, direct comparison with the studies of Mellors *et al.* (1993) and McKenzie (1994) are inappropriate as they studied meadows of structurally large seagrass species in resolutely established meadows.

There is a paucity of data on recovery of seagrass meadows owing to a lack of data from long term seagrass monitoring programs. A study on the recovery of a similar meadow to those in this study found that full recovery, from a disturbance to the reappearrance of seasonal patterns, took up to three years (Campbell and McKenzie 2004), a time frame much longer than the one of the current study. A more in-depth inspection of the data at individual meadows may reveal the subtleties of seasonal growth and nutrient acquisition and use; however this was beyond the scope of this study.

The ability to classify different meadows according to their disturbance regime and level of recovery will take us a step closer to understanding these intertidal seagrass meadows of structurally small seagrasses. To be able to achieve this, a diagnostic tool is required. Mellors (2003) and McMahon (2005) observed an increase in rhizome elongation as measured by internode length from disturbed meadows. This was a characteristic also noted

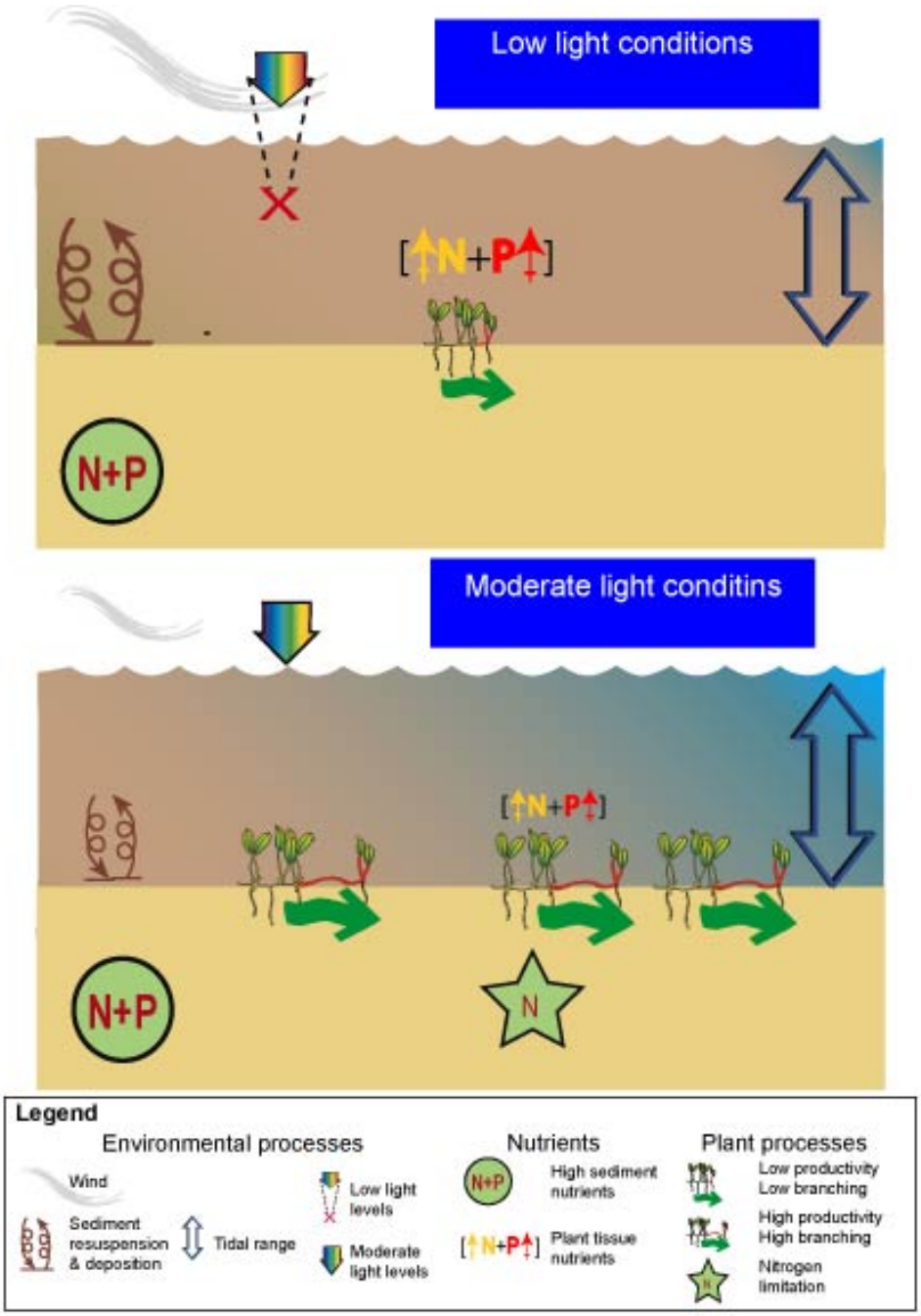
by Campbell and MeKenzie (2004) during recovery of a meadow in the Great Sandy Straits. The use of this characteristic will require testing to check its validity. To be able to classify meadows according to age, will enable a grouping of meadows that may eliminate some of the variability created by differences in location.

Despite the lack of seasonal influences on seagrass biomass and plant tissue nutrients, and the overwhelming evidence that location dictates seagrass meadow structure, some relationships did exist between sediment nutrients and seagrass properties. Porewater NH_4^+ was the best predictor of seagrass biomass and tissue nutrients (Table 9.5, Fig. 9.9). Porewater NH_4^+ had a positive relationship with plant tissue N, indicating that as NH_4^+ increases, plant tissue N also increases. The negative relationship between porewater NH_4^+ and biomass implies that the acquisition of NH_4^+ within the seagrass plant is not being translated into an increase in biomass. Total biomass was driven by the large contribution of below ground biomass.

An increase in below-ground biomass as porewater NH_4^+ decreases may be indicative of the plants need to increase their major site (root and rhizomes) of nutrient acquisition/adsorption in areas of low nutrients (Short 1983). Leaf biomass also declined and this combined with an increase in leaf tissue N with increasing porewater NH_4^+ indicates that some other factor is limiting seagrass growth at these locations. Plant tissue content may be a good indicator of water quality, particularly N, as a positive relationship has been established between porewater NH_4^+ and tissue N (Fig. 9.9b) particularly leaf N (Fig 9.9b). If we are looking at the health of the seagrass meadow, then some measure of seagrass abundance needs to be included (Fig 9.9a) as nutrients are not the only factor structuring seagrass meadows. If nutritional state of a meadow is the main objective of the monitoring program then measures that combine both tissue nutrients and abundance are required ($gN\ m^{-2}_{seagrass}$).

The relationship between nutrients and plant parameters is more complex than these two factors. Closer inspection shows that it is the specific locations that are influencing this relationship. The muddy wetter locations of Bolger Bay (Fig 9.10a) and Meunga Creek (Fig 9.10b) were characterised by low biomass and high tissue nutrients and high porewater NH_4^+. This suggests that nutrients at these sites were being acquired by the plants and being stored rather than transforming the nutrients into components required for structural growth. Therefore, something else is limiting growth at these locations. The most likely factor is light. The finer sediments associated with muddy substrata are easily resuspended, creating turbid conditions and increasing light attenuation (Fig 9.11), More specific knowledge is required on the interaction between nutrients and light in relation to seagrass abundance in this region. This is probably best dealt with in a mesocosm experiment before trying to elucidate these effects in the field.

Based on the evidence presented in this study we suggest that the disturbance regime of a location, that is, the localised aspects of exposure to predominate winds, turbidity and hence light availability, and to a lesser degree the frequency and intensity of herbivory, particularly that of dugong grazing (Preen 1995), dictates the level of abundance for these seagrass meadows. The lack of intra-annual pattern but evidence of temporal change within the meadow on an inter-annual scale is most likely the result of the stage of recovery the meadow is at in association with the extent of the disturbance experienced. Recovery from dugong grazing is less likely to be as intense as recovery from a cyclone. Meadows of high abundance will act as filters of nutrients from catchments, but their capacity is limited by the frequency and extent of the disturbance the meadow encounters. Disturbances that cause loss of seagrass will result in the nutrients being released from the meadow. Meadows of low abundance will not act as filters as nutrients are not being bound up in the plants and resuspension of sediment within the seagrass meadow will release nutrients to the water column.



Conceptual diagram of controls and key processes limiting growth of structurally small seagrasses

Figure 9.11. A conceptual diagram of the processes that form and limit growth of intertidal seagrass meadows of structurally small species in the central region of the Great Barrier Reef World Heritage Area. In low light conditions resulting from strong winds causing resuspension and increasing turbidity, plants store nutrients but do not grow. When light is adequate plants are able to convert stored nutrient into biomass and may become nutrient limited (N limitation).

By comparing a greater number of similar communities (characterised on environmental, climatic geographical conditions and meadow age), over longer time frames than the present study, it should be possible to develop an abstract model in which all local features can be accounted for and long term temporal differences incorporated. Whether this model will conform to traditional views or lead to the development of new paradigms warrants further investigation, in light of the importance of the temporally dynamic seagrass meadows of structurally small species that predominate along the coastline of the central region of the GBRWHA.

It is also important to realise that this study only concentrated on a subset of coastal seagrass habitats; the intertidal meadows of the central region of the GBRWHA. Within the GBR region, four seagrass habitat types have been recognised: 'River estuaries' 'Coastal', 'Reef' and 'Deepwater' (Carruthers *et al.* 2002). Whilst all these habitats are influenced by disturbance, they are both spatially and temporally variable. Each of these habitats is moderated by different processes and therefore has different ecological functions and will respond differently to environmental stressors. It is important to expand our knowledge base to encompass all these different seagrass habitat types.

This study demonstrates the complexity of these systems. Continuing to amass information on this habitat through Seagrass-Watch and the RWQPP Seagrass monitoring program can only enhance our chances of understanding these dynamic habitats.

9.5 References

Baker DE, Eldershaw VJ. 1993. Interpreting soil analysis for agricultural land use in Queensland. (Department of Primary Industries: Queensland) Project Report Series QO93014.

Blake S. 1996. The distribution of sediments and nutrients throughout the Whitsunday Islands inner-shelf region, Great Barrier Reef. In: Larcombe. P., Woolfe, KJ., Purdon, RG. (Eds) Great Barrier Reef: Terrigenous Sediment Flux and Human Impacts—Second Edition November 1996 CRC Reef Research Centre Current Research, Townsville, Australia. pp 24–32.

Boon PI. 1986. Nitrogen pools in seagrass beds of *Cymodocea serrulata* and *Zostera capricorni* of Moreton Bay, Australia. Aquatic Botany 25: 1–19.

Bray RM, Kurtz LT. 1945. Determination of total organic and available forms of phosphorus in soils. Soil Science 59: 39–45.

Bridges KW, Phillips RC, Young PC. 1982. Patterns of some seagrass distribution in the Torres Strait, Queensland. Australian Journal Marine and Freshwater Research 33: 273–283.

Brix H, Lyngby JE. 1985. Uptake and translocation of phosphorus in eelgrass (*Zostera marina*). Marine Biology 90: 11–116.

Brodie J. 1996. River Flood plumes in the Great Barrier Reef Lagoon. In: Larcombe P, Woolfe KJ, Purdon RG (Eds) Great Barrier Reef: Terrigenous Sediment Flux and Human Impacts—Second Edition November 1996 CRC Reef Research Centre Current Research, Townsville; Australia pp 33–40.

Bulthius D, Woelkerling WM. 1981. Effects of in situ nitrogen and phosphorus enrichment of the sediments on the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den

Hartog in Western Port Victoria, Australia. Journal of Experimental Marine Biology and Ecology 53: 93–207.

Campbell SJ, McKenzie LJ. 2004. Flood related loss and recovery of intertidal seagrass meadows in southern Queensland, Australia. Estuarine Coastal and Shelf Science 60:47-490

Carruthers TJB, Dennison WC, Longstaff BJ, Waycott M, Abal EG, McKenzie LJ, Lee Long WJ. 2002. Seagrass habitats of north east Australia: Models of key processes and controls. Bulletin of Marine Science 71: 1153–1169.

Coles RG, Poiner IR, Kirkman H. 1989. Regional studies—seagrasses of north-eastern Australia. In: Larkum, A., McComb, A, Shepherd, S. (Eds). Biology of Seagrasses (Elsevier: Amsterdam) pp 261–278.

De'ath G. 2007. Boosted regression trees for the analysis of ecological data. Ecology (in press)

Duarte CM. 1999. Seagrass ecology at the turn of the millennium: challenges for the new century. Aquatic Botany 65: 7–20.

Duarte CM, Kirkman H. 2001 Methods for the measurement of seagrass abundance and depth distribution. In: Short F, Coles R (eds) 2001 Global Seagrass Research Methods (Elsevier Science:Amsterdam) pp 141-154.

Folk RL. 1974. Petrology of Sedimentary Rocks (Hemphill Publishing Co: Texas).

Fourqurean J, Zieman J, Powell G. 1992. Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. Marine Biology 114: 57–65.

Friedman GM. 1978. Principles of Sedimentology (John Wiley & Sons: Canada).

Furnas M, Mitchell A. 1995. River discharge to and water column concentrations of sediments and nutrients in the GBR. Abstract from CRC/GBRMPA Researcher Days, September 1995.

Hemminga MA, Duarte CM. 2000. Seagrass ecology. Cambridge University Press, Cambridge. 298pp.

Hemminga MA, Harrison PG, Van Lent FA. 1991. The balance of nutrient losses and gains in seagrass meadows. Marine Ecology Progress Series 71: 85–96.

Hillman K, Walker DI, Larkum AWD, McComb AJ. 1989. Productivity and nutrient limitation. In: Larkum AWD, McComb AJ, Shepherd SA (Eds) Biology of Seagrasses: A treatise on the biology of seagrasses with special reference to the Australian region (Elsevier: Amsterdam) pp 635–685.

Iizumi H, Hattori A. 1982. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan: The kinetics of nitrogen uptake. Aquatic Botany 12: 245–256.

Kirkman H, Cook IH, Reid DD. 1982. Biomass and growth of *Zostera capricorni* Aschers in Port Hacking, N.S.W., Australia. Aquatic Botany 12: 57–67.

Lanyon J, Marsh H. 1995. Temporal changes in the abundance of some tropical intertidal seagrasses in northern Queensland. Aquatic Botany 49: 217–237.

Larkum AWD, Collett LL, Williams RJ. 1984. The standing stock, growth and shoot production of *Zostera capricorni* Aschers in Botany Bay, New South Wales, Australia. Aquatic Botany 19: 307–327.

Lee Long WJ, Mellors JE, Coles RG. 1993. Seagrasses between Cape York and Hervey Bay, Queensland, Australia. Australian Journal of Marine and Freshwater Research 44(1): 19–33.

Marba N, Cebrain J, Enriquez S, Duarte C. 1996. Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. Marine Ecology Progress Series 133: 203–215.

McKenzie LJ. 1994. Seasonal changes in biomass and shoot characteristics of a *Zostera capricornii* Ashers dominant meadow in Cairns harbour, northern Queensland. Australian Journal of Marine and Freshwater Research 45: 1337–1352.

McMahon K 2005. Recovery of subtropical seagrasses from natural disturbance. PhD thesis University of Queensland. 224 pp

Mellors J, Marsh H, Coles R. 1993. Intra-annual changes in seagrass standing crop, Green Island, northern Queensland. Australian Journal of Marine and Freshwater Research 44(1): 33–42.

Mellors J. 2003. Sediment and nutrient dynamics in coastal intertidal seagrass of north eastern tropical Australia. PhD Thesis, James Cook University. 278 pp. Available from <www.jcu.edu.au>.

Mellors JE, Waycott M, Marsh H. 2005 Variation in biogeochemical parameters across intertidal seagrass meadows in the central Great Barrier Reef region. Marine Pollution Bulletin 51: 335–342

Mengel K, Kirkby EA. 1987. Principles of Plant Nutrition (International Potash Institute: Switzerland). 687 pp.

Moriarty DJW, Boon PI. 1989. Interactions of Seagrasses with Sediment and Water. In: Larkum AWD, McComb AJ, Shepherd SA. (Eds) Biology of Seagrasses: A treatise on the biology of seagrasses with special reference to the Australian region (Elsevier: Amsterdam). pp 500–535.

Morrissette N 1992. Identifying areas of seagrasses within the Great Barrier Reef region threatened by anthropogenic activities. MSc Qualifying Thesis (James Cook University: Australia).

Murray L, Dennison WC, Kemp WM. 1992. Nitrogen versus phosphorus limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.) Aquatic Botany 44: 83–100.

Pailles C, Moody PW. 1995. Effect of experimental conditions on phosphorus extracted from estuarine and marine sediments, Australian Journal of Marine and Freshwater Research 46: 435–440.

Preen AR. 1995. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. Marine Ecology Progress Series 124: 201-213.

Purves W, Sadava D, Orians G, Heller H. 2001. Life: the Science of Biology. Sixth edition. (W.H. Freeman and Company: Massachusetts) pp 1044

Rayment GE, Higginson FG. 1993. Australian laboratory handbook of soil and water chemical methods. (Inkata Press: Sydney).

Ryle VD, Mueller HR, Gentein P. 1981. Automated analysis of nutrients in tropical sea waters AIMS Data Report III (AIMS OS 81 2: Townsville).

Short FT. 1983. The seagrass *Zostera marina* L.: Plant morphology a bed structure in relation to sediment ammonium in Izembek Lagoon, Alaska. Aquatic Botany 16: 149–161.

Short FT. 1987. Effects of sediment nutrients on seagrasses: Literature review and mesocosm experiment. Aquatic Botany 27: 41–57.

Short FT, McRoy CP. 1984. Nitrogen uptake by leaves and roots of the seagrass *Zostera marina* L. Botanica Marina 27: 547–555.

Strickland JDH, Parsons TR. 1972. A practical handbook of seawater analysis. Fisheries Research Board of Canada Bulletin No. 167 (2nd Edition), Ottawa. 310pp.

Touchette BW, Burkholder JM. 2000. Review of nitrogen and phosphorus metabolism in seagrasses. Journal of Experimental Biology and Ecology 250: 135–167.

Udy JW, Dennison WC. 1996. Estimating nutrient availability in seagrass sediments. In: Kuo J, Phillips RC, Walker DI, Kirkman H (Eds) Seagrass Biology: Proceedings of an International Workshop Rottnest Island, Western Australia, 25–29 January 1996. pp 163–172.

Udy JW, Dennison WC. 1997a. Growth and physiological responses of three seagrass species to elevated nutrients in Moreton Bay, Australia. Journal of Experimental Marine Biology and Ecology 217: 253–257.

Udy JW, Dennison WC. 1997b. Seagrass physiological responses used to identify anthropogenic nutrient inputs. Marine and Freshwater Research 48: 605–614.

Udy JW, Dennison WC, Lee Long WJ, McKenzie LJ. 1999. Responses of seagrasses to nutrients in the Great Barrier Reef, Australia. Marine Ecology Progress Series 185: 257–271.

Walker DI, Dennison WC, Edgar G. 1999. Status of seagrass research and knowledge. In: Bulter A, Jernakoff P (eds) Seagrass in Australia; Strategic review and development of an R & D plan. (FRDC 1999).

Walker DI, McComb AJ. 1988. Seasonal variation in the production, biomass and nutrient status of *Amphibolis antarctica* and *Posidonia australis* Hook F. in Shark Bay, Western Australia. Aquatic Botany 31: 259-275.

Young PC, Kirkman H. 1975. The seagrass communities of Moreton Bay, Queensland. Aquatic Botany 1: 191–202.

Chapter 10: Conclusions

Around the world, an increasing proportion of coral reefs are in a disturbed state, with the greatest cause of disturbance being climate change (Hoegh-Guldberg 1999);(Berkelmans *et al.* 2004). Many coral reefs are also under immense pressure from destructive fishing and overfishing, especially in nations where coral reefs provide daily subsistence to coastal communities (Hughes *et al.* 2003). Reduction in fish abundance can severely compromise the resilience of coral reefs, potentially shifting the ecological balance from corals to algae (Hixon 1997). It is important to remember that Australia is the only 'economically developed' country that combines an extensive and diverse coral reef system with an affluent economy and a low population density; fortunately these advantageous settings are further strengthened by a modern management system based on a license system for commercial activities and a network of 'no-take' zones covering 30% of the GBR. High water quality standards and high fish abundances are two immensely important factors to protect the future of coral reefs in the face of global warming (Wooldridge *et al.* 2005), (Salm *et al.* 2006).

In this study we have determined biophysical and biological measures that consistently change along environmental gradients in the field, and after exposure to contrasting water quality conditions in laboratory experiments. The results and data presented in this Interim Report form the knowledge basis to choose the most suitable measures as indicators that allow us to measure and detect changes in exposure to changing water quality in inshore reefs of the GBR. We identified and started prioritising physico-chemical, genetic, physiological, population and community-based measures that could become sensitive, specific and cost-effective monitoring tools. Responses in biofilms, corals and seagrasses were investigated in the context of varying levels of light from turbidity, particulate and dissolved nutrients and chlorophyll in both the water column and sediments. The data-sets collected during surveys and in controlled experiments will now be used to complete the process of indicator tool development. Once priority indicator candidates are chosen within each group, we will quantify their dose-response relationships to the most critical water quality parameters through controlled laboratory tests and field verifications. These experiments will also serve to identify threshold concentrations for use in Ecosystem Health Guidelines and Water Quality Objectives.

To help decide whether a measure is suitable as an indicator of exposure or the effects of exposure, we have compiled a number of criteria we consider essential. These are derived from a similar set of criteria routinely used to ascertain the existence of a causal relationship based on the weight of evidence in epidemiology (U.S._Department_of_Health 1964); (U.S._Department_of_Health 1998). As a general rule, the more of these criteria that are met, the more useful the indicator is likely to be:

- The relationship between dose and response should be monotonic and ideally strong;
- The response should be specific to the cause;
- There should be a sound conceptual basis (e.g. the response should agree with known biological facts);
- The response should be consistent across time and space;
- Ideally, the measure should be scale-independent, i.e. it is useful at regional and local scales;
- Ideally, the measure should be important in the public's perception;
- The response should be easy and/or cheap to measure, and measurements are observer-independent; and
- The measure could be a proxy for another more complicated or costly measure.

These criteria will now be used to identify priority indicator candidates. After a qualitative assessment of each potential indicator measured against a number of criteria, the scores will result in a ranking. Indicators with a maximum rank will be assigned a 'high recommendation'; they are considered most useful for use in monitoring programs. Those with lowest ranks may still provide useful (often complimentary) information about the disturbance regime, but will be classed as 'low recommendation'.

A preliminary assessment showed that several indicators had a maximum score, and on this basis, they would be considered appropriate for inclusion in a 'toolbox' to assess the effects of water quality on ecosystem health on the GBR. These indicators were: the presence of phototrophic foraminifera and other biofilm attributes, coral colour, abundance of bioeroders, changes in abundance of macroalgae, the taxonomic richness of octocorals and coral juvenile densities, and the presence of octocoral indicator species. All these variables change strongly along spatial water quality gradients on nearshore reefs of the GBR. The physiological response in coral colour becomes evident within ~20 days exposure and provides evidence of sublethal effects from changes in environmental conditions. The Coral Health Monitoring Chart is an efficient method to quantify changes in colour in response to changes in water quality; portable spectrometers may further improve precision in assessing coral colour, and warrant further study. Abundances of internal macro-bioeroders in massive *Porites*, reduced taxonomic richness and abundances of susceptible species, and reduced coral recruitment, may all provide quantitative information on the extent of change in the exposure of benthic communities to changing water quality. For such quantification, specificity, effect sizes, response times, and potential thresholds will have to be considered for the indicators. If hypotheses about changing water quality are to be addressed, then indicators that are specific to disturbances such as sedimentation, turbidity and light will be of greater value than those with lower levels of specificity. While coral physiology and biofilms most likely provide sublethal or 'early warning' indicators of changing water quality on coral reefs, their readings will return to background levels within a period of days to weeks after exposure stops. In contrast, ecosystem level indicators may only change after severe or prolonged disturbance, but will carry the signal over prolonged periods of time. A quantitative comparison of indicators that incorporates sampling in the field over different spatial and temporal scales, coupled with manipulative experiments, has now commenced to identify a suite of complementary indicators suitable for inclusion in a monitoring toolbox.

This series of research projects, reviews and experiments has shown that, given the complex nature of coral reefs and of the disturbance by water quality, no single indicator on its own will provide sufficient information about environmental change. This Interim Report of potential indicators provides a platform from which to complete the development of an integrated indicator system. Research is presently underway to further prioritise and test potential indicators, to better understand their quantitative responses to environmental change, and to develop protocols for inclusion in future monitoring programs on inshore ecosystems of the GBR.

10.1 References

Berkelmans R, De'ath G, Kininmonth S, Skirving WJ. 2004. A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns, and predictions. Coral Reefs 23: 74-83

Hixon MA. 1997. Effects of reef fishes on corals and algae. In: Birkeland C (ed) Life and death of coral reefs. Chapman and Hall, New York, pp 230-248

Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50: 839-866

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystroem M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J. 2003. Climate Change, Human Impacts, and the Resilience of Coral Reefs. Science 301: 929-933

Salm RV, Done T, McLeod E. 2006. Marine Protected Area Planning in a Changing Climate. Americal Geophysical Union, Washington, DC

U.S._Department_of_Health E, _and_Welfare. 1964. Smoking and health: report of the advisory committee to the Surgeon General of the Public Health Service. Public Health Service Publication. No. 1103, Washington, D.C., USA

U.S._Department_of_Health E, _and_Welfare. 1998. Guidelines for ecological risk assessment. U.S. Environmental Protection Agency. Federal Register 63(93) 26 846–26 924, Washington, D.C., USA

Wooldridge S, Done T, Berkelmans R, Jones R, Marshall P. 2005. Precursors for resilience in coral communities in a warming climate: a belief network approach. Marine Ecology Progress Series 295: 157–169

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