Coral bioindicators of environmental conditions on coastal coral reefs

Thesis submitted by
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Chapter 2 is included without abstract and published as Cooper TF, Uthicke S, Humphrey C, Fabricius KE. (2007). Gradients in water column nutrients, sediment parameters, irradiance and coral reef development in the Whitsunday Islands, central Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 74: 458-470. The data was collected by all authors during field work undertaken over a 2-year period from 2004 to 2006. S Uthicke collected, processed and wrote the sediment sections. TF Cooper compiled and analysed the water quality and irradiance data, and wrote the manuscript. The manuscript (and this chapter) was submitted after editorial contributions from all co-authors.

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Publications

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Cooper TF, De'ath G, Fabricius KE, Lough JM. (2008). Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef. *Global Change Biology* 14: 529-538

Cooper TF, Uthicke S, Humphrey C, Fabricius KE. (2007). Gradients in water column nutrients, sediment parameters, irradiance and coral reef development in the Whitsunday Islands, central Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 74: 458-470

Peer-reviewed journal articles relevant but not associated with this thesis

Humphrey C, Weber M, Lott C, **Cooper TF**, Fabricius KE. (2008). Effects of different types of sediment, dissolved inorganic nutrients and salinity on fertilisation and embryo development in the coral *Acropora millepora* (Ehrenberg, 1834). *Coral Reefs* doi 10.1007/s00338-008-0408-1

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Fabricius KE, De'ath G, Puotinen ML, Done TJ, **Cooper TF**, Burgess, SC. (2008). Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. *Limnology and Oceanography* 53: 690-704

Conference abstracts

Cooper TF, Slivkoff M, Fabricius KE. (2006). Coral colour responds to changes in water quality: validation of a bioindicator using reflectance spectrometry. International Society for Reef Studies: European Meeting, 19 – 22 September 2006, Bremen, Germany.

Conference abstracts contd.

Cooper TF, Slivkoff M, Fabricius KE. (2006). Coral colour responds to changes in water quality: validation of a bioindicator using reflectance spectrometry. Australian Marine Sciences Association, 9 – 13 July 2006, Cairns, Australia. *Ron Kenny Prize for Highly Commended student oral presentation.*

Cooper TF, Fabricius KE, Humphrey C, Neale S. (2005). Coral based indicators of the effects of water quality on nearshore reefs of the Great Barrier Reef. Rainforest meets Reef: Joint conference of CRC Reef and Rainforest CRC, 22 – 24 November 2005, Townsville, Australia.

“I thought of that while riding my bicycle”

— Albert Einstein, on the theory of relativity.

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ABSTRACT

Reversing the decline in water quality is a key priority for the protection of the Great Barrier Reef (GBR). Strategies to improve the water quality of the GBR include conservation of riparian zones and the adoption of ecologically sustainable practices in the catchments. The implementation of these strategies requires feedback to resource managers and the community through monitoring programmes aimed at detecting biological responses to changes in water quality. This thesis investigates a range of coral indicators at different spatial and temporal scales and identifies those most suitable for inclusion into a toolbox for monitoring the condition of coastal coral reefs on the GBR. The approach combines *in situ* studies of coral indicators in different regions and environmental gradients on the GBR with controlled manipulative experiments exposing corals to differing water quality to examine causality of correlations observed in the field.

An environmental gradient was identified in the Whitsunday Islands where water column variables (especially chlorophyll *a*, total suspended solids, particulate organic carbon and particulate nutrients) and irradiance variables (Secchi and optical depth) differed significantly from nearshore to the outer islands. For example, mean concentrations of chlorophyll *a* were up to 1.9 times greater at nearshore (Repulse Island; RI: 0.59 ± 0.12 μg L^{-1} mean ± SE) compared with outer islands (Edward Island; EI: 0.31 ± 0.06 μg L^{-1}) averaged over five sampling events from 2004 to 2006, whereas mean Secchi depth was approximately 3 times lower at nearshore (RI: 4.0 ± 0.8 m) than outer locations (EI: 15.3 ± 3.3 m). Some of the coral indicators showed significant relationships with a water quality index (WQI) derived for the Whitsunday Islands. Responses of photo-physiological measures of *Symbiodinium* associated with *Pocillopora damicornis* along the gradient were consistent with patterns of light acclimatisation and suggested deep corals (i.e. below 5 – 6 m depth) on nearshore reefs in the Whitsunday Islands are light-limited. Both colony brightness and tissue thickness of massive *Porites* spp., and the maximum depth of reef building corals, increased from nearshore to outer locations along the gradient. Similarly, a 50-fold decrease in the density of macro-bioeroders in massive *Porites* from nearshore to outer locations was indicative of increased particle loads on the nearshore reefs. The data of the maximum depth limit for coral reef development at locations where suitable settlement substrata were available suggest that the absolute minimum of light required for a coral reef to persist is in the range of 6 – 8 % of surface irradiance in the Whitsunday Islands.

The model that color brightness of corals responded to changes in water quality was validated with manipulative experiments in the laboratory and by transplantation of small nubbins along the environmental gradient. The experiments showed nubbins of massive *Porites* became darker, i.e. concentrations of pigments increased, within 20 – 40 days of exposure to elevated nutrients and

reduced irradiances compared with corals kept in filtered sea water and unshaded conditions. The response in colony brightness was consistent with other studies of photo-acclimatisation to enhanced nutrients and light limitation. However, a 2.5-fold decrease in symbiont density of *P. damicornis* during the wet compared with the dry season, which in turn influenced colony brightness, was related strongly to seasonal changes in sea surface temperature (SST). Thus, effects of seasonal variation of a range of environmental parameters need to be considered if physiological measures such as colony brightness are used in water quality monitoring programmes.

The simultaneous *in situ* measurement of benthic irradiance and turbidity at a shallow depth (~3.5 m) on a coastal coral reef for 2 years allowed the quantification of potential thresholds of concern for turbidity. The linear relationship between the attenuation coefficient for downward irradiance K_d (PAR) and turbidity showed that a change from 0 to 3 nephelometric turbidity units (NTU) at 3.5 m results in a decrease of 88% of benthic irradiance to levels around 200 µmol photons m^{-2} s^{-1}. The minimum saturating irradiance (E_k) of *Symbiodinium* associated with *P. damicornis* was approximately 206 ± 8 µmol photons m^{-2} s^{-1} at shallow depths on nearshore reefs of the Whitsunday Islands. Thus, levels of turbidity greater than 3 NTU can result in environmental conditions that are light limiting, and hence sublethal photo-physiological stress, for *P. damicornis*. Levels of turbidity of 4.5 NTU corresponded to 6 – 8% of surface irradiance, which was a critical level of irradiance required for coral reef development in the Whitsunday Islands. Thus, long-term turbidity >3 NTU could be used as a threshold of turbidity for sublethal photo-physiological stress, while long-term turbidity >5 NTU for severe stress effects on *P. damicornis* at shallow depths (~3.5 m) on coastal reefs.

Temporal variation in the growth parameters of massive *Porites* from two nearshore regions of the GBR were not consistent with regional differences in water quality. Mean annual SST increased by ~0.38°C over a 16 year study period that correlated with a decline of ~21% in coral calcification rates. A decline in calcification of this magnitude with increasing SST contrasts with results of previous studies and is unprecedented in recent centuries. Changes in the growth parameters were linear over time, while SST had no effect on skeletal density, but a modal effect on annual extension and calcification with maxima at ~26.7°C. The findings were consistent with other experimental studies of the synergistic effect of elevated seawater temperatures and CO_2 partial pressure (pCO_2) on coral calcification and suggest that monitoring of seawater chemistry should be undertaken on the GBR.

Defining a set of key selection criteria and assessing the characteristics of candidate indicators in a matrix against changes in water quality, allowed the identification of coral indicators for a monitoring toolbox. The most suitable bioindicators were: symbiont photo-physiology, colony

brightness, skeletal and tissue growth, and bioeroder density in massive *Porites*, coral recruitment, community structure of corals, indicator organisms other than corals and the maximum depth of coral reef development. As each of these measures has a different sensitivity and response time to changes in environmental conditions, a combination of measures, i.e. a composite indicator system, is recommended for use in assessments of the condition of coastal reefs on the GBR.

Chapter 1.0 General introduction, review of literature and thesis outline

1.1 General Introduction

Coral reefs are recognised as being amongst the most diverse of the world's ecosystems. They provide a source of food and income in many countries, they have important tourism values and they may provide the next generation of pharmaceuticals used by humans. There is increasing concern, however, about the status of coral reefs with recent estimates suggesting that approximately 20% of the world's reefs have been destroyed with a further 50% are under threat of ecosystem collapse (Wilkinson 2004). Threats to coral reefs include the effects of climate change (Hughes et al. 2003), diseases (Sutherland et al. 2004), outbreaks of crown of thorns starfish (*Acanthaster planci;* Birkeland and Lucas 1990), changes in water quality (Rogers 1990; Fabricius 2005) and destructive fishing practices. On the Great Barrier Reef (GBR), there is considerable concern about the influence of runoff of nutrients, sediments and agrochemicals on coral reefs (Bell and Elmetri 1995; Haynes and Michalek-Wagner 2000). The coastal zone of the Great Barrier Reef World Heritage Area, with an area of 30,000 km^2 and a water volume of 300 km^3, receives an average annual input of water and sediment on the order of 66 km^3 and 7 – 28 Mt, respectively (Furnas 2003; Alongi and McKinnon 2005). Nutrient and sediment input have increased several-fold over the past 150 years (Moss et al. 1992; McCulloch et al. 2003). Current estimates of annual inputs of nitrogen and phosphorus from land are ~43,000 t and 7,000 – 11,000 t, respectively; a significant proportion of these nutrients are associated with particulate matter (Furnas 2003). Enrichment of nutrients and sediments can alter trophic structures of coral reefs (Grigg 1994; Lapointe 1997). Colony measures such as tissue thickness and growth rates of the massive coral *Porites* (Risk and Sammarco 1991; Barnes and Lough 1992; Lough and Barnes 2000), concentrations of chlorophyll *a* and symbiont densities (Hoegh-Guldberg and Smith 1989) as well as lipid and protein content in corals (Anthony and Fabricius 2000; Anthony 2006) differ along environmental gradients. At the ecological level, nutrient enrichment and sedimentation can have negative effects on reproduction (Loya et al. 2004), inhibit rates of coral fertilization (Gilmour 1999; Harrison and Ward 2001), reduce levels of coral recruitment (Loya 1976; Babcock and Davies 1991; Wittenberg and Hunte 1992) and alter biodiversity (van Woesik et al. 1999; Fabricius and De'ath 2004; Fabricius et al. 2005). These processes can transfer the competitive advantage on nearshore reefs from corals to macroalgae leading to trophic dominance by assemblages of macroalgae (Schaffelke 1999) once productivity exceeds rates of grazing (McCook 1999; Hughes et al. 2007).

Numerous studies have developed and applied indicators as measures of coral condition in the past, however, with some exceptions few have aimed at comparing proposed indicator measures against each other. The exceptions include Risk et al. (2001) who highlighted the need for early warning, cost-effective indicators that can be used at large spatial scales. They proposed a toolbox

comprising assessments of the diversity of stomatopods, amphipods and other invertebrates, and measurements of bioerosion and geochemical markers to identify intensity and origin of stress. Using a rapid assessment method, DeVantier et al. (1998) showed that a two-tiered examination of ecological indicators (benthic cover and taxonomic composition of scleractinian corals) could discriminate sites with high conservation value in the Whitsunday Region of the GBR. Jameson et al. (2001) described the value of using a multimetric index to assess ecosystem health and developed the Index of Biotic Integrity (IBI), combining measures such as sessile epibenthos, benthic macroinvertebrates, fish, marine vegetation, phytoplankton and zooplankton, to produce an environmental score of the condition of coral reefs. No studies have undertaken a quantitative comparison of coral indicators to identify those suitable for assessing changes in environmental conditions on coastal coral reefs of the GBR.

1.2 Review of literature

The types of indicators that could be used to assess the status coral reefs range from responses at the molecular- to community-level. The aim of this review is to summarise the types of indicators that have been, or could be, used in monitoring programmes of the effects of changes in water quality on coral reefs. I define a change in water quality broadly as some change in concentrations of dissolved and/or particulate nutrients, rates of sedimentation, levels of turbidity, or any associated changes in levels of benthic irradiance (light) and an overview of the effects of these stressors on corals is provided below. A review on how to sample or design response/validation experiments is not included, as this topic has received much attention elsewhere (e.g. Andrew and Mapstone 1987; Underwood 1997).

1.2.1 Effects of water quality on corals

1.2.1.1 Nutrient availability

The main sources of new nutrients (N and P) in the GBR are upwelling from the Coral Sea and terrestrial runoff (Furnas 2003; McKergow et al. 2005). Corals are exposed to nutrients in a variety of forms that include particulate matter, and dissolved inorganic and organic nutrients (DIN and DON). Since dissolved inorganic nutrients (both N and P) are assimilated rapidly by phytoplankton, only a fraction of DON is bio-available, and the majority of nutrients are discharged in terrestrial runoff as particulate matter, particulate nutrients are the most common bio-available form of nutrients for corals in the coastal zone (Furnas 2003). Concentrations of nutrients on coral reefs vary widely with differing spatial and temporal scales. Nutrient concentrations are generally higher on coastal than offshore reefs (Brodie et al. 2007; Chapter 2) and higher in the Austral summer than in winter (Brodie et al. 2007).

The effects of nutrients on corals depend on the concentration and duration of exposure. Moderate levels of dissolved inorganic nutrients and particulate nutrients can enhance rates of gross photosynthesis (Kinsey and Davies 1979; Hoegh-Guldberg and Smith 1989; Ferrier-Pages et al. 2000), increase symbiont density (e.g. Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989) and tissue thickness (Barnes and Lough 1992; Lough and Barnes 2000), but reduce rates of calcification (Kinsey and Davies 1979; Marubini and Atkinson 1999). At higher concentrations, however, light attenuation negates the advantages of heterotrophic nutrition due to down-regulation of photosynthesis and reduced rates of calcification (Marubini 1996), which may alter reef metabolic processes leading to changes in community structure and diversity (Fabricius 2005).

1.2.1.2 Sedimentation

Sedimentation is defined as the deposition of particulate material onto the benthos, with the origin of the particles either resuspension from the seafloor or new imports through terrestrial runoff (Rogers 1990; Wolanski et al. 2005). Levels of sedimentation on coral reefs vary widely with differing spatial and temporal scales. Rates of sedimentation are usually greatest near the coast where wind waves can re-suspend seafloor sediments, and near river mouths, and decrease with distance from the shore (Rogers 1990; Todd et al. 2001; Lirman et al. 2003). At smaller scales, sedimentation is usually greatest in sheltered, wave-protected lagoons, bays, or deeper reef slopes and lowest in shallow wave-exposed areas (Wolanski et al. 2005). Sedimentation rates also vary temporally, and are high after periods of strong winds, waves and terrestrial runoff (Wolanski et al. 2008).

Increased concentrations of particulate materials can have contrasting effects on corals. Feeding on fine sediment particles may enhance coral growth in some species (Anthony 1999). However, the ability of corals to utilise particulate organic matter as a source of nutrition varies among species and types of sediment (Anthony and Fabricius 2000). In general, however, settling particulate matter represents a stress to corals. Energy investment into sediment rejection stresses corals in a variety of ways including down-regulation of photosynthesis and increasing their rates of respiration and mucus production (Riegl 1995; Telesnicki and Goldberg 1995; Yentsch et al. 2002; Philipp and Fabricius 2003). Photo-physiological stress occurs within hours of exposure to sedimentation (Philipp and Fabricius 2003) and is strongly related to the quality of the sediment (Weber et al. 2006), and is thus considered a useful sublethal indicator of changes in water quality. Accumulation of sediment on corals may ultimately result in tissue necrosis leading to injury and partial mortality (Lasker 1980; Rogers 1983; Peters and Pilson 1985; Gilmour 2002, Bak, 1978), which can lead to whole-colony mortality thereby altering the demography, percentage cover and community structure on coral reefs. Changes in community structure occur because susceptibility

to sedimentation varies among coral species according to tissue thickness, polyp sizes and growth forms (Abdel-Salam et al. 1988; Stafford-Smith 1993; Riegl 1995; Wesseling et al. 1999).

1.2.1.3 Turbidity and light attenuation

Turbidity refers to the amount of suspended particulate matter (SPM) in the water column (and to a lesser extent some dissolved organic compounds) and their effect on light attenuation (Te 1997; Fabricius 2005). Suspended particles include both inorganic and organic matter (bacteria, phytoplankton, zooplankton and detritus), or inorganic particles with organic coating. Turbidity and thus light attenuation may vary over small spatial and temporal scales depending on the proximity of sources of terrestrial runoff (Fabricius 2005) as well as changes in local weather conditions (Larcombe et al. 1995; Orpin et al. 2004; Wolanski et al. 2005).

Turbidity and light attenuation can have contrasting effects on corals. Some species gain a substantial proportion of their energy budgets from heterotrophic feeding on SPM, while others obtain most of their nutrition from autotrophy regardless of the availability of particulate matter (Anthony and Fabricius 2000). At deeper depths, the energy gained from utilising SPM is most likely offset by the energy lost from reduced light availability (Fabricius 2005). Corals are able to photo-acclimate to changes in light levels by adjusting the concentration of photosynthetic pigments and/or the density of their symbionts. The coral-symbiont association can adapt to low irradiance by increasing concentrations of photosynthetic pigments and/or the density of the symbionts (Falkowski and Dubinsky 1981; Dubinsky et al. 1984; McCloskey and Muscatine 1984; Porter et al. 1984; Chapter 4). Symbionts acclimated to high irradiance have less photosynthetic pigments and/or occur at lower cell density and thus exhibit lower light absorption characteristics (e.g. PAR-absorptivity; Ralph et al. 2005; Chapter 3). Corals that are not able to compensate energetically from reduced light availability may experience decreased rates of calcification and thinner tissue in the coral host (Rogers 1979; Telesnicki and Goldberg 1995; Anthony and Hoegh-Guldberg 2003a). Due to variable abilities of corals in deeper water to compensate for low light, increased turbidity may lead to reduced density and diversity of corals, thus reducing the limit of depth distribution in coral communities (Birkeland 1987; Yentsch et al. 2002; Chapter 2).

1.2.2 Characteristics of suitable indicators

Monitoring programmes examine biological responses to determine the status, trends and the effects of specific stressors on ecological systems. Bioindicators and/or biomarkers are often used to detect such responses. A biomarker refers to measures at the biomolecular or biochemical level (McCarty et al. 2002), whereas a bioindicator (hereafter indicator) refers to those at higher colony, population and/or community levels. The use of biological indicators provides a number of

significant advantages over direct measurements of water quality. For example, a direct measurement of water quality provides information about the condition of the water column at that particular point in time only. Moreover, if sampling is weather-dependant and constrained by safety considerations, then important information on the effects of episodic events, e.g. terrestrial discharges during floods or the resuspension of sediments during strong winds, may be missed. These issues are overcome, however, with the use of biological indicators that can provide a time-integrated measure (from time periods of minutes to years) of the effects of changes in water quality on coral reefs. Indictors that respond rapidly to a stressor can be used to detect sublethal effects, while indicators with high specificity can provide ecologically relevant information about the exposure particularly if the stressors can not be quantified. Given the wide variety of natural and anthropogenic factors that can influence a complex ecosystem such as a coral reef, it is unlikely that a single indicator exists that could sufficiently describe the condition of a coral reef (Erdmann and Caldwell 1997; Jameson et al. 1998). Rather, a composite of indicators (*sensu* Risk et al. 2001) incorporating responses from different ecological levels of organisation (i.e. colony to communities) that can be combined to form an index (e.g. Jameson et al. 2001) has greater potential for success in assessments of the condition of coastal coral reefs.

To select a biological indicator objectively, requires a set of selection criteria. Here, five key criteria are defined (Table 1.1) as modified from Jones and Kaly (1996), Erdmann and Caldwell (1997) and Jameson et al. (1998) that were considered to characterise desirable features of indicators necessary for assessing the condition of coastal coral reefs. An important criterion in the selection of any indicator is the response time over which the biological response is manifest in the colony, population or community. Both the times for the onset of a response and the period until full recovery of a response can range from near-instantaneous to decades. An important distinction, therefore, is to differentiate between methods suitable for detecting effects during or shortly after exposure to the stressor (rapid, with onset of response and recovery from an event within hours to weeks), and those better suited to detecting cumulative effects over prolonged periods of time (slow: onset and recovery taking months to years). An example of a method providing an immediate indication of stress is a change in the photo-physiology of *Symbiodinium* (Jones et al. 1999; Philipp and Fabricius 2003), whereas variation in the density and composition of macro-bioeroders due to changes in water quality may occur on a time-scale of years (Hutchings and Peyrot-Clausade 2002). Both types of indicators have advantages and disadvantages. A rapid response following exposure to a stressor is considered a desirable feature of an indicator as the response could be used as a sublethal indicator particularly for environmental impact assessments (e.g. of the effects of dredging) or acute disturbances such as episodic runoff events. This is offset, however, by the high level of sampling intensity and replication required in monitoring programmes to obtain accurate estimates of a response that

could change on a time-scale of days to weeks; important events may be missed if recovery is too quick. Equally, whilst an indicator responding on a slower time-scale may not provide an early warning of change, they are still considered useful particularly for monitoring of chronic effects, as these types of indicators are likely to have low natural variability, and require lower sampling intensity to detect ecological change. Thus, in addition to response time, the importance of which will depend on the question being addressed, outlined below are five criteria that can be used to select indicators for assessments of the condition of coral reefs:

1. *Response specificity* is the extent to which the biological response is specific to the stressor (either chronic or acute) of interest and not to variation due to other causes. For example, the maximal depth of reef building corals was strongly related to a water quality gradient in the Whitsunday Islands and is considered highly specific to changes in water quality, particularly light attenuation associated with turbidity (Chapter 2), but is unlikely to respond to other stressors, e.g. warming sea temperatures. The photo-physiological parameter PAR-absorptivity, which indicates a more densely pigmented coral tissue layer possibly due to greater density of symbionts and/or concentration of chlorophyll (Ralph et al. 2005), was also strongly related to differences in water quality (Chapter 3). However, symbiont loss is a well known response to a range of stressors including high sea temperatures (e.g. Glynn and D'Croz 1990; Hoegh-Guldberg 1999), thus changes in PAR-absorptivity due to changing water quality can at times be confounded by bleaching stress.

2. *Monotonic* refers to the shape of the dose-response relationship, in which the magnitude of the response reflects the intensity (and/or duration) of the stress. A decrease in the photosynthetic yield (F_v/F_m) of *Symbiodinium* exposed to increasing levels of a stressor (Jones et al. 1999; Philipp and Fabricius 2003; Negri et al. 2005) is an example of a monotonic response indictor.

3. *Variability* refers to indicators that demonstrate patterns of low variation in the absence of the stressor. An indicator that displays patterns of seasonal or temporal variability such as symbiont density (Fitt et al. 2000) or lipid content (Leuzinger et al. 2003) might still be suitable for inclusion into an indictor system provided that the variability is understood and can be accounted for in statistical analyses.

4. *Practicality* refers to indicators that are easily quantified, low cost, require a low level of expertise and are applicable over a range of spatial and temporal scales (e.g. Risk et al. 2001). The cost factor includes consideration of the amount of labour required to collect data in the field and for laboratory analyses, and the cost of equipment and reagents required to process the samples. The colour chart developed by Siebeck et al. (2006) is an example of an economic, simple tool that can be used by a range of end-users.

5. *Relevant* refers to indicators that are both ecologically relevant and also important in public perception. Relevance assists in the communication of the results to a wide range of end-users. Measures such as the shift from a diverse hard coral to a macroalgal dominated reef community, are readily communicated to the public (e.g. Hughes 1994).

Table 1.1. Summary of criteria for selection of indicators to assess effects of stressors on corals and coral communities. Modified from Jones and Kaly (1996), Erdmann and Caldwell (1997) and Jameson et al. (1998).

Attribute	Criteria
Specificity	Indicator should be specific to the cause (the stressor of interest), hence clearly attributable to that stressor.
Monotonic	The relationship between the disturbance intensity and the response size should be monotonic (rather than modal).
Variability	Indicator should be consistent at a range of scales in time and space. Ideally, there should be low background variability.
Practicality	Indicator should be cost effective, easy to measure and a proxy for another, more complicated or costly measure. Measurements should be observer-independent and carried out by a range of users, ideally requiring a low level of expertise.
Relevance	Indicator should be ecologically relevant and ideally important in public perception to assist communication.

A schematic of desirable features of an indicator is presented in Fig. 1.1 showing the responses of a *hypothetical* indicator to hypothetical disturbances (e.g. chronic or episodic runoff events). A suitable indicator must display a response to a disturbance (either chronic or acute) that differs with the response at reference areas. Under chronic conditions, this would be a long-lasting or permanent response (Fig. 1.1a). For acute disturbances, the response would last as long as the disturbance in question (shaded area; Fig. 1.1b), or for a period of time following the disturbance, but eventually the indicator would return to levels measured at reference areas. Further, it should demonstrate specificity by not responding to other types of disturbances (Fig. 1.1b). Ideally, the indicator should provide information on the intensity of the disturbance. A monotonic relationship is shown in Fig. 1.1c where the indicator responds to a disturbance by changing direction (either positive or negative) as the size of the disturbance changes but returns to values comparable to reference areas once the disturbance is over. An indicator that displays patterns of seasonal or temporal variability might still be suitable for monitoring programmes provided that (at the time of the disturbance) the measure at the area of interest is different in some way compared with that at reference areas (Fig. 1.1d). Finally, any measure that does not respond to a specific disturbance

would obviously not represent a suitable indicator (Fig. 1.1e). An ideal indicator would show a response similar to the one described in Fig. 1.1c, quantifying the extent of disturbance and showing rapid recovery following cessation of the disturbance.

Among the most important features of an indicator is that it demonstrates patterns of low unexplained variability in the absence of the disturbance. The responses of potential indicators must be validated with both manipulative experiments and sampling programmes in the field to ensure they are specific to the disturbance of interest. Measuring and validating such responses in the field is, however, a complex process given the natural spatial and temporal variability inherent in biological systems. Notwithstanding this, it is clear that sampling at a range of spatial and temporal scales is an appropriate way to measure environmental responses (e.g. Green 1979; Stewart-Oaten et al. 1986; Underwood 1991). This approach allows comparisons of estimates of the response variability at disturbed areas with natural variability at reference areas, which have not been affected by the disturbance but are otherwise comparable in nature. If, following a disturbance, the response measure at the disturbed area differs in some way from the variability measured at reference areas, then it can be assumed that the response was due to the disturbance.

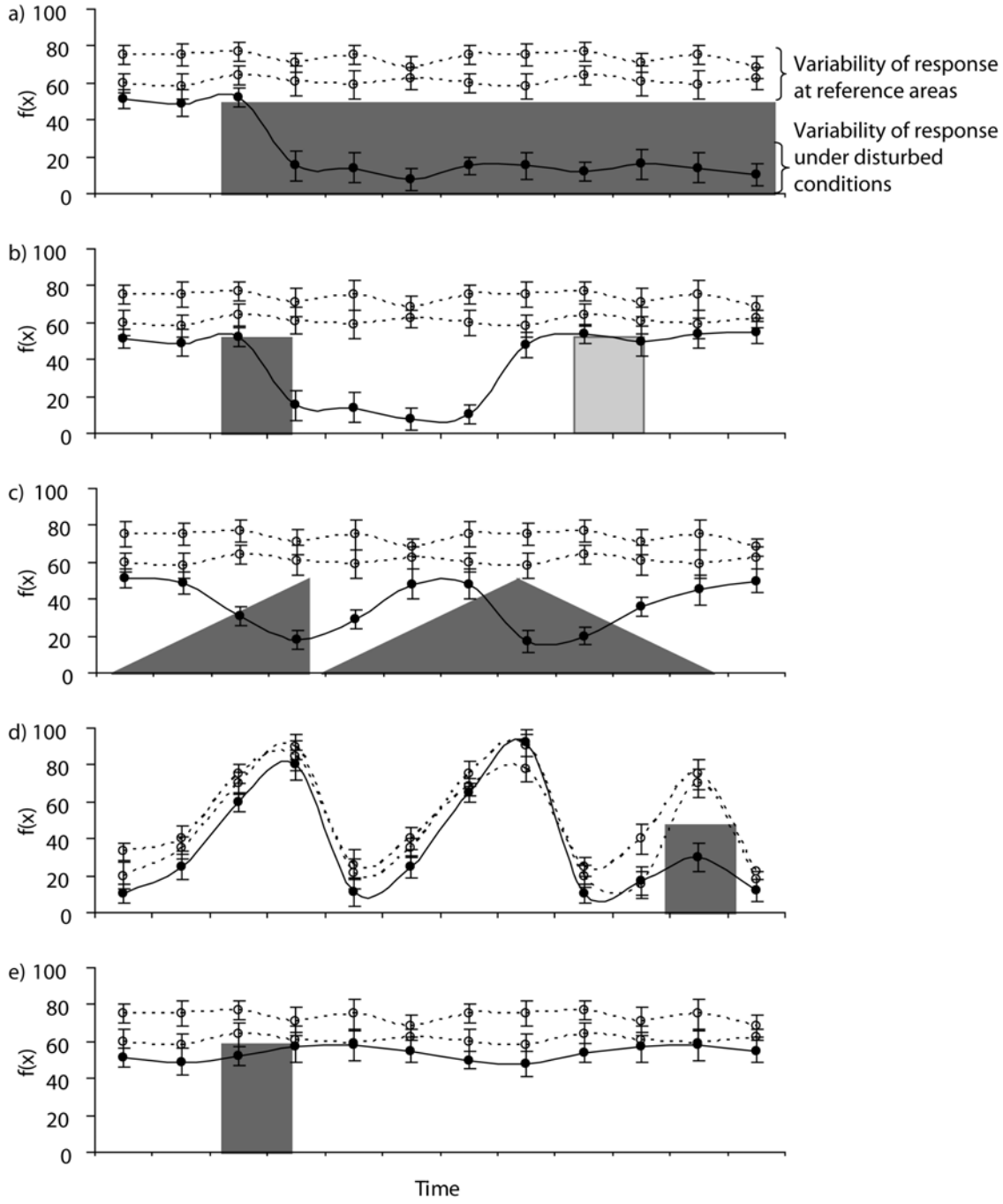

Fig. 1.1. Response of a hypothetical indicator to a disturbance (dark grey areas represent the disturbance in question; light grey areas represent other disturbances). A suitable indicator must detect differences between a disturbed state (solid line) and reference states (dashed lines). The situations described in a), b) c) and d) would be appropriate for inclusion into a monitoring program.

1.2.3 Indicators and indices in other aquatic ecosystems

The use of validated indicators of ecosystem health, numerical indices and predictive models are well developed in other aquatic ecosystems. For this reason, the following section highlights examples from estuarine and freshwater ecology that have incorporated methods that could potentially be adapted for use on coral reefs.

Assessments of estuarine health have focused on different components of the ecosystem including seagrasses (Abal and Dennison 1996; Dennison and Abal 1999), foraminifera (Saraswat et al. 2004), filter feeders such as bivalves (Bayne 1989) and fish assemblages (Scott and Hall 1997; Blaber 1999). For example, light attenuation is considered to be a limiting factor for the distribution of seagrasses (Duarte 1991; Masini et al. 1995). Elevated levels of turbidity from episodic runoff events (Preen et al. 1995; Longstaff and Dennison 1999), the resuspension of sediments due to currents, wind and wave activity (Larcombe et al. 1995; Dennison and Abal 1999), or from anthropogenic disturbances such as dredging, reduces light penetrating to the seafloor and may contribute to seagrass decline. Abal and Dennison (1996) found seagrasses (mainly *Zostera capricorni*) extended to deeper depths at locations with low turbidity, light attenuation and concentrations of nutrients than turbid locations in Moreton Bay (Australia). Recent work has proposed to use the relationship between the maximal depth of seagrasses and water quality as an indicator of estuarine health (e.g. Carruthers et al. 1999; Dennison and Abal 1999).

There is widespread use of trophic or pollution indicators in freshwater ecology, each measuring specific components of the ecosystem such as bacteria (Godlewska-Lipowa 1976), diatoms (Chessman et al. 1999; Taffs 2001), macroinvertebrates (Krieger 1984; Growns et al. 1995; Lamberti and Berg 1995; Wright et al. 1995; Chessman 1999; Klemm et al. 2002) or fish (Harris 1995; Soto-Galera et al. 1998). Other studies range from indicators based on the proportion of deformities found in certain taxa (Bird 1994) to those that have measured the abundance of elephants (*Elephas maximus)* to assess the effects of unregulated mining discharge into a river in Northern India (Singh and Chowdhury 1999).

Many studies have further developed the use of indicators into an integrated framework to assess the health of freshwater ecosystems. Models such as RIVPACS (Wright 1995) and AUSRIVAS (Turak et al. 1999, Simpson, 2000) use information collected for ‘predictor variables’, which are considered unlikely to be affected by anthropogenic impacts, to predict the assemblage of macroinvertebrates that could be expected to occur at a particular location in the absence of anthropogenic disturbances. The predicted assemblage is then compared with that sampled to provide a basis to assess the health of the system.

Other approaches to assess freshwater ecosystem health have been the development of tools such as the SIGNAL index that correlate biotic and abiotic data to produce an environmental quality score for a particular site. Chessman (1995) developed the SIGNAL biotic index, which was later modified (Chessman et al. 1997), to determine the health of rivers in south-east Australia using the presence or absence of families of macroinvertebrates. The grade-numbers for each macroinvertebrate family or taxon were derived from their responses to chemical pollutants. Thus, the SIGNAL index is designed to provide an assessment of ecological health based on water quality.

1.2.4 Indicators of the condition of coastal coral reefs

1.2.4.1 Colony indicators

Photosynthetic efficiency

Chlorophyll *a* fluorescence of Photosystem II (PSII) using pulse-amplitude-modulation (PAM) technology of coral symbionts has been used widely to infer environmental impacts on the regulation of photosynthesis (e.g. Warner et al. 1996; Jones et al. 1999; Fitt et al. 2001; Hill et al. 2004a). However, in recent years, PAM has also been applied to test photo-physiological responses of symbionts in relation to various components of water quality. Recent studies have shown that maximum quantum yield (F_v/F_m) decreases depending on the duration and quantity of sediment exposure (Philipp and Fabricius 2003), sediment type (Weber et al. 2006) and hypo-saline conditions (Kerswell and Jones 2003). Similarly, toxicants have been found to negatively influence the maximum quantum yield depending on quantity and exposure duration (Jones et al. 1999; Markey et al. 2007; Table 1.2).

Imaging-PAM chlorophyll *a* fluorometers (Schreiber 2004), which are essentially a two-dimensional version of the more conventional chlorophyll fluorometers, are capable of mapping the chlorophyll *a* fluorescence yield with a spatial resolution of ~0.5 mm. They can perform all standard routines of saturation pulse quenching analysis (Schreiber 2004), such as determination of maximum and effective ($\Delta F/F_m'$) quantum yield as well as measurements of fluorescence induction and rapid light curves (White and Critchley 1999; Ralph and Gademann 2005). Rapid light curves can provide detailed information on photo-acclimatory responses of corals to changes in the light regime on coral reefs. Quantitative parameters derived from the fitting of rapid light curves include apparent photosynthetic rate (PS_{max}), minimum saturating irradiance (E_k) and light utilisation coefficients (α). Under high irradiance, symbionts are characterised by high PS_{max}, E_k and low α (White and Critchley 1999; Ralph and Gademann 2005; Ulstrup et al. 2006b). In contrast, symbionts acclimated to low irradiance are characterised by having low PS_{max} and E_k, and high α (White and Critchley 1999; Ralph and Gademann 2005).

Colony brightness

The colour of scleractinian corals is determined by photosynthetic pigments contained in the algal endosymbionts (e.g. Jeffrey and Haxo 1968) and light absorbing compounds in the coral tissue (Dove et al. 2001). Photo-acclimatisation by the symbionts to changes in environmental conditions (e.g. water quality, seawater temperatures, irradiance) may lead to changes in density of symbionts and/or the concentration of photosynthetic pigments at time-scales of days to weeks (Falkowski and Dubinsky 1981; Dubinsky et al. 1984; McCloskey and Muscatine 1984; Porter et al. 1984). Generally, there is an inverse relationship between light availability and concentrations of pigments thus corals become darker as irradiance decreases and vice versa as irradiance increases. Symbiont density (and hence colour brightness) increases in response to exposure to elevated nutrients (Hoegh-Guldberg and Smith 1989; Stambler et al. 1991) and decreases in response to sedimentation (Nugues and Roberts 2003; Table 1.2). Hence, coral colour measured using a newly developed colour chart (Siebeck et al. 2006) and colour brightness (the amplitude of the reflectance spectrum at the chlorophyll *a* absorption maxima wavelength), which can be measured using reflectance spectrometry (Hochberg et al. 2004, 2006), demonstrate potential as indicators of environmental conditions prevailing at a coral reef.

Lipid content

The lipid content of corals is an indication of their energy reserves. Corals are mixotrophic organisms that assimilate carbon from their symbionts (Muscatine 1980), the capture of zooplankton (Porter 1974) and the digestion of organic particulate matter (Tomascik and Sander 1985; Anthony 1999; Anthony 2000). Any carbon that is surplus to metabolic requirements can be excreted, or is stored as energy reserves in the form of lipids (Crossland 1987; Anthony and Fabricius 2000).

Changes in lipid content can occur with mucus production (Crossland 1987), exposure to dissolved nutrients (Achituv et al. 1994), altered light availability (Stimson 1987) and turbidity (Anthony and Fabricius 2000; Table 1.2). Lipid content also varies seasonally (Oku et al. 2003), and is lowest at times of high metabolic demand, such as during periods of rapid growth or reproduction. Energy investment into gamete production has been shown to influence the lipid content of brooding (Stimson 1987) and spawning corals (Ward 1995), and was lowest following spawning events (Ward 1995; Leuzinger et al. 2003). Importantly, lipid content has been reported to vary widely among replicate samples taken from within individual corals (Harriott 1993). Recently, Anthony (2006) found that the lipid content of corals on a nearshore reef was greater compared with conspecifics on an adjacent mid-shelf reef and concluded that environmental conditions on reefs in the coastal zone did not necessarily imply negative physiological consequences on the corals living there. The quantification of lipid content requires small samples

to be collected from the coral colony, followed by analytical techniques such as gravimetric determinations, thin layer chromatography or gas chromatography-mass spectrometry. Lipid content is usually normalised to surface area or the protein content of the sample (Harland et al. 1992; Edmunds and Gates 2002).

Skeletal and tissue growth

Responses in the skeletal growth parameters skeletal density, linear extension and calcification rate have been best described for massive corals, for which growth can be analysed retrospectively using skeletal cores or slices (Knutson et al. 1972; Knutson and Buddemeier 1973). These parameters have also been tested in corals with other growth forms (e.g. Ferrier-Pages et al. 2000; Koop et al. 2001; Bongiorni et al. 2003; Table 1.2).

Skeletal growth is influenced by physical parameters, such as the availability of light, and the clarity, flow, temperature and salinity of seawater (e.g. Goreau and Goreau 1959; Bak 1974; Buddemeier and Kinzie 1976; Highsmith 1979; Lough and Barnes 2000), in addition to biological processes such as photosynthetic rates (Barnes and Chalker 1990). Other changes in environmental conditions such as increases in sedimentation, turbidity and resuspension of bottom sediments (Dodge and Vaisnys 1977; Cortes and Risk 1985) and eutrophication (Dodge and Brass 1984; Tomascik and Sander 1985) can influence skeletal density, linear extension and calcification rate. On the GBR, skeletal density increased (Risk and Sammarco 1991), but the rates of linear extension and calcification decreased (Lough and Barnes 1992), with increasing distance from the coast (Table 1.2). There are, however, several studies that have suggested that coral growth parameters may be insensitive to changes in water quality (e.g. Brown et al. 1990; Edinger et al. 2000). Skeletal growth is also influenced by variation in other physical parameters such as the availability of light, and water clarity, flow, temperature and salinity (e.g. Goreau and Goreau 1959; Bak 1974; Buddemeier and Kinzie 1976; Highsmith 1979; Lough and Barnes 2000), in addition to biological processes such as photosynthetic rates (Barnes and Chalker 1990). Techniques for quantifying coral growth include gamma densitometry to determine skeletal density (Chalker and Barnes 1990), the distance between the peaks of adjacent density bands to determine linear extension, and the product of these two parameters to estimate calcification rate.

The thickness of tissue and the surface rugosity (topographical complexity) of *Porites* colonies have also been suggested as potential indicators of environmental condition (Barnes and Lough 1992; Scoffin et al. 1992). Tissues of massive *Porites* were found to be thicker on coastal reefs of the GBR than offshore reefs, possibly due to the greater concentrations of nutrients and particulate organic matter at nearshore locations (Barnes and Lough 1992; Table 1.2). Tissue thickness can be best determined in massive *Porites* by removing a small short core from the upward-facing coral surface and measuring the depth of the skeleton occupied by living tissue with callipers.

Massive *Porites* increase their rugosity when skeletal growth is unable to provide sufficient surface area to accommodate ample tissue growth. *Porites* colonies were found to be more rugose on nearshore than offshore reefs, theoretically due to increased availability of nutrients and particulate organic matter in the coastal zone (Darke 1991; Scoffin et al. 1992; Table 1.2). Surface rugosity can be determined by placing a piece of chain of known length on the upper surface of the colony and calculating the ratio between the horizontal and vertical length (Darke 1991).

Skeletal chemistry

Chemical elements incorporated from the water column into the coral skeleton can be used as retrospective indicators of environmental conditions at the time of skeletal growth (e.g. Goreau 1977; Cohen and McConnaughey 2003; McCulloch et al. 2003). For example, the reconstruction of past sea surface temperatures using strontium to calcium ratios has been the focus of much attention (Smith et al. 1979; Gagan et al. 2000; Cohen et al. 2004). Other geochemical tracers have been used to hindcast changes in water quality on coral reefs. For example, barium to calcium ratios were used as proxies to record sediment input to the coastal zone of the GBR that coincided with European settlement and the onset of farming (McCulloch et al. 2003). Similarly, the ratio of the stable nitrogen isotopes $^{15}N/^{14}N$, known as $\delta^{15}N$, has been used to identify anthropogenic sources of nitrogen in many ecosystems including coral reefs (Mendes et al. 1997; Sammarco et al. 1999; Heikoop et al. 2000; Lapointe et al. 2004). The main sources of anthropogenic nitrogen: sewage effluent, terrestrial runoff and synthetic fertilisers, each produce nitrate and ammonium with characteristic $\delta^{15}N$ signatures that allows the source of the nitrogen in the ecosystem to be identified (Heaton 1986). Sewage effluent is generally enriched with the heavier ^{15}N isotope and has $\delta^{15}N$ values in the range +10 to +22 ‰, whereas values for soil-organic nitrogen are in the range of +4 to +9 ‰ with synthetic fertilizers –4 to +4 ‰ (Heaton 1986).

In a gradient study on the central GBR, Sammarco et al. (1999) found values of $\delta^{15}N$ in tissues of *Porites lobata* were greater on nearshore and offshore reefs but lower on mid-shelf reefs (Table 1.2). They concluded that nearshore corals on the GBR were utilising nitrogen from terrestrial origins while the elevated $\delta^{15}N$ levels in the offshore reefs were most likely due to seasonal upwelling events. Overlaps in $\delta^{15}N$ signatures and complex nitrogen transformations, however, can make it difficult to identify the true source of the nitrogen (Heaton 1986; Lindau et al. 1997). Whether the inshore $\delta^{15}N$ values for *Porites* on the GBR resulted from the uptake of nitrate derived from terrestrial sources (e.g. mangrove detritus), or from the uptake of excess nitrate following the application of fertilisers, could not be determined (Sammarco et al. 1999).

Partial mortality

A partial mortality is a lesion in the living tissue (Hughes and Jackson 1980; Porter et al. 1993; Riegl 1995). Partial mortality can be quantified by estimating the proportion of colony surface free of living tissue, or by using more accurate photographic techniques to measure the area of lesions and colony surfaces. Unless the injury causes infection or disease, lesions do not usually spread to adjacent tissues (Philipp and Fabricius 2003), and adjacent healthy tissues often grow back over the lesion as long as the cause does not persist (e.g. Bak and Steward-Van Es 1980; Hall 1997). Estimates of partial mortality have been used to assess the effects of water quality and sedimentation on coral reefs. Nugues and Roberts (2003) reported increases in partial mortality on corals at sites closest to rivers compared with locations distant from the river discharge (Table 1.2). Importantly, this response was species-specific and likely to be greater in species with poor sediment-rejection abilities (Obura 2001; Nugues and Roberts 2003). In contrast, Ginsburg et al. (2001) found patterns of great variability for partial mortality on massive corals and suggested it was not an optimal indicator of changes in water quality along the Florida Reef Tract (Table 1.2).

1.2.4.2 Population indicators

Bioerosion

Bioerosion is the process of erosion of substrata by biological activity and comprises internal bioerosion (boring by micro and macroborers) and external erosion due to grazing (Neumann 1966; Hutchings 1986; Bellwood 1995). The rate of bioerosion on coral reefs have long been suggested as a potential indicator of coral reef condition because it comprises an important component of the carbonate budget, i.e. the growth of reefs is compromised if the rate of bioerosion exceeds that of carbonate accretion (Hutchings 1986). Rose and Risk (1985) found an increased abundance of the boring sponge *Cliona delitrix* associated with the discharge of untreated sewage on reefs in the Cayman Islands. A greater abundance of macroborers, such as polychaetes and sipunculans, were found in experimental blocks of coral skeletons on eutrophic fringing reefs of French Polynesia than were found on oligotrophic atolls (Hutchings and Peyrot-Clausade 2002). The inverse relationship between the abundance of internal bioeroders and distance to the coast in *Acropora formosa* and massive colonies of *Porites* was attributed primarily to a greater exposure to terrestrially derived nutrients on nearshore reefs on the GBR (Sammarco and Risk 1990; Risk et al. 1995; Table 1.2). In Indonesia, more bioeroders were present on eutrophic reefs in both live colonies of massive corals and in the rubble fragments of branching coral (Holmes et al. 2000). The coral rubble technique involves sectioning samples of dead branching coral pieces (excluding *Acropora*) along the longitudinal axis and scoring each piece based on the presence or absence of different bioeroder taxa (Holmes et al. 2000; Table 1.2).

Population structure

The structure of a population can be defined as the number of individuals of different life history stages. Most commonly, these stages are size-classes, because the life history traits of corals are strongly influenced by their size (Hughes 1984). Since the structures of populations reflect the life history traits of individuals, they provide an indication of all the physical and biological conditions to which the population has been exposed (Bak and Meesters 1999; Meesters et al. 2001). A population structure can be assessed by measuring and counting the numbers of colonies along transects or within large quadrats. Care must be taken when attempting to infer the effects of certain environmental conditions from a single population structure, and more accurate inferences are obtained by quantifying changes in both environmental conditions and population structure at similar times. For example, the effects of storms (Woodley et al. 1981; van Woesik et al. 1995; Gilmour 2002) and crown of thorns starfish (Done 1987; Fong and Glynn 1998) on coral reefs have been inferred by quantifying changes in the structure of coral populations through time (Table 1.2). The effects of changes in water quality on coral reefs have been inferred by quantifying changes in the structure of coral populations through time. Meesters et al. (2001) found that the size-frequency distributions of populations closest to urban centres were negatively skewed having fewer juveniles and larger colonies than pristine reefs. For some species, however, there was a suggestion that differences in the size-frequency distributions were due to differences in life-history strategies whereby small colonies were shorter-lived than larger colonies (Meesters et al. 2001). Thus, care must be taken when extrapolating information about the effects of stressors on life history traits of corals from changes in their population structure, because they depend on a range of other confounding variables, such as the life-history strategy and the previous history of disturbance (Hughes 1989; Hughes and Connell 1999).

Coral diseases

Coral diseases have only recently been recognised as a major form of disturbance for coral reefs (Garrett and Ducklow 1975; Antonius 1985; Richardson et al. 1998; Garzon-Ferreira et al. 2001; Page and Willis 2006). Currently, approximately 20 diseases have been identified that affect more than 100 species of corals (Sutherland et al. 2004) with some being species-specific and others affecting a wide range of species. Most diseases are transmitted by pathogens such as bacteria, cyanobacteria and fungi, which are dispersed passively through the water column, or transmitted by biological vectors (Sussman et al. 2003), and many are highly infectious. Coral diseases can be assessed by determining the proportion of colonies with visible disease symptoms relative to healthy colonies in large quadrats or along transects (e.g. Cervino et al. 2001).

Corals appear to be more susceptible to diseases when stressed due to changes in environmental conditions such as seawater temperatures, sedimentation, turbidity, salinity, nutrient availability

and pollution (Bruno et al. 2003; Sutherland et al. 2004). Elevated water temperatures increase the growth and virulence of pathogens on high coral cover reefs (Bruno et al. 2007), in addition to reducing the immune response in corals. Pathogenic organisms can be delivered to coral reef via terrestrial runoff (Sutherland et al. 2004) and coral reefs considered to be stressed by anthropogenic influences have been reported to have a greater prevalence of disease (Green and Bruckner 2000). Consequently, monitoring programmes are increasingly quantifying diseases on reefs (Richardson 1995; Sweatman et al. 2002).

1.2.4.3 Community indicators

Larval supply and recruitment

Many spawning corals release gametes synchronously over a few nights each year, which develop into larvae that remain dispersive for hours to months, and then settle and metamorphose into a coral polyp. The number of larvae settling at a site is a measure of larval supply, while the number of small juvenile corals (typically defined as <5 cm) is a measure of recruitment to the community.

A variety of environmental conditions can influence the rates of larval supply and recruitment to reefs (Wittenberg and Hunte 1992; Hughes et al. 1999; Edmunds 2000). Increased turbidity and sedimentation (Babcock and Davies 1991; Gilmour 1999), temperature (Jaap 1979) and eutrophication (Hunte and Wittenberg 1992) are all known to reduce the number of larvae produced by corals, their rates of settlement and early post-settlement survival (Table 1.2). Variation in larval supply and recruitment, therefore, not only reflect the disturbances to which a reef has been exposed, but also the condition of the reefs that supply the larvae (Hughes and Jackson 1985; Hughes and Connell 1987; Babcock 1991). Larval settlement is typically greatest on surfaces that are relatively free of sediment, i.e. vertical or downward-facing horizontal surfaces of settlement plates in areas of high sedimentation (Babcock and Davies 1991; Gilmour 1999). Thus, to monitor local changes in sedimentation despite variable larval supply, the ratio of coral recruits on vertical compared with upward-facing horizontal surfaces may prove a better indicator of changes in sedimentation on coastal coral reefs than settlement density, but field comparisons are required to determine its suitability.

Larval supply can be quantified using larvae traps (Lasker et al. 1998) while coral recruitment is easily quantified with settlement plates and/or transect and quadrat techniques (e.g. Babcock and Davies 1991; Hughes et al. 2002; Smith et al. 2005). Larval supply and recruitment of corals are influenced by the abundance and fecundity of adult corals on the reef and adjacent reefs, the amount of substrata available for settlement, the abundance of predators and competitors, and the physical conditions before, during and after spawning, particularly weather conditions. The

numbers of settling larvae are influenced by predator densities including planktivorous fish (Pratchett et al. 2001) and corals that also prey on planktonic larvae (Fabricius and Metzner 2004), which may be greater at locations least affected by anthropogenic stressors. Consequently, there is great natural variation in the supply and recruitment of larva on a reef that must be accounted for in monitoring programmes.

Benthic cover

Percentage coral cover is commonly used as a measure of reef condition (Marshall and Orr 1931; Dodge and Vaisnys 1977; Smith et al. 1981; Bell and Elmetri 1995; English et al. 1997; Done et al. 2007; Table 1.2). Often, coral cover decreases with declining water quality (e.g. Brown et al. 1990; van Woesik et al. 1999; Fabricius et al. 2005; Dikou and van Woesik 2006). In contrast, Lirman and Fong (2007) found a negative relationship between coral cover and changes in water quality in the Florida Keys where coral cover was significantly higher on inshore than on offshore reefs despite the existence of a water quality gradient. Benthic cover is also influenced by other forms of physical disturbances including cyclones (Fabricius et al. 2008), destructive fishing (Marcus et al. 2007), bleaching events (Golbuu et al. 2007; McClanahan et al. 2007) and predation by *Acanthaster planci* (Lourey et al. 2000).

The percentage cover of organisms is usually assessed using simple methods such as quadrats and/or transects, and determined for broad categories such as hard corals, soft corals, algae and sediment. Hard coral cover is sometimes further differentiated at the level of families, genera, or morphological groups. However, natural variability in benthic cover is likely to be large and using it as a co-variate in water quality assessments will require knowledge of the disturbance history of the area of interest. Thus, estimates of coral cover have limited utility as a response measure to changes in water quality.

Benthic community structure

Benthic community structure can be defined as the relative abundances of different taxonomic groups on coral reefs. A variety of methods can be used to quantify community structure with photo-transects being the most common. Links are often drawn between benthic community structure and the levels of anthropogenic stressors to which the assemblage has been exposed because the abundances of different benthic organisms generally reflect habitat conditions. With increasing distance from major river systems in the Whitsunday Region of the GBR, the coral assemblage changed from one dominated by faviids on nearshore reefs to a diverse assemblage dominated by acroporids, which was correlated to improved water quality at sites more distant from the rivers (van Woesik et al. 1999; Table 1.2). Among the soft corals on inshore reefs, the relative abundances of species from the Family Alcyoniidae were greater on reefs with high

turbidity and sedimentation in contrast to species of the Family Xeniidae and Family Nephtheidae that are common in clear-water conditions (Fabricius and De'ath 2001; Fabricius et al. 2005; Table 1.2). Changes in benthic community structure occur naturally due to factors such as rates of recruitment and history of disturbances (Hughes 1989). Consequently, correlating variation in community structure to levels of anthropogenic stressors requires a high degree of spatial replication and knowledge of the history of the reefs.

Indicator organisms other than corals

The abundance and species composition of bacteria in sediments (Uthicke and McGuire 2007), microphytobenthos and phytoplankton (Bell and Elmetri 1995; Gottschalk et al. 2007), macroalgae (Fabricius et al. 2005), amphipods (Thomas 1993), stomatopods (Koop et al. 2001; Risk et al. 2001) and foraminifera (Cockey et al. 1996; Uthicke and Nobes 2008) have been investigated as potential indicators of the condition of coral communities. Some of these measures have been incorporated into monitoring programmes (e.g. Hallock et al. 2003). Whilst these types of indicators show great potential for incorporation into assessments of the condition of coastal coral reefs, their widespread acceptance will depend on the availability of taxonomic expertise or genetic assays, or simple protocols that overcome the need for species differentiation. For example, the FORAM Index developed by Hallock et al. (2003) has been used to assess the effects of changes in water quality on foraminifera by quantifying the shift from assemblages containing larger species with algal symbionts to assemblages dominated by small and heterotrophic species (Uthicke and Nobes 2008). In the FORAM Index, analyses are based on easily quantifiable size classes rather than species composition, thus it can be used by observers without taxonomic expertise (Hallock et al. 2003).

Patterns of abundance and diversity of macroalgae belonging to the Rhodophyta and Chlorophyta may potentially be explained by responses to water quality (Fabricius et al. 2005; Tsai et al. 2005). Fabricius et al. (2005) reported responses in diversity of these algae at different spatial scales. At the regional level on the GBR, assemblages of Rhodophyta and Chlorophyta were more diverse on nearshore reefs adjacent to a region exposed to flood plumes from catchments with agricultural land uses, compared with a region with minimal land use (Brodie et al. 1997). Within regions, changes in the abundance and diversity of Rhodophyta, and the abundance of Chlorophyta, were correlated significantly with water quality suggesting that these groups of taxa may be sensitive enough to detect differences in water quality not only at large scales (between regions) but at also at finer scales (among reefs) (Fabricius et al. 2005; Table 1.2).

In conclusion, this review has highlighted the diverse range of indicators that are available to assess the effects of changes in environmental conditions on coastal coral reefs, e.g. from the colony to community-level. An integrated comparison that combines information on physiology,

population and community ecology of corals is required to identify indicators responsive to changes in water-quality on the GBR and this thesis addresses this gap. Whilst the ecosystem-wide effects of land-based sources of pollution are considered a significant threat to the GBR, the consequences of changing water quality can not be considered in isolation from those of a changing climate (e.g. Glynn 1991; Hoegh-Guldberg 1999; Kleypas et al. 1999). Thus, in undertaking such a comparison, it will be important to have an understanding not only of the response time of each of the indicators, but also of the specificity to contrasting disturbances such as changes in water quality and climate change. If hypotheses regarding water quality are to be addressed, then those that are specific to disturbances such as nutrient availability, sedimentation and turbidity, and that demonstrate a fast response to provide an 'early warning' of any changes in water quality, will be of greater value than those characterised by patterns of great variability. It is at the colony level that we are most likely to find 'early warning' or sublethal indicators of the effects of changes in environmental conditions on coral reefs. Understanding the processes at these levels will furthermore aid in understanding the responses at the ecological level.

1.3 Thesis outline

The research presented in this thesis aimed to assess a range of coral indicators at different spatial and temporal scales and identify those most suitable for inclusion into a 'toolbox' for monitoring the condition of coastal coral reefs on the GBR. Although the focus of this thesis was to examine responses to changes in water quality, such a comparison could not be done without consideration of the consequences of climate change on corals and coral reefs. Since early warning responses to changing environmental conditions were likely to first occur at the physiological level, most of the research presented here examined responses at the colony level of organisation. The principal objective of this research was to identify environmental gradients of water quality and irradiance on the GBR and then test the general null hypothesis that there would be no difference in a range of coral indicators along the gradients. To test causal effects of changes in water quality on the coral indicators, validation experiments were done using controlled facilities in the laboratory that were followed by *in situ* manipulative experiments in the field.

The outline of the thesis is as follows: **Chapter 1** provides a summary of the main effects of three key components of water quality: nutrients, sedimentation, turbidity and light attenuation, on corals to provide a context against which the proposed indicators can be assessed. This chapter also outlines desirable characteristics of indicators and then reviews a range of response measures that have been proposed as indicators in previous studies. **Chapter 2** identifies the persistence of an environmental gradient in the Whitsunday Islands where levels of a range of nutrients and suspended solids were elevated at nearshore reefs but decreased with distance away from the Australian mainland. Similarly, irradiance parameters such as Secchi- and optical depth were low

at the nearshore reefs but increased with distance away from the mainland indicating differences in water clarity along the gradient. Since many of these water column nutrient and irradiance parameters co-varied with each other, it was necessary to calculate a single parameter against which to test variation of the response measures in the statistical models. Thus, Chapter 2 also details the determination of a water quality index used as an explanatory variable in some of the research that follows. **Chapter 3** examines the spatial variation in the photo-physiology of the dinoflagellate symbionts (*Symbiodinium*) of *Pocillopora damicornis* along the environmental gradient in the Whitsunday Islands. To further understand patterns of spatial variation, response measures such as symbiont density, concentration of chlorophyll *a*, protein content and skeletal density of *P. damicornis*, as well as colony brightness, thickness of the tissue layer, density of macro-bioeroders and surface rugosity of massive *Porites* were investigated in **Chapter 4** along the environmental gradient in the Whitsunday Islands from nearshore to outer islands. This chapter also describes the results of manipulative experiments exposing nubbins of massive *Porites* to increased nutrient availability and decreased irradiance in the form of suspended particulate matter (SPM) in the laboratory, and by transplanting *Porites* nubbins along the environmental gradient in the field, to test causal effects of changes in water quality on coral indicators. Changes in colony brightness due to responses of the pigment-laden symbionts, which can be measured using a simple colour chart, emerged as a useful coral indicator of environmental conditions. **Chapter 5** demonstrated that strong relationships exist between coral reflectance and concentrations of chlorophyll *a* with the perceived brightness of scleractinian corals, and hence provided further validation of the colour chart. To understand patterns of seasonal variation, response measures including symbiont density, concentration of chlorophyll *a*, skeletal density and colony brightness of *P. damicornis*, and the density of macro-bioeroders of massive *Porites*, were examined in **Chapter 6** over a period of 2 years at a coastal (Magnetic Island) and two mid-shelf locations (Davies and Broadhurst Reefs). The growth parameters skeletal density, annual extension and calcification rates of massive *Porites* were analysed in **Chapter 7** to examine spatial and temporal variation in coral growth on the GBR. Finally, **Chapter 8** utilises a matrix of five selection criteria (defined in Chapter 1) to rank and identify potential coral indicators for monitoring programmes. This chapter also provides a general discussion on coral indicators and highlights questions arsing from this research that warrant further investigation.

Table 1.2. Examples of studies examining colony, population and/or community variables on coral reefs and reported responses to various stressors.

Indicator	Stressor	Response	Source
Colony			
Symbiont photo-physiology	Cyanide	6 h exposure caused reductions in quantum yield (F_v/F_m) in *Stylophora pistillata* (70%) and *Acropora aspera* (60%) compared with controls.	(Jones et al. 1999)
Symbiont photo-physiology	Herbicide	Diuron 10 μg l^{-1}, F_v/F_m reduced by 50% compared with controls.	(Jones et al. 2003)
Coral brightness	Dissolved inorganic nutrients	*Seriatopora hystrix*, *S. pistillata* darker in NH_4 treatment compared with control.	(Hoegh-Guldberg and Smith 1989)
Coral brightness	Dissolved inorganic nutrients	Optical density and chlorophyll concentration in *Acropora variabilis* increase with time exposed to NH_4.	(Kizner et al. 1995)
Concentration of chlorophyll *a*	Dissolved inorganic nutrients	Mean chlorophyll *a* (mg g $protein^{-1}$, ± SE): *S. pistillata*, Control 5.6 ± 3.14, NH_4 (20 μM) 19.4 ± 8.97. *S. hystrix*, Control 8.75 ± 4.04, NH_4 (20 μM) 13.5 ± 4.49.	(Hoegh-Guldberg and Smith 1989)
Concentration of chlorophyll *a*	Dissolved inorganic nutrients	Chlorophyll *a* (μg cm^{-2}): *Pocillopora damicornis*, control 9.3, NH_4 (50 μM) 24.8. *Montipora verrucosa*, control 1.9, NH_4 (50 μM) 19.4.	(Stambler et al. 1994)
Density of symbionts	Dissolved inorganic nutrients	Mean symbiont density (10^6 cells mg $protein^{-1}$, ± SE): *S. pistillata*, Control 0.55 ± 0.12, NH_4 (20 μM) 1.49 ± 0.25. *S. hystrix*, Control 2.11 ± 1.03, NH_4 (20 μM) 2.78 ± 1.55.	(Hoegh-Guldberg and Smith 1989)
Lipid content	Light	Lipid content greater in unshaded compared with shaded treatment.	(Stimson 1987)
Lipid content	Inshore-offshore	*Porites porites*, nearshore lipid content ~11% of tissue DW, offshore lipid content ~8% of tissue DW.	(Harland et al. 1992)

Indicator	Stressor	Response	Source
Lipid content	Turbidity	*Goniastrea retiformis* and *Porites cylindrica*, lipid content reduced by shading.	(Anthony and Fabricius 2000)
Skeletal and tissue growth	Field water quality gradient	*Acropora eurystoma*: Three fold increase in growth rates (weight and linear extension) near fish farm compared with reference area.	(Bongiorni et al. 2003)
Skeletal and tissue growth	Dissolved inorganic nutrients	*S. pistillata*: Growth rates (mg d^{-1}) decreased by 25 – 60% during long-term nutrient exposure.	(Ferrier-Pages et al. 2000)
Skeletal and tissue growth	Inshore-offshore	Massive *Porites*: Skeletal density (g cm^{-3}): Central GBR nearshore 1.1, offshore 1.4.	(Risk and Sammarco 1991)
Skeletal and tissue growth	Inshore-offshore	Massive *Porites*: Mean skeletal density (g cm^{-3}, ± SD): Central GBR nearshore 1.35 ± 0.21, offshore 1.57 ± 0.16. Mean extension rate (mm y^{-1}, ± SD): nearshore 13.56 ± 3.5, offshore 8.22 ± 1.02. Mean calcification rate (g cm^{-2} y^{-1}, ± SD): nearshore 1.77 ± 0.26, offshore 1.28 ± 0.12.	(Lough and Barnes 1992)
Skeletal and tissue growth	Inshore-offshore	Mean tissue thickness (mm, ± SD) of massive *Porites* Central GBR: nearshore 6.59 ± 1.19, offshore 5.21 ± 0.95.	(Barnes and Lough 1992)
Skeletal and tissue growth	Inshore-offshore	Surface rugosity of massive *Porites* greater on nearshore compared with offshore reefs. Mean tissue growth (mm y^{-1} ± SE): nearshore 9.20 ± 1.66, mid-shelf 7.42 ± 1.32, offshore 6.87 ± 0.14.	(Darke 1991)
Skeletal chemistry	Inshore-offshore	*Porites lobata*: $\delta^{15}N$: nearshore ~5.5 ‰, mid-shelf ~3.8 ‰, offshore ~5.2 ‰.	(Sammarco et al. 1999)
Skeletal chemistry	Sewage	*Porites lobata*: $\delta^{15}N$ levels greater on reefs with sewage input compared with 5 of 7 Indo-Pacific reference locations.	(Heikoop et al. 2000)
Partial mortality	River exposure	More colonies with >50% partial mortality adjacent to river mouths than sites distant from riverine discharge.	(Nugues and Roberts 2003)

Indicator	Stressor	Response	Source
Population			
Bioerosion	Inshore-offshore	Total bioerosion in *Porites*: nearshore 11%, offshore 1.3%.	(Sammarco and Risk 1990)
Bioerosion	Sewage, terrestrial runoff, sedimentation	Rates of bioerosion in branching coral rubble (excluding *Acropora* spp.) greater on polluted than reference areas.	(Holmes et al. 2000)
Bioerosion	Dissolved inorganic nutrients	NH_4, PO_4 addition (ENCORE experiment): no effect on bioerosion.	(Koop et al. 2001)
Bioerosion	Terrestrial runoff, inshore-offshore	More polychaetes and sipunculans in experimental blocks after 60 months at fringing reefs compared to atolls in French Polynesia.	(Hutchings and Peyrot-Clausade 2002)
Bioerosion	Inshore-offshore	Lower rates of bioerosion inshore compared with offshore sites of the GBR.	(Hutchings et al. 2005)
Population structure	Field water quality gradient	High Island (high exposure to flood plumes) low density of colonies (0.13 m^{-2}), similar proportion across size-classes. Fitzroy Island (low exposure to flood plumes) greater density of colonies (2.46 m^{-2}) dominated (>73%) by juvenile size-classes.	(Smith et al. 2005)
Coral diseases	Dissolved inorganic nutrients	Nutrient enrichment associated with increased aspergillosis of *Gorgonia ventalina* and yellow band disease of *Montastraea annularis* and *M. franksii*.	(Bruno et al. 2003)
Community			
Larval supply and recruitment	Sedimentation	Elevated sedimentation reduced coral recruits to upper horizontal surfaces.	(Babcock and Davies 1991)
Larval supply and recruitment	Sedimentation	Larval survival and settlement reduced in experimental treatments of high (100 mg l^{-1}) and low (50 mg l^{-1}) sediments compared with controls (0 mg l^{-1}).	(Gilmour 1999)

Indicator	Stressor	Response	Source
Larval supply and recruitment	River exposure	Recruitment greater on reefs distant from a river in the northern GBR compared with those adjacent to river discharge.	(Smith et al. 2005)
Benthic cover	Sedimentation	Adjacent to logged areas on Cahuita (Costa Rica), mean coral cover 40% compared with mean cover of 63% at reference sites at Grand Cayman.	(Cortes and Risk 1985)
Benthic cover	Sedimentation	Sedimentation >10 mg DW cm^{-2} d^{-1} associated with decline in coral cover.	(Rogers 1990)
Benthic cover	Dredging	Coral cover decreased by 30% adjacent to a dredging operation. Recovery of coral cover within 22 months.	(Brown et al. 1990)
Benthic cover	Field water quality gradient	Increasing distance from two rivers, Central GBR: From reefs near the river to those >80 km way, macroalgae cover decreased from 70% ± 10% to 0%, octocoral cover increased from 1% ± 1% to 19% ± 10% and hard coral cover increased from 4% ± 2% 31% ± 14%.	(van Woesik et al. 1999)
Community structure	Field water quality gradient	Increasing distance away from two rivers, Central GBR: 24 hard coral taxa at location near rivers, 64 hard coral taxa at reefs >80 km.	(van Woesik et al. 1999)
Community structure	Herbivory, inshore-offshore	Abundance of *Sargassum* greater on nearshore reefs of the GBR than on offshore reefs.	(McCook 1996)
Indicator species	Field water quality gradient	Increased abundance of Rhodophyta and Chlorophyta along water quality gradients in regions receiving runoff from agriculture catchments compared with reference locations.	(Fabricius et al. 2005)

Chapter 2.0 Gradients in water column nutrients, sediment parameters, irradiance and coral reef development in the Whitsunday Islands, central Great Barrier Reef

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 4-fold increase in the input of nutrients (Moss et al. 1992; Neil et al. 2002), a 5 to 10-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 runoff 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 increases (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 photo-physiology. Exposure of corals to sedimentation by nutrient-rich silt resulted in greater photo-physiological stress (i.e. lower maximum quantum yield, 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 primarily autotrophic when light is not limiting (Muscatine 1990), with a shift toward heterotrophy in some (but not all) species as sediment influence increases (Anthony and Fabricius 2000). Light is, therefore, amongst the most significant resources 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 2003b; Anthony et al. 2004). 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 nearshore 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 objective of this study was to estimate the spatio-temporal variation of a range of key resources utilised by corals. The variables characterised included nutrients, sediment and irradiance at twelve different locations in the Whitsunday Islands on five separate occasions over a two-year period. The measured changes in water quality were then related to the depth of coral reef development on reefs along the gradient.

2.2 Materials and methods

2.2.1 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. 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). Tides within the Whitsunday region are semidiurnal and the tidal range can exceed 4.0 m, which is higher than most other areas on the GBR. Rainfall within the region occurs mostly during the Austral summer (December to April) and varies inter-annually between 1200 – 2000 mm. Episodic flood events are an important influence on the water quality in the Whitsunday Islands, as illustrated by a flood event on 28th January 2005 shown on a satellite image (Fig. 2.1a). The image highlights the complex nature of flood plumes in the region including retention through eddy formation 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.

This study focused on twelve locations in the Whitsunday Islands (Fig. 2.1b). These sites 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. The locations naturally separated into nearshore locations (directly influenced by rivers and within 20 km of the Australian mainland: Repulse, Lindeman, Long and Dent Islands), outer islands (>20 km from the coast and sheltered from direct coastal influences but potentially indirectly exposed to resuspended and materials transported further offshore: Whitsunday, Hook, Deloraine, Edward and Border Islands), 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.

2.2.2 Water column

Surface water was sampled at each location to measure the following variables: chlorophyll *a*, particulate nitrogen, particulate phosphorus, particulate organic carbon, total suspended solids, dissolved inorganic nutrients (NH_4, NO_2, NO_3, PO_4, $Si(OH)_4$), total dissolved nutrients (total dissolved nitrogen [TDN] and total dissolved phosphorus [TDP]) and dissolved organic nutrients (dissolved organic nitrogen [DON] and dissolved organic phosphorus [DOP]). For each of chlorophyll *a*, particulate nitrogen, particulate phosphorus and particulate organic carbon, replicate water samples (250 ml) 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 Turner 10AU fluorometer following acidification with 0.1M HCl and a 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 a 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 a standard reference material (BCSS-1 and MESS-1, Institute for Environmental Chemistry, Canada). To determine concentrations of total suspended solids, replicate water samples (1 L) were filtered through pre-weighed polycarbonate filters (0.45 μm). Each filter was oven dried at 60°C for 24 h and reweighed. For analysis of dissolved inorganic and organic

nutrients, replicate water samples (10 ml) were collected with a syringe and filtered through sterile polycarbonate filters (0.45 μm). Concentrations of dissolved inorganic nutrients and total dissolved nutrients 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.

2.2.3 Sediments

Grain size distribution, sediment colour and inorganic carbon content 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 in the back (sheltered) and front (exposed) of ten of the study reefs. During all other times, only two sites were selected on the back of each reef. The sediment samples were taken in triplicate 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).

Concentrations of organic carbon, nitrogen and sediment pigment 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).

2.2.4 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 cosine-corrected light sensor (LI-192, LI-COR, Nebraska, 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 below the surface, 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:

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

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 downward irradiance and z is depth in metres. By rearranging Equation (1), K_d (PAR) was estimated 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 Deloraine Islands

(Fig. 2.1b) for 4 diurnal cycles each in January and February 2006. The Odyssey light loggers were calibrated against the LI-192 light sensor. Data of surface irradiance were obtained from the AIMS weather station at Hardy Reef (http://www.aims.gov.au/pages/facilities/weather-stations/weather-index.html).

2.2.5 Maximum depth of coral reef development

The lowest depth limit of coral reef development was estimated by observers using each of two transects across the entire reef profile at each of two sites per reef. The lowest limit of reef development was recorded, 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, allowed estimates of the percent of surface irradiance that would limit the depth distribution of coral reef development in the Whitsunday Islands.

2.2.6 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 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 clearer water with fewer nutrients than the sample average, whereas a positive z-score indicates turbid and nutrient-rich conditions. Linear models (fitted by restricted maximum likelihood estimation; Pinheiro and Bates 2000) were used to test for relationships of the response variables (water column, sediment and irradiance; $\log_2$ transformed) with distance from the coast (determined as the distance from the nearest mainland coast) and among time of sampling. The factors Distance and Time were considered random and orthogonal 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. For all ANOVAs, data were tested for deviations from the assumption of homogeneity of variances and data were transformed if necessary. Pooling procedures involving elimination of terms from the mean square estimates were done if a term was non-significant at $P > 0.25$ (Underwood 1997). 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. 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).

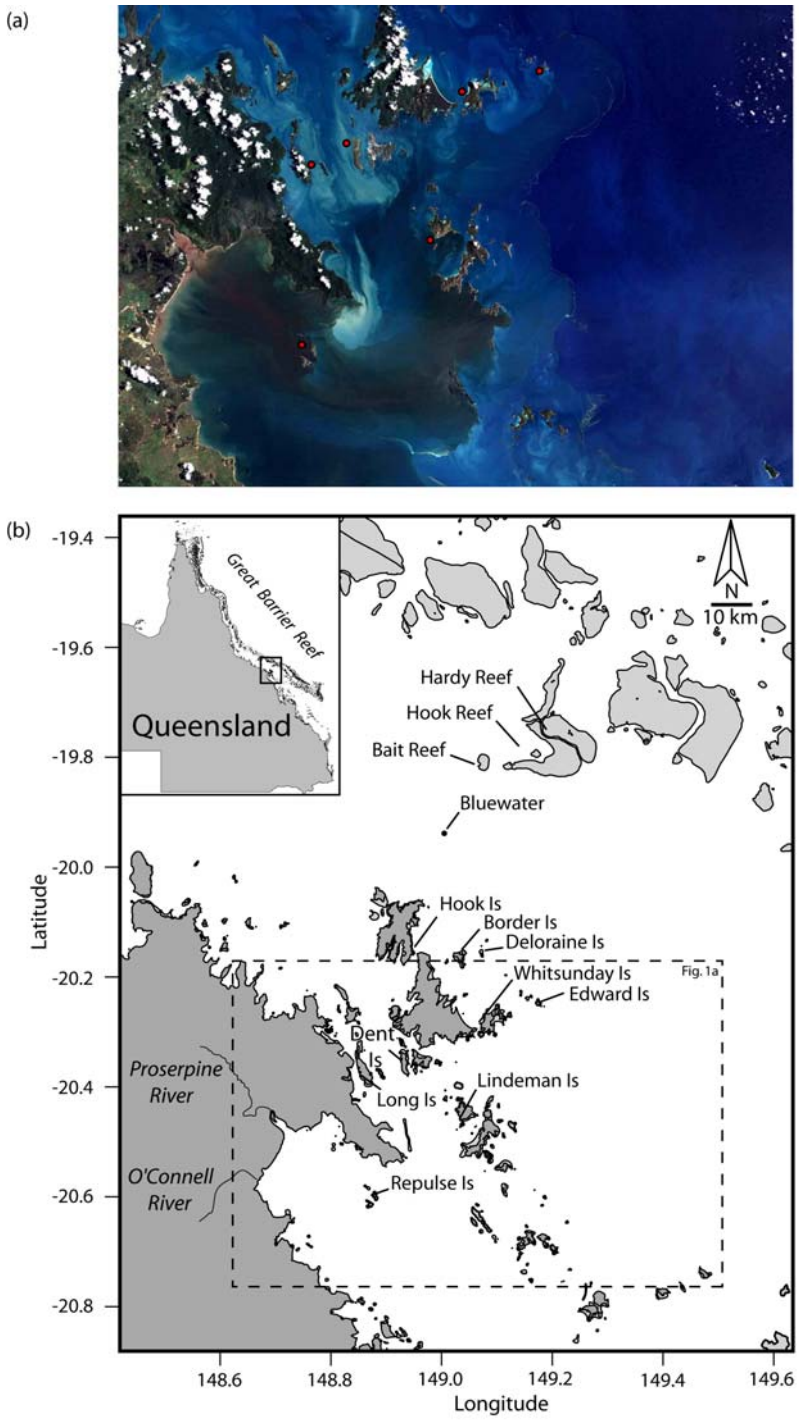

Fig. 2.1. (a) Satellite image (Landsat 5 TM) of the Whitsunday Islands showing a flood plume emerging from the Proserpine and O'Connell Rivers, 28th January 2005. Areas of elevated suspended solids are visible near the mouths of the rivers, with areas of increased phytoplankton abundance indicative of nutrient enrichment that extend through the islands. Red circles indicate some of the sampling locations; (b) Map of study locations in the Whitsunday Islands of the Great Barrier Reef, Australia. Dashed area represents area shown in Fig. 1a. Image courtesy K. Rohde (Department of Natural Resources and Water, Queensland Government).

2.3 Results

2.3.1 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 Fig. 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 ± 0.12 μg L^{-1}, mean ± SE, *n*=6) compared with the outer Edward Island (EI) (0.31 ± 0.06 μg L^{-1}, *n*=4) when averaged over all times of sampling (Table 2.1). Similarly, mean concentrations of total suspended solids were approximately 2.9 times greater at Repulse Island (3.97 ± 0.49 mg L^{-1}, *n*=6) than at Edward Island (1.36 ± 0.12 mg L^{-1}, *n*=5). Particulate phosphorus (RI: 0.11 ± 0.01 μmol L^{-1}, *n*=6; EI: 0.06 ± 0.01 μmol L^{-1}, *n*=5) and particulate organic carbon (RI: 20.35 ± 2.78 μmol L^{-1}, *n*=5; EI: 12.95 ± 1.24 μmol L^{-1}, *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 2.2, Fig. 2.2). In addition to these differences in magnitude among sampling events, levels of chlorophyll *a*, particulate phosphorus, 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 (Fig. 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 among the sampling times.

Concentrations of total suspended solids, dissolved inorganic nitrogen, and the ratio between both particulate nitrogen and particulate organic carbon with total suspended solids, varied inconsistently with distance from the coast and among times of sampling (Distance x Time interaction). For example, the slopes for total suspended solids were negative for all five field trips but the slopes were distinctly steeper in August 2004, 2005 and 2006 compared with the other times of sampling (Fig. 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 (Fig. 2.2). There was no difference with distance from the coast or among times of sampling in the ratio of carbon to nitrogen.

Table 2.1. Summary of mean water column, sediment and irradiance parameters (± standard error) at each of the 12 study locations in the Whitsunday Islands. Data for each location are averaged over sampling events from August 2004 to February 2006.

		Repulse	Lindeman	Long	Dent	Whitsunday	Hook	Border	Deloraine	Edward	Bluewater	Bait Rf	Hook Rf
GPS		20° 35'S 148° 52'E	20° 28'S 149° 02'E	20° 23'S 148° 51'E	20° 21'S 148° 56'E	20° 14'S 149° 02'E	20° 09'S 148° 57'E	20° 10'S 149° 04'E	20° 10'S 149° 04'E	20° 15'S 149° 10'E	19° 48'S 149° 04'E	19° 48'S 149° 05'E	20° 09'S 148° 57'E
Distance to coast (km)		5	14	2.5	10	20.5	21	27.5	31	37.5	47.5	57.5	62
Water													
Chlorophyll *a* (µg L^{-1})	Mean	0.59	0.55	0.47	0.46	0.44	0.38	0.24	0.34	0.31	0.49	0.25	0.42
	SE	0.12	0.16	0.07	0.06	0.07	0.07	0.04	0.06	0.06	0.38	0.04	0.08
Phaeophytin (µg L^{-1})	Mean	0.35	0.30	0.34	0.35	0.28	0.21	0.28	0.22	0.21	0.2	0.18	0.26
	SE	0.04	0.04	0.04	0.04	0.03	0.02	0.10	0.04	0.04	0.12	0.01	0.03
Total suspended solids (mg L^{-1})	Mean	3.97	2.05	2.33	2.30	1.72	1.86	1.89	1.45	1.36	1.23	1.34	1.43
	SE	0.49	0.25	0.36	0.65	0.23	0.14	0.32	0.17	0.12	0.58	0.30	0.24
Total organic carbon (µmol L^{-1})	Mean	18.06	14.35	15.41	12.08	14.01	13.98	15.42	10.79	13.99	13.49	8.78	14.99
	SE	2.02	1.38	3.42	1.44	5.69	2.94	8.43	1.18	0.79	0.74	1.97	1.91
Particulate N (µmol L^{-1})	Mean	1.40	1.03	1.10	1.12	0.97	1.21	0.72	0.97	1.32	1.14	0.82	1.10
	SE	0.23	0.20	0.19	0.23	0.11	0.31	0.03	0.15	0.18	0.34	0.09	0.07
Particulate P (µmol L^{-1})	Mean	0.10	0.08	0.09	0.06	0.07	0.09	0.07	0.05	0.06	0.07	0.05	0.07
	SE	0.02	0.01	0.02	0.01	0.01	0.01	0.04	0.01	0.01	0.01	0.02	0.01
DIN (µmol L^{-1})	Mean	0.14	0.25	0.44	0.45	0.11	0.27	0.17	0.16	0.21	0.04	0.29	0.27
	SE	0.02	0.14	0.17	0.15	0.04	0.09	0.07	0.03	0.06	0.01	0.08	0.10
DIP (µmol L^{-1})	Mean	0.11	0.10	0.11	0.11	0.09	0.10	0.11	0.11	0.11	0.07	0.11	0.10
	SE	0.02	0.01	0.01	0.02	0.02	0.01	0.01	0.01	0.02	0.01	0.02	0.01

		Repulse	Lindeman	Long	Dent	Whitsunday	Hook	Border	Deloraine	Edward	Bluewater	Bait Rf	Hook Rf
DON ($\mu mol\ L^{-1}$)	Mean	6.61	6.69	6.55	6.52	6.73	7.37	5.42	6.45	7.14	5.45	4.44	6.97
	SE	0.99	0.68	0.66	0.60	0.86	1.13	1.49	1.02	0.73	0.10	0.66	0.47
DOP ($\mu mol\ L^{-1}$)	Mean	0.23	0.24	0.19	0.16	0.16	0.15	0.23	0.15	0.16	0.15	0.16	0.27
	SE	0.04	0.03	0.02	0.01	0.02	0.03	0.06	0.03	0.02	0.01	0.01	0.11
Silicate ($\mu mol\ L^{-1}$)	Mean	2.83	2.52	1.89	1.34	1.12	1.25	1.02	1.35	0.86	0.5	0.93	0.60
	SE	0.39	0.39	0.27	0.08	0.02	0.03	0.04	0.28	0.01	0.01	0.26	0.05
Sediment													
Chlorophyll *a* ($\mu g\ gDW^{-1}$)	Mean	2.45	3.09	2.34	1.80	2.12	4.17	1.21	1.35	1.23	-	3.65	2.14
	SE	0.31	0.28	0.48	0.20	0.77	0.39	0.01	0.25	0.19	-	1.02	0.72
Phaeophytin ($\mu g\ gDW^{-1}$)	Mean	2.95	4.59	3.28	3.60	3.07	2.72	1.50	4.04	3.08	-	2.96	4.58
	SE	0.79	1.60	0.74	0.63	2.16	1.29	0.01	1.11	0.37	-	2.85	0.41
Organic carbon (%)	Mean	0.30	0.33	0.30	0.36	0.29	0.28	0.25	0.25	0.26	-	0.27	0.30
	SE	0.00	0.02	0.01	0.02	0.09	0.07	0.00	0.04	0.00	-	0.06	0.00
Nitrogen (%)	Mean	0.05	0.05	0.04	0.05	0.04	0.04	0.05	0.04	0.04	-	0.04	0.05
	SE	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	-	0.00	0.00
Light													
Secchi depth (m)	Mean	4.50	5.30	7.17	10.10	8.75	7.00	10.67	12.20	12.00	12.67	16.50	17.00
	SE	0.80	1.24	1.19	2.14	1.53	1.02	1.45	1.02	1.22	1.20	4.50	5.00
K_d	Mean	0.29	0.21	0.18	0.14	0.15	0.18	0.12	0.11	0.12	0.10	0.07	0.11
	SE	0.06	0.04	0.04	0.03	0.03	0.02	0.02	0.01	0.00	0.00	0.01	0.01
Optical depth (m)	Mean	3.77	5.52	6.84	8.45	7.48	5.65	9.09	9.41	8.57	10.31	14.22	9.25
	SE	0.60	1.04	1.43	1.29	1.71	0.54	1.41	0.76	0.25	0.49	2.31	0.77

Table 2.2. 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	MS	*F*	*P*	df	MS	*F*	*P*	df	MS	*F*	*P*	Residual
Chlorophyll *a* (μg L^{-1})	1,46	3.7930	19.78	0.0001	4,46	3.4621	18.05	<0.0001	4,46	0.1187	0.62	0.6514*	0.1918
Total suspended solids (mg L^{-1})	1,4	9.4716	6.34	0.0022	4,4	0.6352	0.43	0.1365	4,49	1.4945	7.79	0.0001	0.1919
Particulate N (μmol L^{-1})	1,3	0.2776	1.53	0.1506	3,3	3.9998	22.11	0.0042	3,42	0.1809	2.40	0.0809	0.0753
Particulate P (μmol L^{-1})	1,4	5.3824	14.17	0.0038	4,4	2.8032	7.38	0.0073	4,49	0.3799	2.56	0.0503	0.1486
Particulate Organic C (μmol L^{-1})	1,4	2.4256	15.49	0.0003	4,4	2.3513	15.01	0.0000	4,47	0.1906	1.22	0.3162*	0.1566
Dissolved inorganic N (μmol L^{-1})	1,3	0.8250	0.19	0.4569	3,3	2.6670	0.62	0.2509	3,40	4.3360	3.81	0.0170	1.137
Dissolved inorganic P (μmol L^{-1})	1,40	0.0056	0.12	0.7281	3,40	1.4761	32.16	<0.0001	3,40	0.0299	0.65	0.5869*	0.0459
Dissolved organic N (μmol L^{-1})	1,3	0.1417	1.16	0.2151	3,3	1.8673	15.33	0.0087	3,40	0.1218	2.11	0.1142	0.0577
Dissolved organic P (μmol L^{-1})	1,40	1.0209	4.23	0.0463	3,40	0.4304	1.78	0.1659	3,40	0.2907	1.20	0.3205*	0.2414
C:N	1,3	0.5917	3.32	0.1170	3,3	0.3107	1.74	0.2356	3,40	0.1781	1.43	0.2469	0.1242
PN:TSS	1,3	7.2387	6.30	0.0097	3,3	2.3348	2.03	0.0385	3,42	1.1481	5.55	0.0027	0.2069
POC:TSS	1,4	2.1436	2.82	0.0459	4,4	2.5621	3.37	0.0242	4,47	0.7599	2.90	0.0316	0.2618
Sediment chlorophyll *a* (μg gDW^{-1})	1,2	0.0309	0.03	0.8288	2,2	0.1034	0.09	0.8321	2,51	1.1135	2.17	0.1242	0.5123
Sediment phaeophytin (μg gDW^{-1})	1,2	0.0020	0.00	0.9682	2,2	37.6130	26.77	<0.0001	2,51	0.3940	0.28	0.7564*	1.405
Sediment pigment (μg gDW^{-1})	1,2	0.0419	0.15	0.6970	2,2	0.0460	0.17	0.8456	2,51	0.3400	1.24	0.2967*	0.2732
Sediment organic C (%DW)	1,2	0.4398	3.04	0.0873	2,2	1.6678	11.53	0.0001	2,50	0.0273	0.19	0.8285*	0.1446
Sediment N (%DW)	1,2	0.0236	0.24	0.6251	2,2	0.0465	0.48	0.6245	2,50	0.0117	0.12	0.8874*	0.0977
Secchi depth (m)	1,3	9.8739	44.96	<0.0001	3,3	2.6184	11.92	<0.0001	3,33	0.1898	0.86	0.4694*	0.2196
Optical depth (m)	1,3	5.8009	27.60	<0.0001	3,3	1.5086	7.18	0.0008	3,33	0.1969	0.94	0.4340*	0.2102

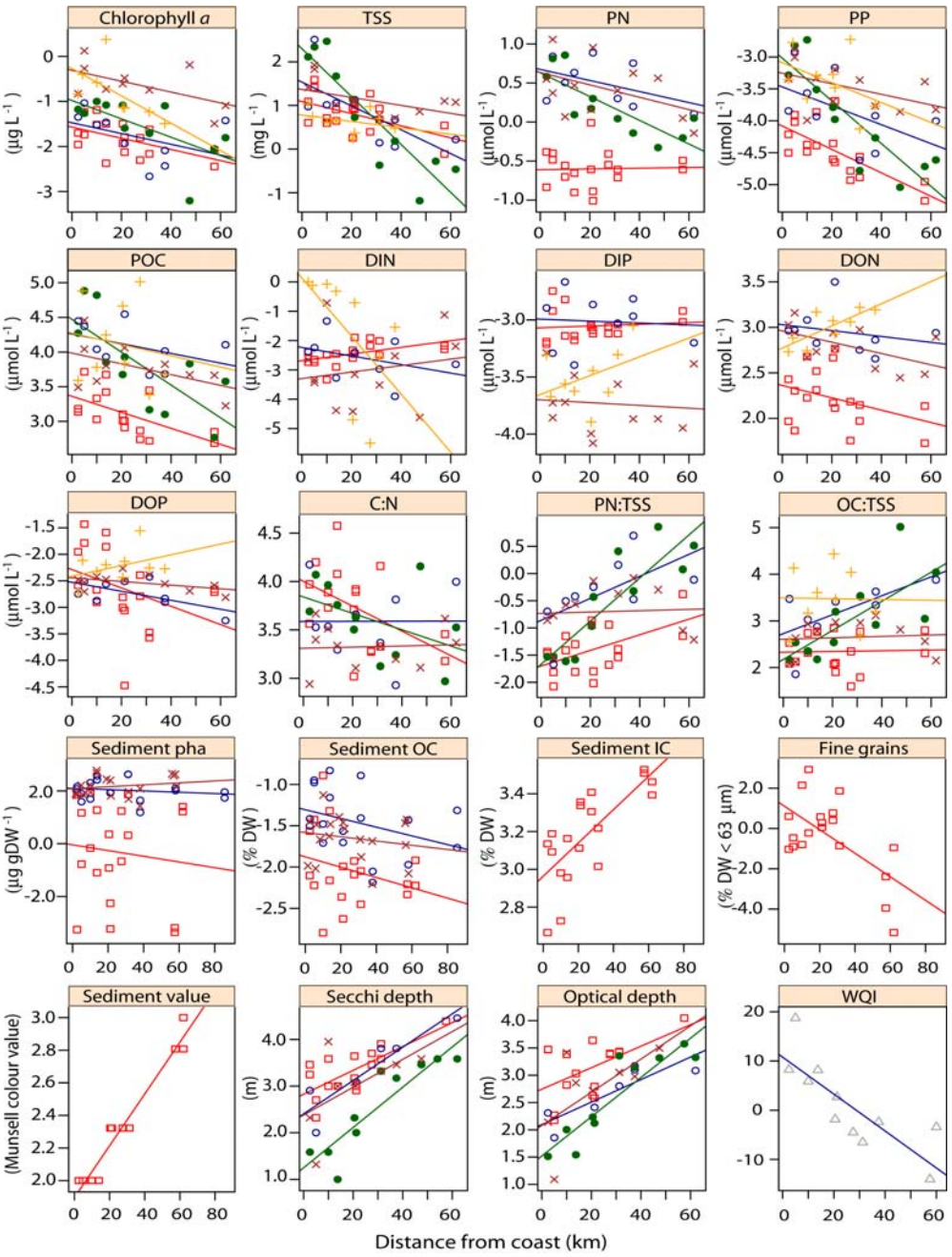

Fig. 2.2. Summary of the relationships between each of the water column, sediment and irradiance variables and nearest distance from the coast. Samples collected from five sampling events between August 2004 and August 2006. Response variables are $\log_2$ transformed, except for the Water Quality Index. 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, Pha = phaeophytin. 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.

A PCA further illustrated the relationships of the water column variables among each other and their distribution across the locations. The nearshore 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 (Fig. 2.3). These nearshore islands also associated strongly with high values of the water quality index. In contrast, the outer islands and mid-shelf 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 (Fig. 2.3). Only the dissolved inorganic nutrient forms DIP and DIN showed no clear correlation with distance from the coast in the PCA.

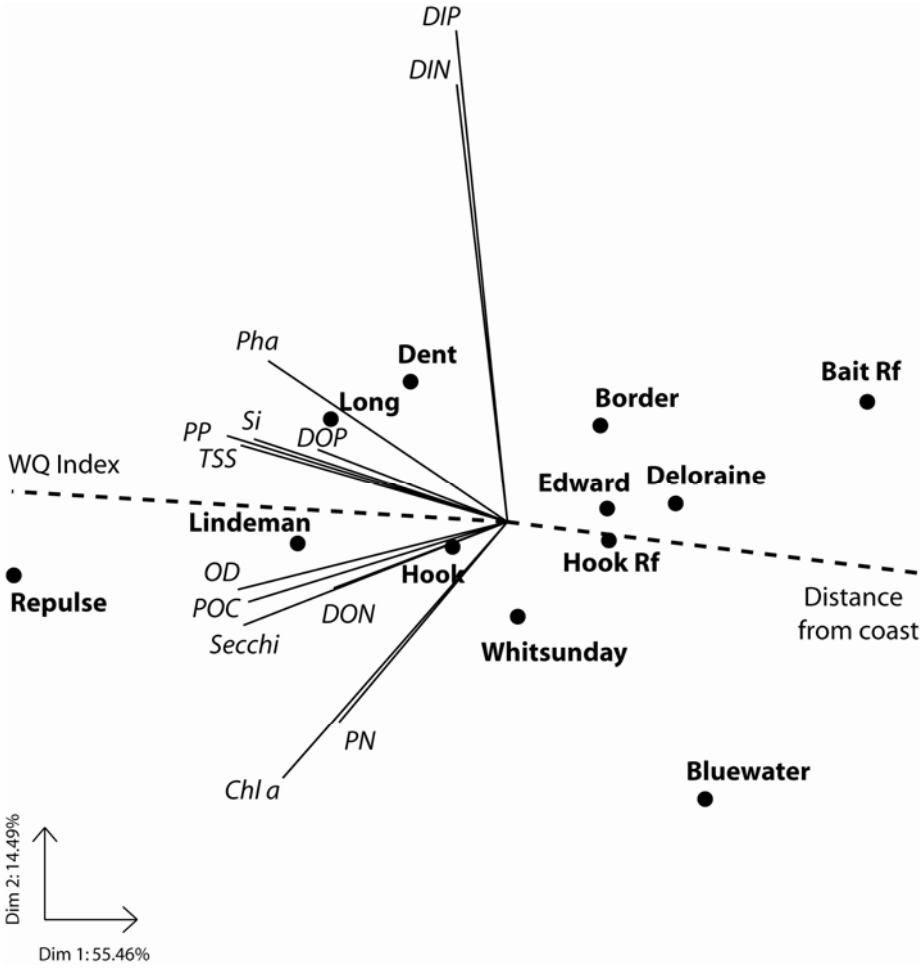

Fig. 2.3. Principal components analysis of water column and irradiance variables sampled at the Whitsunday Islands for all sampling events. *Chl a*=chlorophyll *a*, *Pha* = Phaeophytin, *TSS* = total suspended solids, *PN* = particulate nitrogen, *PP* = particulate phosphorus, *POC* = particulate organic 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.

2.3.2 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 (<63 μm) decreased significantly with distance from the coast ($F_{1,17} = 10.28$, $P = 0.0051$, $r^2 = 0.34$; Fig. 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 nearshore and not at outer islands ($F_{1,17} = 10.28$, $P < 0.0001$, $r^2 = 0.95$; Fig. 2.2).

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

Similarly, sediment 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 nearshore reef sediments were dominated by inorganic carbon with values >50%, whereas outer shelf reef sediments reached values of over 90%.

Linear models of sediment 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 2.2). 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 ± 0.021 %DW, *n*=19), when compared with August 2005 (0.376 ± 0.024 %DW, *n*=18) and February 2006 (0.322 ± 0.014 %DW, *n*=19). In addition, there was a trend for concentrations of organic carbon to decrease with increasing distance from the coast (Table 2.2, Fig. 2.2).

Concentrations of sediment nitrogen varied considerably among reefs and sites. 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 concentrations of nitrogen in sediments and distance from the coast (Table 2.2; overall average, 0.044 ± 0.001 %DW, *n*=57).

The relationships among the sediment variables and the reefs were illustrated in a PCA (Fig. 2.4). 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 positively with distance from the coast.

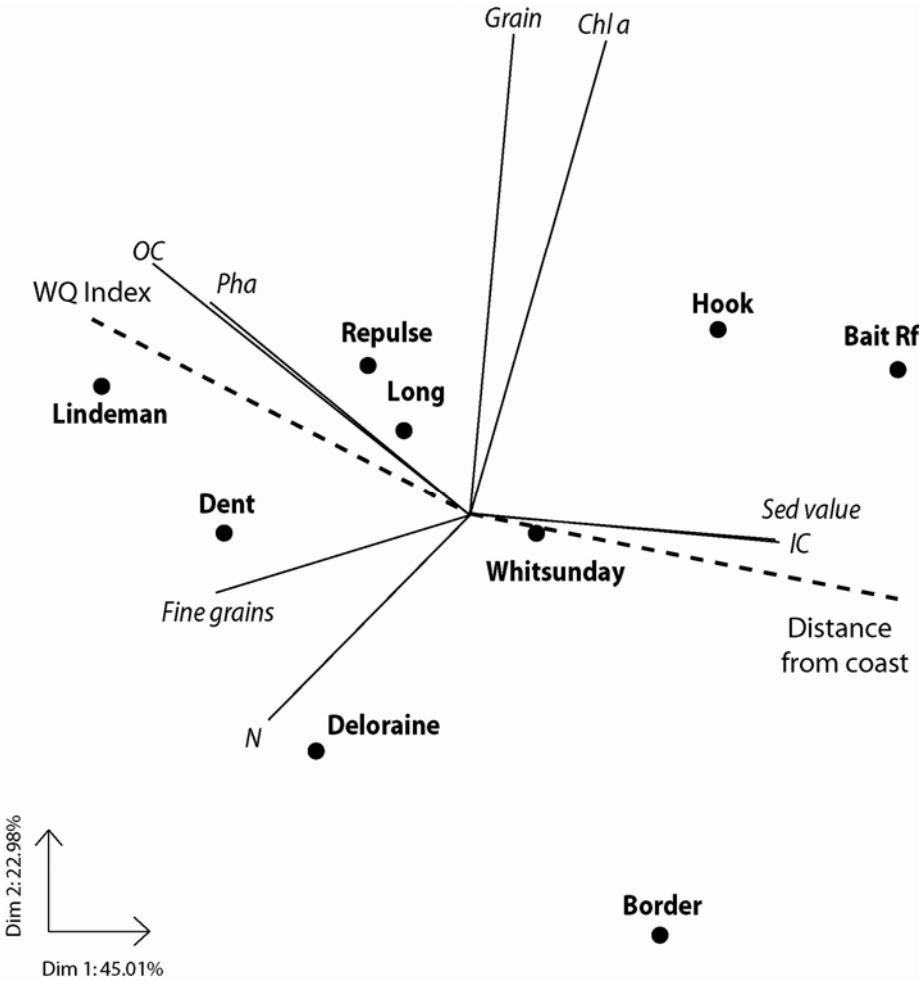

Fig. 2.4. Principal components analysis of sediment variables at the Whitsunday Islands. *Chl a* = chlorophyll *a*, *Pha* = phaeophytin, *N* = nitrogen, *IC* = inorganic carbon, *OC* = organic carbon, *Sed value* = Munsell colour value, *Grain* = average grain size, *fine grains* = sediments<63 μm. WQ 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.

2.3.3 Irradiance

Secchi depth differed among times of sampling and with distance from the coast in the Whitsunday Islands (Table 2.2). Mean Secchi depth increased from 4.0 ± 0.8 m (*n*=5) at Repulse

Island to 12.3 ± 1.0 m (*n*=4) at Edward Island and 15.3 ± 3.3 m (*n*=3) at the mid-shelf reefs (Fig. 2.2). Similarly, the optical depth of the water column differed among times of sampling and with distance from the coast (Table 2.2) with the mean optical depth increasing from 3.77 ± 0.60 m (*n*=4) at Repulse Island to 8.92 ± 0.49 m (*n*=4) at Edward Island and was 11.97 ± 2.62 m (*n*=3) at the mid-shelf reefs (Fig. 2.2). The patterns of variation in Secchi and optical depth were 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, $F_{1,9} = 17.85$, $P = 0.0022$, $r^2 = 0.66$; Fig. 2.2).

Total daily irradiance received by the benthic community of three of the islands are summarised in Table 2.3. At any given depth, total daily benthic irradiance was 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 benthic irradiance at 6 m depth at Deloraine Island was similar to that at shallow depths of Long and Lindeman Islands (means: 23.2 ± 1.3 mol photons m^{-2} d^{-1}, versus 24.1 ± 2.2 and 25.3 ± 3.0 mol photons m^{-2} d^{-1}, respectively; Table 2.3).

2.3.4 Maximum depth of coral reef development

The maximal depth of coral reef development increased almost 5-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 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 chlorophyll *a*, particulate nitrogen, particulate phosphorus, particulate organic carbon, total suspended solids and dissolved organic nitrogen, and positive correlations with Secchi and optical depths, and sediment colour (Table 2.4). Moreover, many of the water column variables were correlated with the irradiance parameters (Table 2.4). Thus, the derived water quality index was used as the explanatory variable in the linear model that showed the lower limit of reef development increased significantly with decreasing water quality index, i.e. from turbid to clear water conditions ($F_{1,9} = 26.86$, $P = 0.0006$; Fig. 2.5).

Table 2.3. Total daily irradiance (mol photons 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 parentheses are % of surface irradiance at Hardy Reef. Mean ± standard error.

	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	63.2	23.0	13.8	33.1	16.4	47.6	25.8
SE	0.4	3.3	1.7	3.2	0.7	4.7	0.7
Mean February 06	58.9	25.7	15.4	19.5	8.1	33.5	21.3
SE	2.5	3.2	2.0	0.5	0.3	3.6	1.6
Overall mean	60.8	24.1	14.7	25.3	11.7	39.5	23.2
SE	1.6	2.2	1.3	3.0	1.7	3.9	1.3

Table 2.4. 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, Sed value = Munsell colour value, Sed org C = sediment organic carbon, Sed pha = sediment phaeophytin, Sed inorg C = sediment inorganic carbon, Fine grains = %grains <63 μm. Bold: P <0.05.

Variable	Max depth	Chl *a*	PN	PP	POC	TSS	DIN	DIP	DON	DOP	Secchi	OD	Sed value	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					
Sed value	**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

Incorporating the estimates of the lower depth limits of reef building 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 2.5). In contrast, at Lindeman, Long, Dent and Hook Islands, this limit was at 20 – 30% of surface irradiance (Table 2.5). At Hook Reef, there was approximately 4% of surface irradiance at the maximal depth limit of coral reef development (Table 2.5).

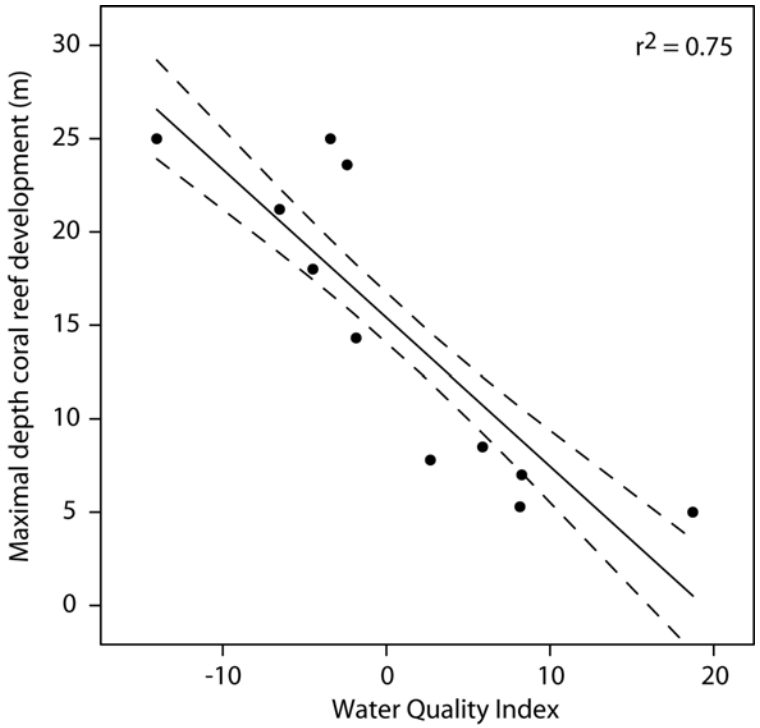

Fig. 2.5. Relationship between maximal depth of coral reef development and the water quality index for the Whitsunday Islands. Dashed lines are ± 1 standard error (SE).

Table 2.5. 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.

Parameter	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
SE	(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 (µmol photons m^{-2} s^{-1})	107	432	224	410	123	284	115	104	62
% 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 a strong relationship exists between the water quality index (WQI) 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 islands 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). None of the wet season sampling events captured any flood plumes associated with monsoonal activity.

2.4.1 Water column

The doubling of water column chlorophyll *a* along the gradient is consistent with cross-shelf patterns typically found in the central GBR (Brodie et al. 2007). Analysis of a long-term chlorophyll *a* dataset for the GBR found mean chlorophyll *a* concentrations of 0.37 μg L^{-1} at inner locations compared with 0.15 μg 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 μg L^{-1} at inshore locations of the Whitsunday/Pompey section of the GBR compared with 0.69 ± 0.04 μg L^{-1} at the outer reefs. The time-averaged results are about half those of Brodie et al. (1997), but approximately 2-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). Although not tested statistically, concentrations of chlorophyll *a* were distinctly greater during the two wet season sampling events similar to Brodie et al. (2007).

Wind driven resuspension events are important influences on water column characteristics in the coastal zone (Alongi and McKinnon 2005). Total suspended solids increased 2- to 3-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 10.2 ± 0.8 m s^{-1} (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 levels from

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 (7.8 ± 0.8 m s^{-1}), which had similar wind conditions to the other times of sampling, i.e. August 2004 (7.1 ± 0.7 m s^{-1}), August 2005 (7.3 ± 1.1 m s^{-1}) and January 2006 (7.9 ± 0.4 m s^{-1}). Thus, other factors such as tides and currents (particularly within channels between islands) also have important influences on levels of total suspended solids in the Whitsunday Islands as was demonstrated in the coastal zone of Broad Sound located in the southern GBR (Kleypas 1996). 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.

2.4.2 Sediments

The clearest trends in the sediment variables investigated here were the changes in sediment colour and inorganic carbon, two variables that 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.

Concentrations of sediment chlorophyll *a* 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 that may exist in the upper photic levels of the sediment.

Although not statistically 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 levels of nitrogen and organic carbon on the four reefs nearest the coast were noted in August 2004 (Uthicke 2006). However, nitrogen concentrations on these reefs were only about 10% higher than the average from 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.

2.4.3 Irradiance

Corals on the nearshore reefs received lower total daily benthic irradiance compared with corals on reefs on the outer islands in both survey periods. Total daily benthic irradiance decreased by 47% at Lindeman Island and 15% at Deloraine Island after a weather change when wind speeds reached 10 – 15 m s^{-1} in February 2006 and clouds decreased surface irradiance at Hardy Reef by approximately 15% (Table 2.3). Thus, the increase in cloud cover most likely contributed to a proportion of the decreased irradiance recorded on the outer island. However, the greater reduction in irradiance on the nearshore reefs suggests that resuspension of bottom sediments additionally contributed to the 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, although the processes contributing to such declines in irradiance in the Whitsunday Islands should be quantified with deployments of *in situ* turbidity loggers (e.g. Orpin et al. 2004).

2.4.4 Maximum depth of 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 into the patterns of variation in the depth

distribution of coral reefs. Water clarity increased around 3-fold along the 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. Similarly, Kleypas (1996) noted that decreasing coral reef development coincided with increased concentrations of suspended sediments (derived from AVHRR imagery) as well as increased tidal ranges in the southern GBR. 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 substrata were 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. The 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 minimum 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. This 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 the 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 1989). In the outer Whitsunday Islands, corals are likely to cover much of their energetic requirements from photosynthates whereas nearshore corals may be light-limited at all but shallow depths due to turbid conditions. 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 Whitsunday 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 nearshore 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-acclimatisation of biofilms, suggests that photo-acclimatisation 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 condition 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.

Chapter 3.0 Spatial variation in the photo-physiology of a coastal coral along an environmental gradient of the Great Barrier Reef

3.1 Introduction

Reef-building corals (Scleractinia) are important contributors to the physical structure of coral reefs. The success of corals can be attributed to their symbiotic association with unicellular dinoflagellate algae (genus *Symbiodinium*). Photo-physiological characteristics of these symbiotic dinoflagellates are determined by the optical environment in which they live (Falkowski and Dubinsky 1981; Chalker et al. 1983; Barnes and Chalker 1990) but may also be influenced by stress from sedimentation (Philipp and Fabricius 2003; Weber et al. 2006), pollutants (Jones et al. 1999; Jones et al. 2003), salinity (Kerswell and Jones 2003), temperature (Coles and Jokiel 1977) and flow-regime (Nakamura et al. 2005; Ulstrup et al. 2005).

The optical environment of coral symbionts is governed by light scattering and light absorption properties of the coral tissue (Kühl et al. 1995; Salih et al. 2000) and the water column (Kirk 1994) as well as backscatter of the coral skeleton (Enriquez et al. 2005). The transparency of the water column is determined by water quality (Kirk 1994). Water quality is characterised by the content of nutrients (dissolved inorganic/organic and particulate forms of N and P), sediments, pollutants (e.g. herbicides and pesticides), which may vary spatially depending on distance from terrestrial runoff (Devlin and Brodie 2005; Fabricius 2005) and temporally between seasons, during weather-dependent resuspension of sediments and episodic flood events (Alongi and McKinnon 2005; Devlin and Brodie 2005; Brodie et al. 2007). Water quality is also characterised by irradiance, which may vary spatially with depth and reef topography, and temporally with tidal regimes, cloud cover and weather-dependent resuspension of sediments (Larcombe et al. 1995; Anthony and Hoegh-Guldberg 2003; Anthony et al. 2004).

Changes in water quality due to terrestrial runoff containing nutrients, sediments and pollutants are considered a significant threat to coral reefs in the coastal zone (Bell and Elmetri 1995; Haynes and Michalek-Wagner 2000). Coral cover, diversity and maximal depth of coral reef development has been shown to decline with decreasing water quality (elevated water column nutrients, sediments and pollutants as well as reduced irradiance) on the Great Barrier Reef (e.g. van Woesik et al. 1999; Fabricius et al. 2005). Corals may respond physiologically to elevated levels of nutrients by increases in symbiont density (e.g. Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989) and tissue thickness (Barnes and Lough 1992; Lough and Barnes 2000), but reduced rates of calcification (Kinsey and Davies 1979), while exposure to suspended particulate matter can result in increased energy stores (Anthony and Fabricius 2000; Anthony 2006). However, different components of water quality have contrasting photo-physiological effects on corals. For example, dissolved inorganic nutrients and particulate organic matter can enhance rates of gross photosynthesis, whereas light-limitation due to increased turbidity and sedimentation can have negative consequences on coral photo-physiology (Fabricius 2005).

Chlorophyll *a* fluorescence of Photosystem II (PSII) has been measured using pulse-amplitude-modulation (PAM) technology to test photo-physiological responses of coral symbionts in relation to various components of water quality. Laboratory experiments have shown decreasing maximum quantum yield (F_v/F_m) depending on the duration of exposure and quantity (Philipp and Fabricius 2003) as well as the quality of sediment (grain-size and organic content; Weber et al. 2006). Similarly, pollutants negatively influence F_v/F_m depending on quantity and duration of exposure (Jones et al. 1999; Jones et al. 2003; Markey et al. 2007). Such studies suggest that photo-acclimatisation may in part be influenced by water quality and not by irradiance alone.

Corals are able to persist in variable light environments of the coastal zone due to photo-acclimatory responses of *Symbiodinium* that occur at different levels of organisation. These range from variation in the surface density of thylakoids per symbiont (Stambler 1998) and changes to the size and number of photosynthetic units (Iglesias-Prieto and Trench 1994), to variation in the concentration of photosynthetic pigment and/or cell density (Falkowski and Dubinsky 1981; Dubinsky et al. 1984; McCloskey and Muscatine 1984; Porter et al. 1984) and coral morphological responses (Anthony and Hoegh-Guldberg 2003). Consequently, the local light regime determines the photo-physiology of *Symbiodinium*. Symbionts acclimatised to high irradiances are characterised by high maximum photosynthetic rate, minimum saturating irradiance (E_k) and low light utilisation efficiency (α) (White and Critchley 1999; Ralph and Gademann 2005; Ulstrup et al. 2006) and photosynthetically active radiation (PAR)-absorptivity (Ralph et al. 2005). In contrast, symbionts acclimatised to low irradiance are characterised by low maximum photosynthetic rate and E_k, and high α and PAR-absorptivity (White and Critchley 1999; Ralph and Gademann 2005; Ralph et al. 2005). Corals may experience photo-inhibition if excess light energy results in a reduction in the rate of electron transfer in PSII, which may be dynamic (reversible) or chronic (Brown et al. 1999; Gorbunov et al. 2001). The dissipation of excess energy during photosynthesis via non-photochemical quenching (NPQ) has been shown to be greater for symbionts acclimatised to high irradiance compared with symbionts acclimatised to low irradiance (e.g. Gorbunov et al. 2001). Finally, the photo-physiological performance of the symbionts can also be assessed by determination of excitation pressure (Q_m) over PSII, which examines the magnitude of reduction in effective quantum yield ($\Delta F/F_m'$) relative to F_v/F_m (Iglesias-Prieto et al. 2004).

Most photo-physiological studies of corals in the field have focused on relatively small spatial scales and generally tested hypotheses about the effects of irradiance on the photo-physiology of *Symbiodinium*. Photochemical and non-photochemical processes of symbionts have been shown to perform differently between sun- and shade-acclimatised colonies (Falkowski and Dubinsky 1981; Porter et al. 1984; Gorbunov et al. 2001; Anthony and Hoegh-Guldberg 2003), between

sun- and shade-acclimatised surfaces of individual colonies (Jones et al. 1998; Ralph et al. 2005) and between polyp and coenosarc tissue (Kühl et al. 1995; Ralph et al. 2002; Ulstrup et al. 2006) where polyp tissue was characterised as shade-acclimatised in comparison to coenosarc tissue. Further, Iglesias-Prieto et al. (2004) found a significant negative relationship between Q_m and depth, but with differences between intercepts for two dominant corals, which suggested that symbionts adapted to different light environments could explain the vertical distribution patterns of their host in the Gulf of California. Recent studies have also found photo-physiological differences in benthic biofilms along known environmental gradients covering large spatial scales, i.e. 10's km (Underwood 2002; Uthicke 2006). However, no studies have examined the photo-physiology of corals over similar scales.

The aim of this study was to examine mesoscale (i.e. 10's km) variation in photo-physiology of the ubiquitous scleractinian coral *Pocillopora damicornis*. The study was undertaken in the Whitsunday Islands along an environmental gradient where a range of irradiance variables and water column nutrients (e.g. particulate and dissolved inorganic/organic nutrients) differed with increasing distance from the Australian coast and the discharge of two rivers (Chapter 2).

3.2 Materials and methods

3.2.1 Study area and sampling design

The study locations were selected along a cross-shelf transect through the Whitsunday Islands (20° 00' – 30'S and 148° 45' – 149° 15'E) as data from previous studies indicated the persistence of an environmental gradient with increasing distance away from the coast (Kleypas 1996; van Woesik et al. 1999; Brodie et al. 2007). Two rivers (Proserpine and O'Connell Rivers) flow into Repulse Bay to the south west of the Whitsunday Islands and provide a point-source discharge of terrestrial runoff into the study area. Corals were sampled at seven fringing reefs along the gradient and included: Repulse, Lindeman, Long, Dent, Haslewood, Hook and Deloraine Islands (Fig. 3.1). Sampling was carried out between 8th – 18th January 2007. At each location, apical branches (~8 cm long) of *P. damicornis* were collected during the afternoon using pliers from the centre of six colonies (n=6) at each of two depths (Shallow: 2 – 3 m, and Deep: 5 – 6 m below lowest astronomical tide, LAT). The maximal depth of coral reef development at Repulse and Lindeman Islands is 5.0 and 5.3 m, respectively (Chapter 2), thus 5 – 6 m was considered the so-called 'deep depth' among all locations. Coral branches were acclimated under low-light conditions (<10 µmol photons m^{-2} s^{-1}) in flow-through seawater tanks on board a research vessel for at least 2 h until dusk. All photo-physiological measurements were then carried out after 30 min of dark-acclimation.

3.2.2 Environmental gradient

Concentrations of water column nutrients have been shown to be highly correlated with irradiance parameters such as Secchi- and optical depth in the Whitsunday Islands (Chapter 2). Thus, a water quality index (WQI) was calculated for use as an explanatory variable in the analyses using the sum of a z-score transformation for thirteen irradiance and water-column nutrient variables measured at each location over six times of sampling from August 2004 to January 2007 following Fabricius and De'ath (2004) and Fabricius et al. (2005). The parameters used to calculate the WQI included: Secchi- and optical depth, chlorophyll *a*, phaeophytin, particulate nitrogen, particulate phosphorus, particulate organic carbon, dissolved organic and inorganic nitrogen and phosphorus, dissolved silicate and total suspended solids. The sampling procedures and analytical techniques for all parameters are described in Chapter 2. For each of the thirteen water quality parameters at each location, the WQI was calculated by:

$$\mathrm{WQI} = \sum_{i=13}^{N} x_i = \frac{(X_i - \overline{X})}{s_X} \qquad (1)$$

where X_i is the mean of a parameter for all sampling events at a location, $\overline{X}$ is the overall sample mean among locations, s_X is the standard deviation, and x_i is the z-score for each water quality parameter. A z-score is negative when the data point is below the sample mean and positive when above it. A negative (low) WQI thus indicates clear, nutrient-poor water whereas a positive (high) WQI indicates turbid, nutrient-enriched conditions.

To further characterise the light regime on a nearshore and an outer island, Odyssey light loggers (Dataflow Systems, Christchurch, New Zealand) attached to star-pickets were deployed at two depths (tide corrected; 3 m below lowest astronomical tide [LAT]; 6 m below LAT) on the leeward sides of Long and Deloraine Islands (Fig. 3.1) between 11th – 15th January 2007. The Odyssey light loggers were calibrated against a cosine-corrected light sensor (LI-192; LI-COR, Nebraska, USA).

3.2.3 Relative PAR-absorptivity

PAR-absorptivity and chlorophyll *a* fluorescence of PSII was measured to characterise the photo-physiology of *Symbiodinium* in *P. damicornis* using an Imaging-PAM (MAXI Imaging-PAM, Walz, Effeltrich, Germany). A feature of the Imaging-PAM is that it can provide an image of estimated PAR-absorptivity and that for every image pixel the corresponding pixel values of the maximum quantum yield can be obtained. Measurements were performed on branches submerged in a shallow bath of seawater. For each replicate branch (n=6), three circular 'areas of interest' (AOIs) were selected approximately 1 – 2 cm from the tip of the branch using the software

ImagingWin v 2.00m (Walz, Effeltrich, Germany). Each AOI included both coenosarc and polyp tissue. The average of three AOIs was used to determine photo-physiological variables for each replicate branch.

PAR-absorptivity was measured as the fraction of incident PAR absorbed, from the ratio of reflectance of red light (650 nm) (R) to the reflectance of non-absorbed near-infrared light (780 nm) (NIR) from the tissue surface (Ralph et al. 2005). The measurement is based on the principle that a change in the concentration of photosynthetic pigments will alter absorption of R with respect to NIR resulting in a change of the absorptivity value. It should be noted that this feature of the Imaging-PAM provides an estimate of PAR-absorptivity since it relies on several assumptions; (i) that there is no absorption by photosynthetic pigments at 780 nm; (ii) the absorption at 650 nm is representative for absorption of PAR; (iii) the remission of 650 nm and 780 nm by the sample without pigments is identical to that of the object used to calibrate the instrument. Thus, PAR-absorptivity was estimated as:

$$\text{PAR-absorptivity} = 1-(R/NIR) \quad (2)$$

All measurements were done in the laboratory with a 1 cm pathlength between the sample and the water surface. Although PAR-absorptivity measurements may be affected by differential absorption of 650 and 780 nm by water and coral tissue, no correction factors were applied to the data as the study hypotheses focused on relative changes of photo-physiological parameters along the environmental gradient. Since the measurements for all samples were conducted following the same protocol, this parameter is referred to as relative PAR-absorptivity (rPAR-absorptivity) and it is acknowledged that this should not be considered absolute.

3.2.4 Minimum fluorescence and maximum quantum yield

Quantum yield of PSII was assessed in the dark with the saturating pulse technique (Schreiber 2004) using the Imaging-PAM with the following settings: (Measuring Intensity = 1, Measuring Frequency = 1, Gain = 2, Damping = 2, Saturating Intensity = 8, Saturating Pulse Width = 0.8 s, Red Gain = 185, Fm-Factor = 1.055, F-Factor = 1.000). The saturating pulse in the dark yielded minimum fluorescence, F_0, and maximum fluorescence, F_m. From these parameters maximum quantum yield (F_v/F_m) was calculated:

$$F_v/F_m = (F_m-F_0)/F_m \quad (3)$$

3.2.5 Rapid light curves

Rapid light curves (RLCs) as described by White and Critchley (1999), and Ralph and Gademann (2005), comprised quantum yields at 10 incremental irradiance steps (0, 26, 72, 143, 241, 436,

598, 793, 1040, 1398 µmol photons m^{-2} s^{-1}) of 10 s duration each. At the end of each irradiance a saturating pulse was given, which yielded minimum fluorescence, F, and maximum fluorescence, $F_{m'}$, in the light. From these parameters effective quantum yield was calculated:

$$(\Delta F/F_m') = (F_m'-F)/F_m' \qquad (4)$$

Equation 2 and 4 were used to derive apparent photosynthetic rate (PS) at each irradiance step using the following equation:

$$PS = \Delta F/F_m' \times \text{PAR} \times \text{rPAR-absorptivity} \qquad (5)$$

where PAR denotes the incident irradiance. Information about the partitioning of light energy between PSI and PSII would be necessary in order to determine absolute photosynthetic rates (Schreiber 2004; Ralph and Gademann 2005). The RLCs were fitted to a formula of Platt et al. (1980), whereby descriptive parameters (PS_{max} [maximum apparent photosynthetic rate], α [light utilisation coefficient], E_k [minimum saturating irradiance]) were calculated (further details provided in Ralph et al. 2002). RLCs indicate the actual state of photosynthesis as opposed to the optimal state derived from steady state P–E curves. RLCs, however, not only show the light-acclimatisation state over the past few minutes but are also strongly influenced by the long-term light exposure (Ralph and Gademann 2005). Thus, RLCs were used to provide quantitative insight into the light acclimatisation capacity of corals collected along an environmental gradient.

3.2.6 Relative non-photochemical quenching and relative excitation pressure

Non-photochemical quenching (NPQ) and the excitation pressure over PSII, Q_m, was measured at 241 µmol photons m^{-2} s^{-1} along the RLC according to the following equations:

$$NPQ_{241} = (F_m-F_m')/F_m' \qquad (6)$$

$$Q_{241} = 1 - [(\Delta F/F_m')/(F_v/F_m)] \qquad (7)$$

where F_m' is maximum light-acclimated fluorescence and (7) is modified from Maxwell et al. (1995). The two parameters normally show a dose-dependent response (Ralph and Gademann 2005) until steady-state has taken place. Here, the actual state was examined during an RLC following a strict sampling protocol to investigate relative changes along the environmental gradient. Hence, it is acknowledged that the measurements should not be considered absolute by referring to the parameters as relative NPQ_{241} ($rNPQ_{241}$) and relative Q_{241} (rQ_{241}), where rQ_{241} considers the interaction of photochemical and non-photochemical processes taking place simultaneously in the reaction centres of PSII (Maxwell et al. 1995; Iglesias-Prieto et al. 2004). Values close to 0 indicate that photosynthesis is light limited even at high irradiances, while

values closer to 1 indicate closure of PSII at high irradiances, e.g. due to photoinhibition. Thus, rQ_{241} can be used as a proxy for the physiological performance of the symbionts.

3.2.7 Statistical analyses

Two factor analyses of variance (ANOVA) were used to examine differences among locations and between depths for the photo-physiological variables measured from *P. damicornis* in the Whitsunday Islands. The factors analysed were Location (7 levels; random) and Depth (2 levels; random, orthogonal). For all ANOVAs, data were tested for deviations from the assumption of homogeneity of variances prior to analysis. *Post hoc* comparisons of means for significant terms in the ANOVAs were done using Student Newman Keuls tests. Linear models were used to test for relationships between photo-physiological variables and the water quality index derived for the seven locations sampled in the Whitsunday Islands with the statistical software R (R Development Core Team 2006).

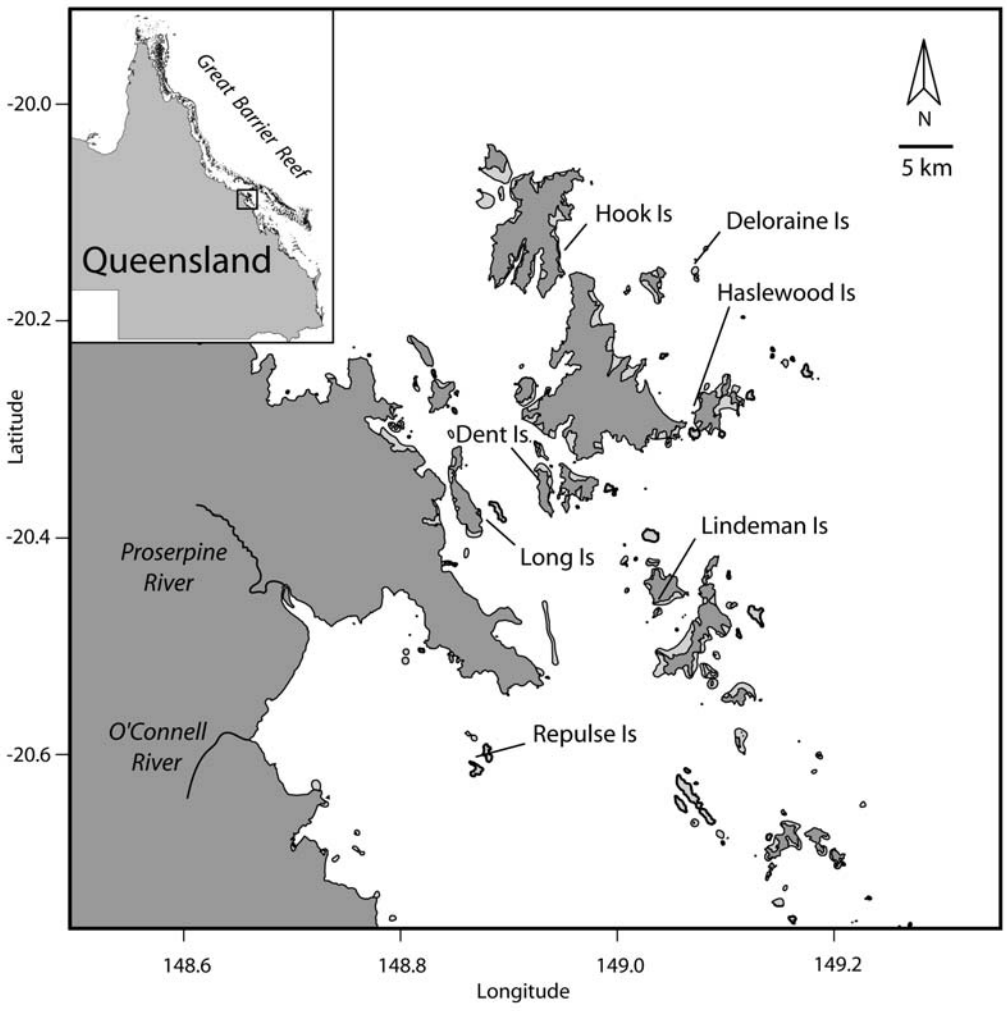

Fig. 3.1. Map of study locations in the Whitsunday Islands, Great Barrier Reef.

3.3 Results

3.3.1 Environmental gradient

Environmental conditions differed significantly along the gradient from nearshore to outer islands. Averaged over all times of sampling, mean Secchi depth was ~2.8-fold lower at nearshore (Repulse Island; RI: 4.4 ± 0.8 m, mean ± SE) than outer locations (Deloraine Island DI: 12.2 ± 1.0 m). Optical depth, which is a measure of the transparency of the water column, increased ~2-fold along the gradient from nearshore (RI: 4.6 ± 0.9 m) to outer islands (DI: 9.4 ± 0.8 m). Similar patterns occurred for the water-column nutrient parameters. For example, mean concentrations of chlorophyll *a* were up to 1.6 times greater at nearshore (RI: 0.56 ± 0.11 μg L^{-1}) compared with outer islands (DI: 0.34 ± 0.05 μg L^{-1}). Levels of total suspended solids were ~2.7-fold greater at nearshore (RI: 3.56 ± 0.58 mg L^{-1}) than outer islands (DI: 1.34 ± 0.18 mg L^{-1}). Similarly, mean concentrations of particulate nitrogen, phosphorus and organic carbon were generally 1.5- to 2-fold greater at nearshore compared with outer locations (for further details see Chapter 2). The rank order of locations from turbid to clear-water conditions was (WQI in parentheses): Repulse (14.83), Lindeman (3.55), Long (3.02), Dent (0.11), Hook (-1.06), Haslewood (-7.55) and Deloraine (-12.90).

There were spatial differences in the daily irradiance received by the benthic community during the sampling period at two of the islands representing opposite ends of the environmental gradient. At the 3 m and 6 m depths, total daily irradiance was 1.3 and 2.1 times greater, respectively, at the outer Deloraine Island compared with the nearshore Long Island. Averaged over the deployment period, the daily irradiance at 6 m depth at Deloraine Island was comparable to that at shallow depth of Long Island (13.3 ± 2.0 mol photons m^{-2} day^{-1} [mean ± SE] versus 16.0 ± 1.9 mol photons m^{-2} day^{-1}, respectively). At Long Island, the maximum daily irradiance ranged from 374 – 970 and 220 – 636 μmol photons m^{-2} s^{-1} at 3 m and 6 m, respectively. At Deloraine Island, the maximum daily irradiance ranged from 589 – 1364 and 263 – 797 μmol photons m^{-2} s^{-1} at 3 m and 6 m, respectively.

3.3.2 Relative PAR-absorptivity

A summary of the photo-physiological variables measured in *P. damicornis* is provided in Table 3.1. Relative PAR-absorptivity of *P. damicornis* varied inconsistently among locations and between depths (Table 3.2). At the shallow depth, mean rPAR-absorptivity was greatest at Repulse (0.918 ± 0.004, mean ± SE, *n*=6) and Long Island (0.912 ± 0.004), followed by Lindeman Island (0.821 ± 0.024) compared with the other reefs, which were not different from each other. At the deep depth, mean rPAR-absorptivity was greatest at Long (0.914 ± 0.004), Repulse (0.904 ± 0.009) and Dent Islands (0.860 ± 0.019) compared with the other reefs (Table 3.2). The linear

models showed that rPAR-absorptivity was greatest in turbid conditions at nearshore islands (high WQI) but decreased as water quality improved at the outer islands (low WQI) (Table 3.3, Fig. 3.2).

3.3.3 Minimum fluorescence and maximum quantum yield

Linear models showed that F_0 was greatest at the deep depth where water quality was lowest (high WQI) but was highly variable with changes in water quality along the gradient at the shallow depth (Fig. 3.3). F_v/F_m differed among locations and between depths (Table 3.2). At the shallow depth, mean F_v/F_m was greatest at Haslewood (0.656 ± 0.010) and Deloraine Islands (0.651 ± 0.003) followed by Hook Island (0.622 ± 0.008) compared with the other islands, which were not different from each other. At the deep depth, however, mean F_v/F_m was lowest at Repulse (0.556 ± 0.009) and Long Island (0.578 ± 0.006) compared with the other reefs, which were not different from each other (Table 3.2). The linear model showed that F_v/F_m was lowest where water quality was lowest (high WQI) but increased as water quality improved along the gradient from nearshore to outer islands (low WQI) (Table 3.3, Fig. 3.3).

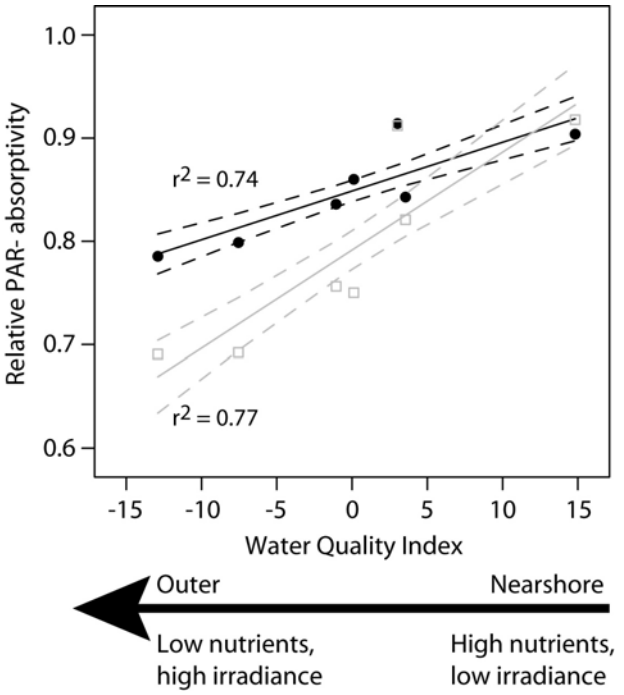

Fig. 3.2. Relationship between relative PAR-absorptivity of *Pocillopora damicornis* and the water quality index (WQI), where □ = shallow depth (3 m) and ● = deep depth (6 m). The WQI is determined by the sum of z-scores calculated from thirteen irradiance and water column nutrient variables collected between August 2004 and January 2007. A low WQI indicates high irradiance, low nutrient conditions whereas a high WQI indicates low irradiance, nutrient-enriched conditions. Arrow indicates direction of change along the environmental gradient from turbid nearshore to clear-water outer locations. Linear regression ± 1 standard error (dashed lines).

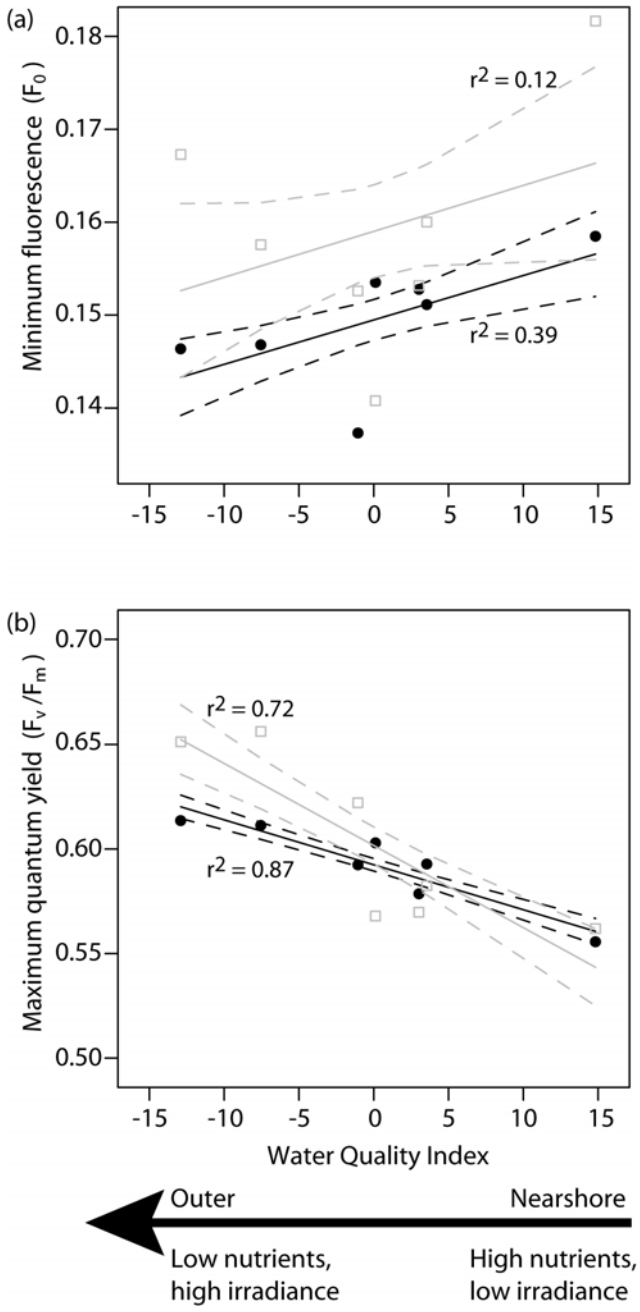

Fig. 3.3. Relationship between (a) minimum fluorescence (F_0) and (b) maximum quantum yield (F_v/F_m), respectively, of *Pocillopora damicornis* and the water quality index (WQI) derived for the Whitsunday Islands. □ = shallow depth (3 m), ● = deep depth (6 m). Linear regression ± 1 standard error (dashed lines).

3.3.4 Rapid light curves

PS_{max} and E_k of *P. damicornis* varied inconsistently among locations and between depths (Table 3.2). At the shallow depth, mean PS_{max} was greatest at Long Island (106.28 ± 5.12), followed by Repulse Island (89.13 ± 4.40), but no differences were detected elsewhere. At the deep depth, however, mean PS_{max} was greatest at Dent (108.09 ± 5.56) compared with Deloraine,

Hook, Long, Haslewood and Lindeman Islands, which were not different from each other, but mean PS_{max} at these reefs was significantly greater than at Repulse Island (81.16 ± 2.22) (Table 3.2). The ANOVAs did not detect any differences in the light utilisation coefficient (α) among locations or between depths (Table 3.2).

Corals at the shallow depth exhibited lower E_k at Deloraine Island (146.01 ± 3.75 µmol photons m^{-2} s^{-1}) compared with Dent, Hook, Haslewood, Lindeman and Repulse Islands, which were not different from each other. Corals at Long Island exhibited the greatest E_k (242.29 ± 14.57 µmol photons m^{-2} s^{-1}). At the deep depth, mean E_k was lowest at Repulse (188.38 ± 5.94 µmol photons m^{-2} s^{-1}) and Lindeman Islands (194.07 ± 9.00 µmol photons m^{-2} s^{-1}), compared with the other reefs, which were not different from each other (Table 3.2). At the deep depth, the linear models showed that PS_{max} and E_k were lowest where water quality was low (high WQI) and increased as water quality improved along the gradient at the outer islands (low WQI). However, both parameters showed the contrasting pattern at the shallow depth and were lowest where water quality was high at the outer islands (Table 3.3, Fig. 3.4).

3.3.5 Relative non-photochemical quenching and relative excitation pressure

Mean levels of $rNPQ_{241}$ and rQ_{241} of *P. damicornis* varied among locations and between depths (Table 3.2). At the shallow depth, mean $rNPQ_{241}$ was lowest at Repulse (0.062 ± 0.007), Long (0.075 ± 0.006) and Lindeman Islands (0.097 ± 0.012) compared with the remaining reefs. At the deep depth, mean $rNPQ_{241}$ was greatest at Dent Island (0.128 ± 0.019) and Hook Islands (0.121 ± 0.013) compared with the other reefs, which did not differ from each other (Table 3.2). For rQ_{241}, mean levels were greatest at Deloraine Island (0.523 ± 0.011) compared with the remaining reefs but there were no differences elsewhere. At the deep depth, however, mean rQ_{241} was greatest at Repulse (0.514 ± 0.009) and Lindeman Islands (0.487 ± 0.015) compared with the other reefs, which were not different from each other (Table 3.2). The linear model showed that $rNPQ_{241}$ increased as water quality improved along the gradient from nearshore to outer islands (Table 3.3, Fig. 3.5). In contrast, rQ_{241} was greatest where water quality was lowest at the deep depth with no correlation present at the shallow depth (Table 3.3, Fig. 3.5).

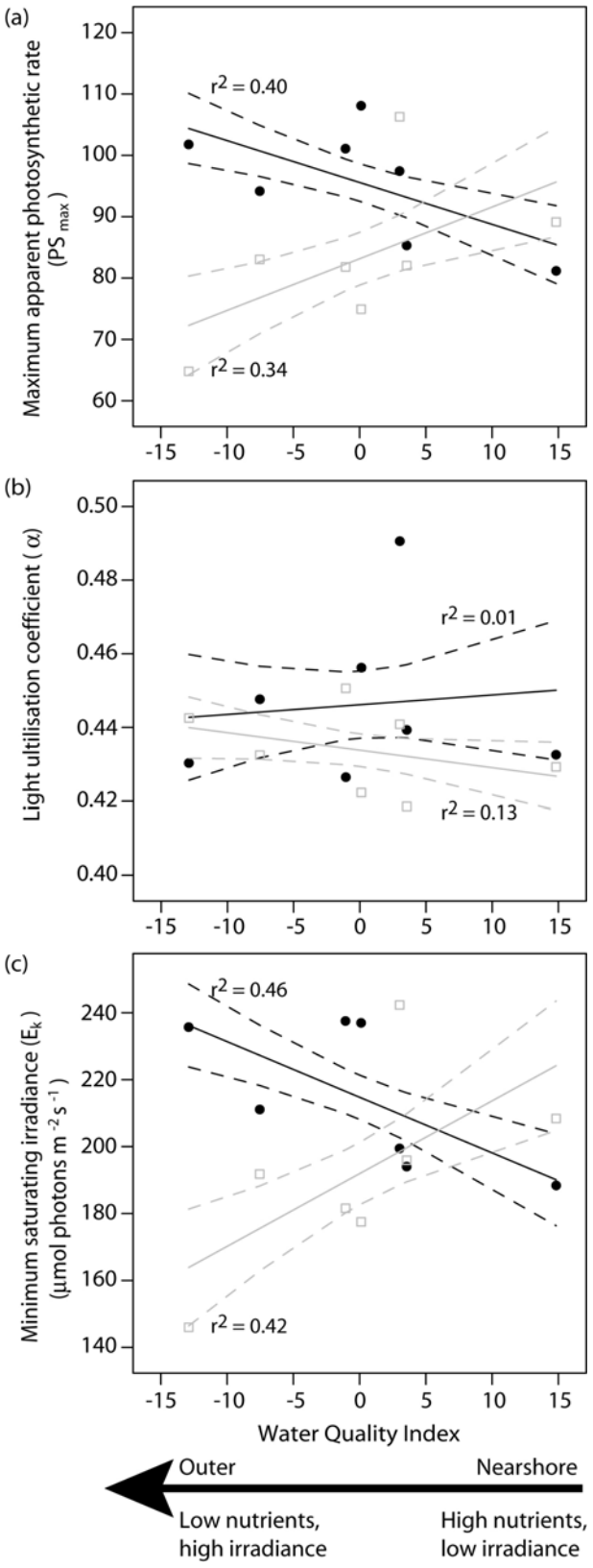

Fig. 3.4. Relationship between (a) maximum apparent photosynthetic rate (PS_{max}), (b) light utilisation coefficient (α) and (c) minimum saturating irradiance (E_k), respectively, of *Pocillopora damicornis* and the water quality index (WQI) derived for the Whitsunday Islands. □ = shallow depth (3 m), ● = deep depth (6 m). Linear regression ± 1 standard error (dashed lines).

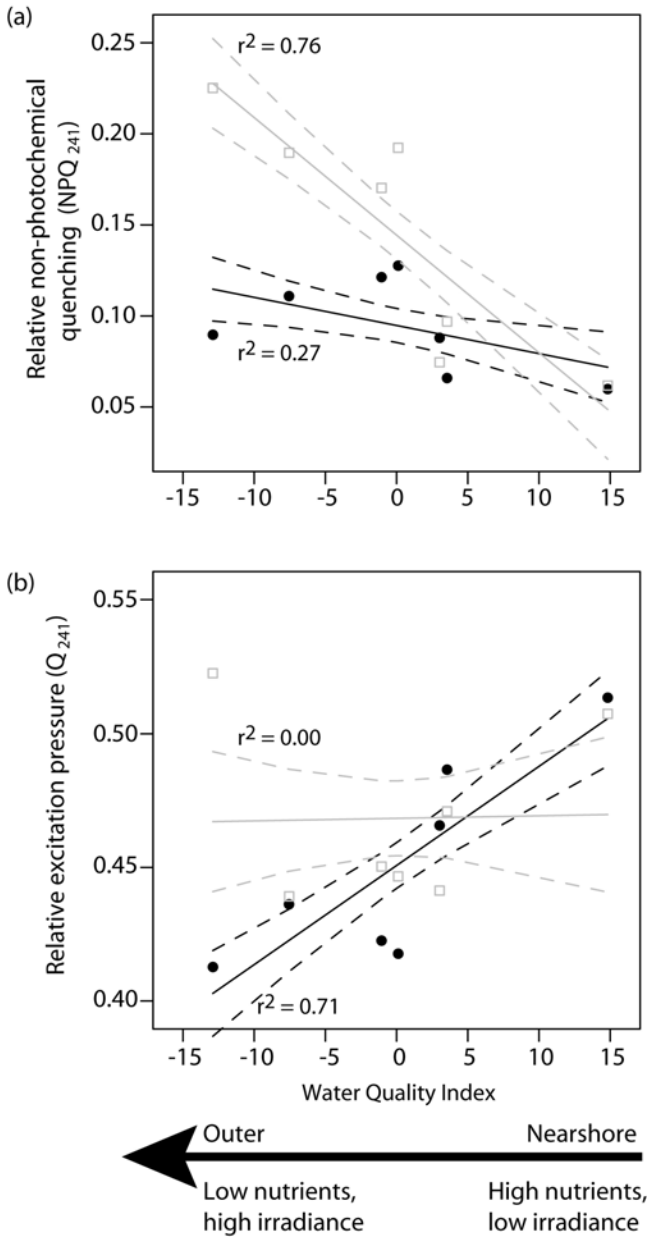

Fig. 3.5. Relationship between (a) relative non-photochemical quenching ($rNPQ_{241}$) and relative excitation pressure over PSII (rQ_{241}), respectively, of *Pocillopora damicornis* and the water quality index (WQI) derived for the Whitsunday Islands. □ = shallow depth (3 m), ● = deep depth (6 m). Linear regression ± 1 standard error (dashed lines).

Table 3.1. Summary of mean photo-physiological variables (± standard error, *n*=6) of *Pocillopora damicornis* at each of the 7 study locations in the Whitsunday Islands, January 2007.

		Repulse		Lindeman		Long		Dent		Haslewood		Hook		Deloraine	
Variate		Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep
rPAR-abs.	Mean	0.918	0.904	0.821	0.843	0.912	0.914	0.750	0.860	0.692	0.799	0.756	0.836	0.691	0.786
	SE	0.004	0.009	0.024	0.013	0.004	0.004	0.028	0.019	0.032	0.014	0.014	0.015	0.026	0.019
F_0	Mean	0.182	0.158	0.160	0.151	0.153	0.153	0.141	0.154	0.158	0.147	0.153	0.137	0.167	0.146
	SE	0.018	0.004	0.004	0.004	0.003	0.004	0.008	0.004	0.014	0.003	0.005	0.003	0.005	0.004
F_v/F_m	Mean	0.562	0.556	0.583	0.593	0.570	0.579	0.568	0.603	0.656	0.611	0.622	0.592	0.651	0.614
	SE	0.011	0.010	0.008	0.004	0.007	0.006	0.012	0.013	0.010	0.007	0.008	0.004	0.003	0.005
PS_{max}	Mean	89.13	81.16	82.03	85.30	106.28	97.44	74.93	108.09	83.03	94.14	81.81	101.09	64.79	101.77
	SE	4.40	2.22	5.53	4.50	5.12	3.42	6.57	5.56	5.56	6.11	4.27	3.79	4.25	6.18
α	Mean	0.429	0.433	0.419	0.439	0.441	0.491	0.422	0.456	0.432	0.448	0.451	0.426	0.443	0.430
	SE	0.005	0.011	0.014	0.008	0.008	0.011	0.009	0.016	0.017	0.015	0.020	0.011	0.021	0.014
E_k	Mean	208.39	188.38	195.93	194.06	242.29	199.44	177.50	236.95	191.79	211.09	181.55	237.54	146.01	235.68
	SE	11.79	5.94	10.72	9.00	14.57	9.84	14.84	9.06	8.81	14.67	5.80	8.18	3.75	9.34
$rNPQ_{241}$	Mean	0.062	0.060	0.097	0.066	0.075	0.088	0.192	0.128	0.190	0.111	0.170	0.121	0.225	0.090
	SE	0.007	0.010	0.013	0.009	0.006	0.005	0.017	0.019	0.025	0.012	0.028	0.013	0.013	0.011
rQ_{241}	Mean	0.507	0.514	0.471	0.487	0.441	0.466	0.447	0.418	0.439	0.436	0.450	0.423	0.523	0.413
	SE	0.019	0.009	0.024	0.015	0.020	0.011	0.026	0.013	0.014	0.021	0.014	0.015	0.010	0.017

Table 3.2. Summary of two factor ANOVAs comparing photo-physiological variables of *Pocillopora damicornis* among reefs and between depths in the Whitsunday Islands. For *post hoc* tests, results are presented in ascending order. Abbreviations: R = Repulse Island; L = Lindeman Island; Lo = Long Island; D = Dent Island; Hs = Haslewood Island; H = Hook Island; Dl = Deloraine Island.

Variate	Source of variation	df	MS	*F*	*P*	*Post hoc* tests
(a) rPAR-absorptivity	Location	6	0.0602	7.32	0.0144	
	Depth	1	0.0688	8.36	0.0276	
	Loc x Dep	6	0.0082	4.09	0.0014	Sh: Dl=Hs=D=H<L<Lo=R
	Residual	70	0.002			Dp: Dl=Hs=H=L<D=R=Lo
(b) F_0	Location	6	0.0008	1.73	0.2614	
	Depth	1	0.0019	4.11	0.0890	
	Loc x Dep	6	0.0005	1.48	0.1982	
	Residual	70	0.0003			
(c) F_v/F_m	Location	6	0.0098	3.80	0.0644	
	Depth	1	0.0018	0.69	0.4385	
	Loc x Dep	6	0.0026	6.21	<0.0001	Sh: R=D=Lo=L<H<Dl=Hs
	Residual	70	0.0004			Dp: R=Lo<H=L=D=Hs=Dl
(d) PS_{max}	Location	6	506.18	0.50	0.7916	
	Depth	1	3242.5	3.19	0.1244	
	Loc x Dep	6	1016.9	6.89	<0.0001	Sh: Dl=D=H=L=Hs<R<Lo
	Residual	70	147.56			Dp: R<L=Hs=Lo=H=Dl<Dl
(e) α	Location	6	0.0018	0.89	0.5540	
	Depth	1	0.0032	1.62	0.2502	
	Loc x Dep	6	0.002	1.80	0.1120	
	Residual	70	0.0011			
(f) E_k	Location	6	1229.4	0.18	0.9722	
	Depth	1	10929.2	1.60	0.2531	
	Loc x Dep	6	6840.9	10.81	<0.0001	Sh: Dl<D=H=Hs=L=R<Lo
	Residual	70	632.77			Dp: R=L<Lo=Hs=Dl=D=H
(g) $rNPQ_{241}$	Location	6	0.0221	2.94	0.1075	
	Depth	1	0.0517	6.87	0.0395	
	Loc x Dep	6	0.0075	5.74	0.0001	Sh: R=Lo=L<H= Hs =D=Dl
	Residual	70	0.0013			Dp: R=L=Lo=Dl=Hs<H=D
(h) rQ_{241}	Location	6	0.0097	1.56	0.3017	
	Depth	1	0.0065	1.06	0.3437	Sh: Hs=Lo=D=H=L=R<Dl
	Loc x Dep	6	0.0062	3.53	0.0041	Dp: Dl=D=H=Hs=Lo<L=R
	Residual	70	0.0018			

Table 3.3. Summary of linear models testing relationships between photo-physiological variables of *Pocillopora damicornis* and the water quality index.

Variate	Slope	SE	t	*P*
(a) rPAR-absorptivity				
Shallow	0.0095	0.0012	7.636	<0.0001
Deep	0.0047	0.0008	6.220	<0.0001
(b) F_0				
Shallow	0.0005	0.0005	1.063	0.2939
Deep	0.0005	0.0001	2.507	0.0163
(c) F_v/F_m				
Shallow	-0.0039	0.0005	-7.243	<0.0001
Deep	-0.0021	0.0004	-5.915	<0.0001
(d) PS_{max}				
Shallow	0.8428	0.2911	2.895	0.0061
Deep	-0.6824	0.2447	-2.789	0.0081
(e) α				
Shallow	-0.0005	0.0007	-0.723	0.4736
Deep	0.0003	0.0007	0.394	0.6954
(f) E_k				
Shallow	2.1739	0.6173	3.522	0.0012
Deep	-1.6624	0.5104	-3.257	0.0023
(g) $rNPQ_{241}$				
Shallow	-0.0065	0.0009	-6.868	<0.0001
Deep	-0.0015	0.0007	-2.367	0.0228
(h) rQ_{241}				
Shallow	0.0001	0.0001	0.093	0.9262
Deep	0.0037	0.0008	4.929	<0.0001

3.4 Discussion

This study is the first to demonstrate large-scale spatial variation in the photo-physiology of *Symbiodinium* of the scleractinian coral *Pocillopora damicornis*. The differences observed here were related to an environmental gradient determined previously for the Whitsunday Islands on the GBR (Kleypas 1996; van Woesik et al. 1999). Similar photo-physiological patterns along a water quality gradient have been reported in benthic biofilms in Fiji (Underwood 2002) and along the gradient sampled here (Uthicke 2006). In Chapter 2, it was found that irradiance and water column nutrients co-vary along the environmental gradient. Hence, a WQI was used as an explanatory factor to analyse the photo-physiological variables discussed here. The magnitude of change in the WQI from nearshore to outer islands was mostly attributed to irradiance variables, and to a lesser extent, water column nutrient variables (Chapter 2). It was predicted, therefore, that the photo-physiology of *P. damicornis* along the gradient would conform to known patterns of light/shade acclimatisation (e.g. Warner et al. 2002; Ralph and Gademann 2005; Ulstrup et al. 2006). The patterns of variability of some photo-physiological parameters were, however, explained more by effects of water quality than by irradiance.

3.4.1 Relative PAR-absorptivity

The greater rPAR-absorptivity observed in locations with a high WQI (low irradiance, nutrient-enriched; Fig. 3.6) indicates a more densely pigmented coral tissue layer possibly due to greater density of symbionts and/or concentration of chlorophyll (Ralph et al. 2005). Concentrations of chlorophyll *a* and density of symbionts in *P. damicornis* were strongly related to a WQI in the central GBR with both parameters greater at nearshore than mid-shelf reefs (Chapter 6). Such photo-acclimatory mechanisms have been documented in response to light-limitation (Falkowski and Dubinsky 1981; Dubinsky et al. 1984; Falkowski et al. 1984) and increased nutrient availability (e.g. Hoegh-Guldberg and Smith 1989). The pattern of variation in rPAR-absorptivity found in this study is consistent with photo-acclimatisation to low irradiances and/or elevated nutrient availability at nearshore compared with the outer islands. The variation in PAR-absorptivity invariably also results in differing spectral properties and intensities of the light reaching the symbionts (Kühl et al. 1995; Enriquez et al. 2005). Downward irradiance absorbed would be expected to correlate with the product of symbiont density and cellular pigment content (Falkowski et al. 1984; Stambler and Dubinsky 2005) although multiple scattering by the skeleton enhancing the light field should also be taken into account (Enriquez et al. 2005). The smaller rPAR-absorptivity at the shallow depth thus indicates a higher contribution of diffuse scattered light from the skeleton to the ambient light field of the symbionts, which can be attributed to the higher translucency of the coral tissue.

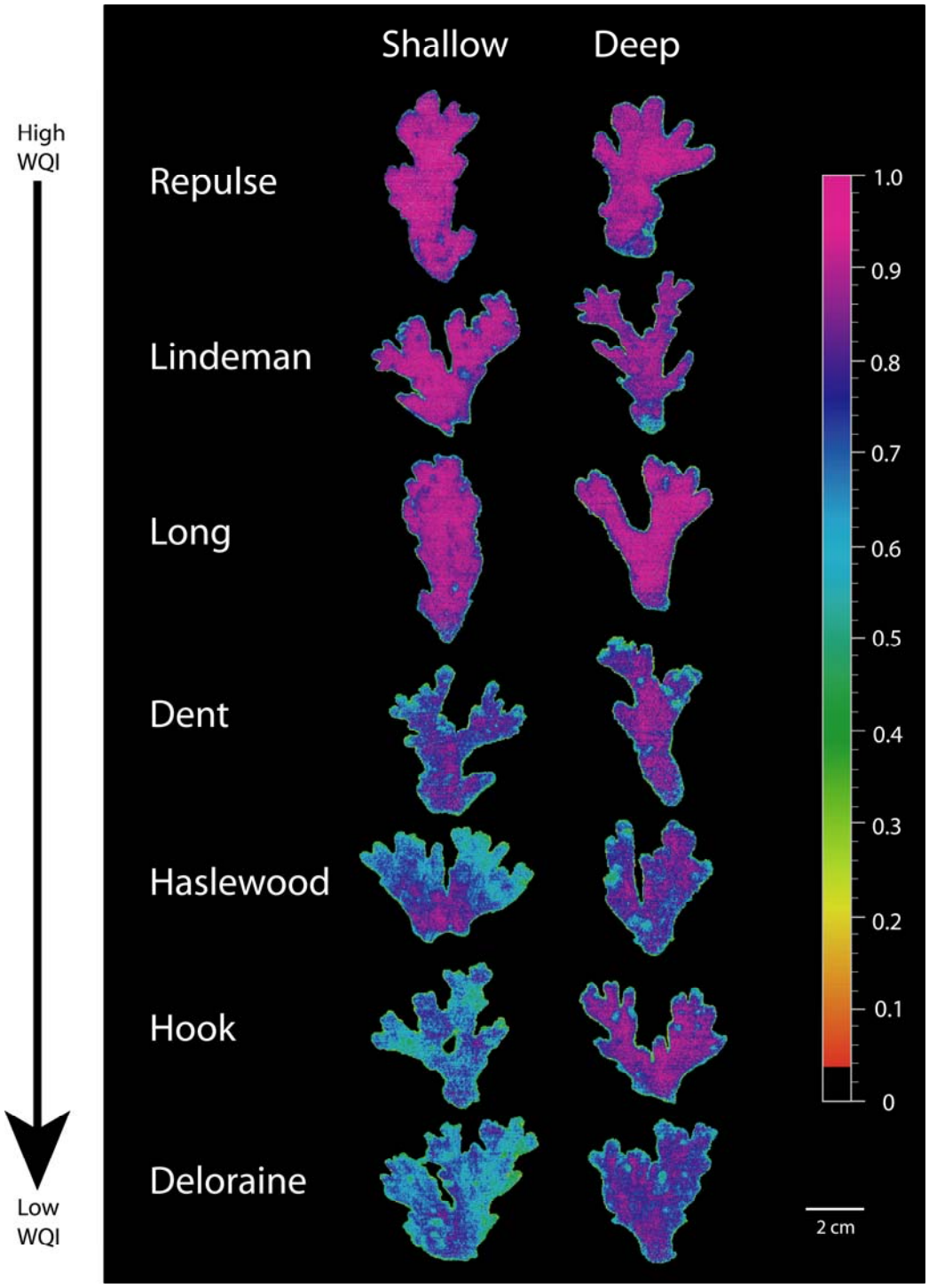

Fig. 3.6. Relative PAR-absorptivity images of *Pocillopora damicornis* collected at shallow (3 m) and deep (6 m) at seven locations along the environmental gradient. Arrow indicates direction of change along the environmental gradient from turbid nearshore (high WQI) to clear-water outer locations (low WQI).

3.4.2 Minimum fluorescence and maximum quantum yield

Minimum fluorescence was characterised by patterns of greater variability along the environmental gradient compared with rPAR-absorptivity. Minimum fluorescence has previously been shown to be an indirect measure of chlorophyll content in benthic biofilms (e.g. Serodio 2003). However, F_0 may be influenced by packaging effects of symbionts in corals (Stambler and Dubinsky 2005; Ulstrup et al. 2006) as chlorophyll *a* fluorescence is likely to be measured from the top layer(s) of symbionts only (Ulstrup et al. 2006). It is possible, therefore, that F_0 was underestimated in the study corals that contained high density of symbionts (as indicated by high rPAR-absorptivity in nearshore locations).

The increase in F_v/F_m along the gradient from nearshore to the outer islands, suggests that photosynthetic efficiency of PSII was inhibited at nearshore compared with the outer islands. Previous studies conducted over micro-scales (i.e. coenosarc vs. polyp; Ralph et al. 2002; Ulstrup et al. 2006) and depth gradients (Warner et al. 2002) have shown greater F_v/F_m in low-irradiance habitats than in high-irradiance habitats. However, F_v/F_m has been shown to be lower at very low irradiances in caves (i.e. maximum 10 – 40 µmol photons m^{-2} s^{-1}) than in open habitats, which was suggested as a photo-acclimatory mechanism for colonising low-irradiance environments (Anthony and Hoegh-Guldberg 2003). Decreases in F_v/F_m, however, may also be due to sedimentation stress. Philipp and Fabricius (2003) reported a rapid (12 h) decline in F_v/F_m in corals exposed to ~150 mg cm^{-2} of sediment. Similarly, Weber et al. (2006) reported a decline in F_v/F_m in corals exposed to nutrient-rich silts, with some capacity for recovery, whereas F_v/F_m did not change when corals were exposed to nutrient-poor sediments. The greater decrease in F_v/F_m exposed to nutrient-rich silts was most likely due to elevated bacterial hydrogen sulphide production and anoxic conditions at the sediment-tissue interface (Weber et al. 2006). Finally, F_v/F_m has also been shown to decrease in corals subjected to herbicides such as diuron (Negri et al. 2005). Although nearshore reefs in the Whitsunday Islands were characterised by reduced irradiance compared with outer islands, the maximum irradiance intensity at the nearshore deep depth during the sampling period ranged from 220 – 636 µmol photons m^{-2} s^{-1}, which is unlikely to result in light limitation and hence down-regulation of photosynthesis. Rather, the observed reductions in F_v/F_m in locations with a high WQI were more likely due to sedimentation and/or pollutant stress rather than a photo-acclimatory mechanism to low irradiance.

3.4.3 Rapid light curves

The interaction detected among locations and between depths for PS_{max} and E_k indicated photo-physiological plasticity to variable conditions of water quality. At the deep depth, corals conformed to typical predictions of photo-acclimatisation to high (outer islands) and low (nearshore islands) irradiances where PS_{max} and E_k increased with improved water quality from

nearshore to outer islands. Similarly, Anthony and Hoegh-Guldberg (2003) found lower relative electron transport rate ($rETR_{max}$, where $rETR = \Delta F/F_m' \times PAR$) and E_k in corals from low-irradiance habitats compared with open habitats. In contrast, shallow corals showed a decline in PS_{max} and E_k with improving water quality (low WQI) indicative of photo-inhibition at the outer islands. Previous studies conducted at micro-scales have shown that coenosarc tissue may have higher $rETR_{max}$ compared to an adjacent polyp (Ralph et al. 2002; Ulstrup et al. 2006) due to the coenosarc generally being directly light-exposed, whilst the polyp is shade-acclimatised (Jokiel and Morrissey 1986; Ralph et al. 2002) but see Hill et al. (2004). In this study, shallow corals appeared to have been photosynthetically down-regulated possibly by a reduction in active PSII reaction centres (Gorbunov et al. 2001) at locations with low WQI, which is also supported by their higher $rNPQ_{241}$ (see discussion below on NPQ). Possible mitigating effects of nutrients on the photo-physiology, as found for phytoplankton under light stress (Longhi et al. 2006), may explain the lack of down-regulation of photosynthesis (PS_{max}) and low $rNPQ_{241}$ in shallow nearshore corals. Interestingly, Uthicke (2006) found no differences in $rETR_{max}$ but an increase in E_k in benthic biofilms along the same gradient studied here. The finding of an increase in E_k in *Symbiodinium* along the same environmental gradient (at the deep depth) thus suggests that photo-acclimatisation to low irradiances can occur within different components of coral reef ecosystems.

3.4.4 Relative non-photochemical quenching and relative excitation pressure

The increase in $rNPQ_{241}$ at the shallow depth with improving water quality (low WQI) along the gradient from nearshore to outer islands suggests that *Symbiodinium* have adjusted to higher irradiances at the outer islands by developing an efficient mechanism for excess energy dissipation. Shallow corals along the gradient showed similar rQ_{241} as indicated by the slope of the relationship between rQ_{241} and the WQI not being significantly different from zero. This suggests that the relative proportion of photochemical and non-photochemical mechanisms remained stable along the environmental gradient. In contrast, deep corals showed less affinity for excess energy dissipation (NPQ) at the outer islands (low WQI) in relation to shallow corals partly reflecting their lower light regime. However, the combination of relatively low $rNPQ_{241}$ and elevated rQ_{241} in deep corals where water quality was low (high WQI) suggests partial reduction of, and/or damage to, primary PSII acceptors. It is unlikely that this would have been induced by irradiance as these deeper corals were exposed to low to moderate illumination (no greater than 636 µmol photons m^{-2} s^{-1}) during the study. Environmental parameters other than irradiance, such as sedimentation and/or pollutants, may have contributed to the reduction of, and/or damage to, primary PSII acceptors.

The contrasting pattern observed between shallow and deep corals for PS_{max} and E_k suggested different mechanisms of photo-acclimatisation. Deep corals conformed to typical patterns of

light/shade acclimatisation (e.g. Warner et al. 2002; Ralph and Gademann 2005; Ulstrup et al. 2006) suggesting light-limitation on nearshore reefs. Moreover, consistency between patterns of variation of E_k along the environmental gradient studied here for both biofilms (Uthicke 2006) and corals at the deep depth suggests that photo-acclimatisation can occur within different components of coral reef ecosystems. In contrast, shallow corals exhibited reduced PS_{max} and E_k as well as greater heat dissipation with improving water quality at the outer islands. The significance of the capacity to dissipate excess heat to reduce the effects of photo-inhibition as well as excitation pressure over PSII of shallow corals on coastal reefs thus requires further investigation. This study examined photo-physiological responses of a coastal coral along a large-scale environmental gradient that is regulated by variation in a range of factors such as nutrient availability, light attenuation and turbidity (Chapter 2) as well as other potential factors including sedimentation and exposure to herbicides and pesticides. Since many of these parameters are known to co-vary with each other under field conditions, it has not been possible to attribute causality of photo-physiological differences to any particular component of water quality, e.g. irradiance, nutrient availability, pollutants. Controlled experiments manipulating different components of water quality are required to determine the relative contribution of these stressors to changes in coral photo-physiology. Moreover, using corals sampled from various locations along the gradient for such experiments would provide valuable insight to contrasting photo-acclimatory strategies that allow corals to persist in variable environmental conditions such as those occurring on coastal coral reefs.

Chapter 4.0 Relationship among coral reflectance, chlorophyll *a* concentration and perceived brightness of scleractinian corals

4.1 Introduction

The colour of scleractinian corals is determined by photosynthetic pigments contained in the algal endosymbionts (*Symbiodinium*), endolithic algae (Fine and Loya 2002; Ralph et al. 2007) and light absorbing compounds in the coral tissue (Dove et al. 2001). The main pigments of the symbionts include chlorophyll *a* and accessory pigments such as chlorophyll c_2, peridinin, xanthophylls and carotenes including β-carotene (Jeffrey and Haxo 1968). The light absorbing compounds of the coral host include green fluorescent proteins (GFPs) that have fluorescent properties also capable of producing the bright colours observed in corals (Lukyanov et al. 2000; Salih et al. 2000; Mazel and Fuchs 2003). Light is a key resource for corals (Barnes and Chalker 1990; Muscatine 1990) yet irradiance and spectral quality on a coral reef are highly variable and depend on factors including depth, reef topography and turbidity (Larcombe et al. 1995; Anthony and Hoegh-Guldberg 2003b; Anthony et al. 2004). Corals may photo-acclimatise over days to weeks to changes in irradiance by modulating the density of symbionts and/or the concentration of photosynthetic pigments within the symbionts (Falkowski and Dubinsky 1981; Dubinsky et al. 1984; McCloskey and Muscatine 1984; Porter et al. 1984). Photo-protective processes such as xanthophyll cycling may also result in changes in pigment concentration on time-scales of hours (Brown et al. 1999a). Pigment concentrations may also change in response to changing seawater nutrient availability (e.g. Hoegh-Guldberg and Smith 1989), seawater temperatures (Glynn 1991; Hoegh-Guldberg 1999), or salinity (Kerswell and Jones 2003). Given that photo-acclimatisation can occur on timescales of days to weeks (Anthony and Hoegh-Guldberg 2003a), changes in the concentrations of photosynthetic pigments within corals, and hence changes in their colour brightness, have been suggested as an appropriate bioindicator of environmental condition (Marubini 1996). This study was directed at coral specimens where photosynthetic pigments were the dominant determinants of colour brightness.

Coral brightness measured using a 'Coral Health Monitoring Chart' has been suggested as a simple method to assess coral health (Siebeck et al. 2006). The chart was developed primarily for monitoring of coral bleaching events. It is based on the principle that a decrease in colour brightness is the result of a decrease in symbiont density and chlorophyll *a* concentration. Validation of the colour chart found significant positive relationships between symbiont density and concentrations of chlorophyll *a* with the colour score of *Acropora* spp. Siebeck et al. (2006). It is not known whether the same relationships exist between coral reflectance and the colour scores since reflectance spectrometry was not a component of the validation of the colour chart (Siebeck et al. 2006).

Several studies have examined the relationship between pigmentation and optical properties of corals to determine if the condition of coral reefs could be monitored using remote sensing

techniques. For example, Joyce and Phinn (2003) examined the relationship between spectral reflectance and different coral reef substrata, including two species of the massive coral *Porites* and found variable relationships between coral reflectance and concentrations of pigment, highlighting the difficulties associated with *in situ* coral reflectance measurements carried out under variable illumination conditions. The compilation of an extensive dataset of *in situ* coral reflectance measurements (>5,000 spectra from 195 species) allowed Hochberg et al. (2004) to characterise two basic modes of coral reflectance: 'brown-mode' coral reflectance resulting from absorption of pigments contained in the zooxanthellae; and 'blue-mode' coral reflectance from absorption by non-fluorescing host pigments. Recently, Hochberg et al. (2006) developed a model that allowed the prediction of photosynthetic pigment concentrations from reflectance spectra using predominately *Porites*. These studies highlight the utility of high-resolution reflectance spectrometry as a non-destructive method to characterise the optical properties of corals, which have the added advantage of being performed by aerial surveys and/or satellites to potentially provide the temporal and spatial coverage unattainable with *in situ* coral reef health monitoring. However, for imaging spectrometry to be useful as a tool for monitoring changes of coral chlorophyll concentrations due to environmental perturbations, a better understanding of the extent of the inter-species variability between coral reflectance and concentrations of the coral pigment chlorophyll *a* is required, as is knowledge of any angular dependencies of the reflected signal that may exist due to morphology (e.g. bidirectional reflectance distribution function, BRDF; Joyce and Phinn 2002).

The aims of this study were to (1) investigate the potential of reflectance spectrometry as a new tool in the rapid quantitation of chlorophyll *a* in scleractinian corals; and (2) assess the inter-species variability between coral reflectance, the concentration of the coral pigment chlorophyll *a* and the colour chart (Siebeck et al. 2006) for a range of coral species with different morphologies. For the purposes of this study, colour brightness was defined as the amplitude of the reflectance spectrum at a local chlorophyll *a* absorption maxima wavelength at 675 nm.

4.2 Materials and methods

Corals were sampled from the Whitsunday Islands (20°00' – 20°30' S, 148°45' – 149°15' E) in the central Great Barrier Reef (GBR). To examine the relationship between coral reflectance, the concentration of chlorophyll *a* and the colour chart, and determine the effect of differing morphologies on coral reflectance, a range of different species were sampled. These included the branching corals *Acropora millepora* (*n*=12), *Pocillopora damicornis* (*n*=10) and *Stylophora pistillata* (*n*=14), the foliaceous *Turbinaria reniformis* (*n*=12) and the massive coral *Porites lobata* (*n*=92). Apical branches (~8 cm long) of the branching corals, as well as flat pieces of the foliaceous coral, were collected with a small hammer and chisel, whereas nubbins from *P. lobata*

(21 mm diameter x approximately 30 mm length) were sampled using a pneumatic drill with a 25 mm diameter hole-saw attachment. An acrylic drilling guide was used to minimise damage to the colony and the core tissue. Following collection, all nubbins were placed immediately into holding tanks with flow-through seawater and their reflectance spectra were measured within 1 h of collection. In the laboratory and prior to the reflectance measurements, all corals were assigned a colour score from 1 to 6 using the colour reference card and the procedures described by Siebeck et al. (2006) whereby measurements were carried out ~2 cm from the tip of each sample. All samples were frozen in liquid nitrogen prior to pigment extraction in the laboratory.

4.2.1 Reflectance measurements

Reflectance spectra were measured in a purpose-built chamber to provide a controlled illumination field (Fig. 4.1). Inside the chamber, two x 50-watt quartz spectrophotometer halogen bulbs were mounted approximately 45° and 10° from the zenith. The surfaces of the chamber were finished with matt black paint as a precaution to reduce specular reflection off the internal surfaces and to decrease stray light contamination. Reflectance measurements were conducted using a USB 2000 fibre optic spectrometer (Ocean Optics Inc. Florida, USA), acquiring dark current corrected spectra from approximately 400 nm to 930 nm. A tube collimated quartz fibre optic probe directed the light reflected from the sample into the SMA fibre optic entrance of the USB 2000. The view angle of the fibre optic was fixed at approximately 5 degrees off nadir. The detector integration time was chosen to maximise the signal to noise ratio of the resultant measurement. For each sample, three different illumination conditions were used to test hypotheses about the effects of shadows due to coral morphology on coral reflectance. The distances between sample and detector varied from ~4 cm to ~6 cm using an adjustable platform, which due to the 9 degree sensor field of view (half angle), represented a coral cross section diameter ranging from approximately 1 to 2 cm in diameter. At no time did the sensor view area exceed the coral cross-sectional area. Each reflectance measurement used for analysis was determined by first calculating a mean reflectance spectrum from 10 to 30 replicate spectra for each sample at each illumination angle. Thus for each sample, three reflectance measurements were recorded corresponding to a side angle (45º lamp illuminated, top lamp off), top angle (10º lamp illuminated, side lamp off) and a measurement when both lamps were illuminated.

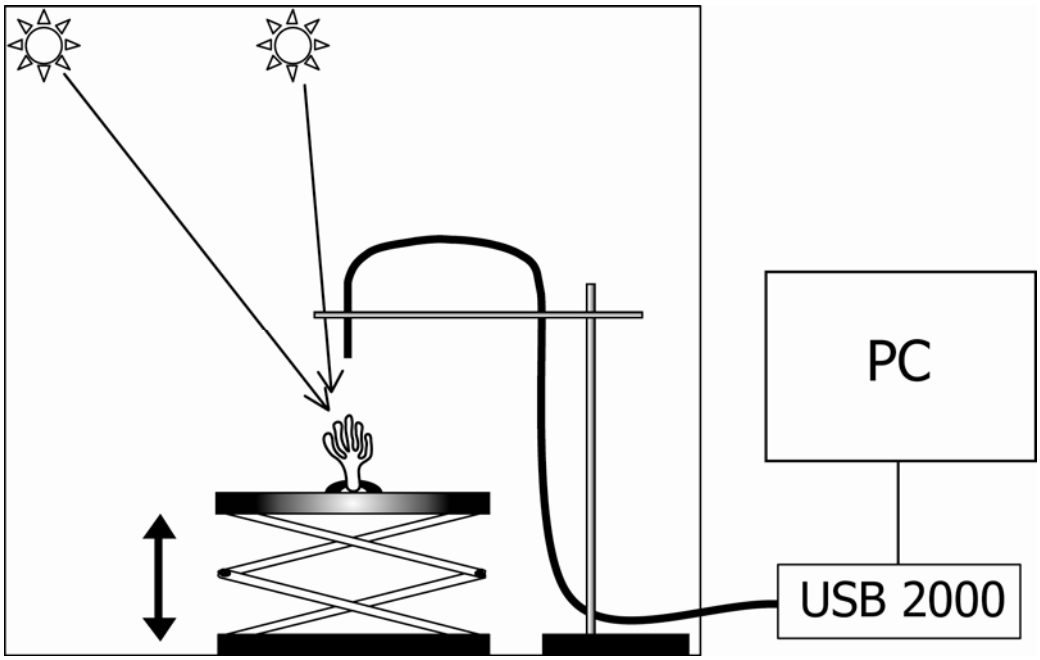

Fig. 4.1. Diagrammatic representation of the coral reflectance measuring chamber. A piece of coral is placed on an adjustable platform and positioned near the detector. A fibre optic cable connects to an Ocean Optics USB 2000 spectrometer, which is connected to a computer.

The USB2000 detector's linearity with integration time was verified for three different brightness targets (brown, grey and a Spectralon SRM-99 99 % Reflectance Standard; Labsphere, New Hampshire, USA). Reflectance from the Spectralon plaque was measured inside the reflectance chamber at 5 different heights for each illumination condition. For each wavelength and illumination condition, the light field counts vs. height measurements were fitted with a log-square model of the form:

$$counts = a_0 + a_1\log(H) + a_2\log(H)^2 \qquad (1)$$

where a_0, a_1 and a_2 are model fit coefficients and H is the sample height. The log-square model was then used to generate an appropriate reference spectrum given the sample height, illumination condition and detector integration time. The spectral log-square model retrieved the Spectralon characterisation reflectance measurements to within 1% through the wavelength region of 400 to 930 nm. This model was then used to normalise each USB2000 coral sample count according to its actual sample height, integration time and illumination condition, to convert the coral count measurements into a percentage reflectance measurement.

To verify that sampling time did not affect the reflectance of the coral, and to verify the temporal stability of the lamps used for illumination, two separate corals were exposed to full illumination for 15 min and a time series of un-averaged reflectance measurements were made. The 15 min

period was approximately 3 times the duration to perform measurements of the illumination combinations. No changes were observed in the reflectance at 675 nm.

4.2.2 Determination of chlorophyll *a*

Following reflectance measurements, each coral sample was placed into a small plastic bag with filtered (0.2 μm) seawater and tissue was stripped from the skeleton with an airbrush, a method that does not allow extraction of endolithic algae within the coral skeletons. The resulting tissue slurry was homogenised for 30 s using a tissue grinder and the total volume recorded. A 5 ml sub-sample of the slurry was centrifuged at 3,500 g for 10 min at 4°C. The supernatant was discarded and chlorophyll *a* extracted from the pellet with a double extraction using 100% acetone in darkness at -20°C for 24 h each. The optical properties of the combined extracts for each sample were measured at 630 nm and 663 nm using a Shimadzu UV-1700 Spectrophotometer (Shimadzu Corporation, Kyoto, Japan). Chlorophyll *a* was determined using the formula from Jeffrey and Humphrey (1975) after correction for the volume of the homogenate and solvent. Concentrations were then normalised to coral surface area determined by wax dipping (Stimson and Kinzie 1991).

4.2.3 Statistical analyses

Linear models were used to test the relationships between coral reflectance, the concentration of chlorophyll *a* and the colour chart. Additional linear models were also used to examine the effects of shadows due to coral morphology on coral reflectance by using thee different illumination angles within the reflectance chamber, and to examine the relationship between coral reflectance (R_{675}) and concentrations of chlorophyll *a* (μg cm^{-2}) for each species. To determine the inter-species variability between coral reflectance and concentration of chlorophyll *a*, analyses of covariance (ANCOVA) were conducted. Tests of the assumption of homogeneity of variances were performed prior to the analyses. Statistical analyses were done using the statistical software R (R Development Core Team 2006).

4.3 Results

In total, 140 coral nubbins of a range of colour brightness (determined by the colour chart) were collected for analysis of reflectance spectra and concentration of chlorophyll *a*. Averaged over all taxa, lightly pigmented corals (colour score 1) reflected approximately 10 times more light compared with darker corals (colour score 6) (side angle: 45.5 ± 5.5% versus 4.5 ± 0.5% (mean ± SE; Fig. 4.2a). There was a significant relationship between reflectance and the colour score ($F_{1,139} = 118.4$, $P < 0.0001$; Table 4.1a) and the model explained 40% of the variance between these two parameters in all species combined. For individual species, the model explained approximately 91% of the variance between reflectance and the colour score in

P. damicornis, followed by *A. millepora* (89%), *T. reniformis* (80%), *S. pistillata* (72%) and *P. lobata* (25%) (Table 4.1a, Fig. 4.2a). The overall pattern of chlorophyll *a* concentration in relation to colour score was inverse to that described for reflectance. Corals that were assigned a colour score of 6 had approximately 26 times more chlorophyll *a* cm^{-2} compared with lighter coloured corals with a colour score of 1 (20.8 ± 3.0 μg cm^{-2} versus 0.8 ± 0.5 μg cm^{-2} (mean ± SE); Fig. 4.2b). There was a significant relationship between concentration of chlorophyll *a* and the colour score ($F_{1,139} = 188.9$, $P < 0.0001$; Table 4.1b) and the overall model explained 57% of the variance between these two parameters across all species examined. For individual species, the model explained approximately 93% of the variance between chlorophyll *a* concentration and the colour score in *P. damicornis*, followed by *A. millepora* (89%), *T. reniformis* (87%), *S. pistillata* (83%) and *P. lobata* (44%) (Table 4.1b, Fig. 4.2b).

Comparisons of the relationship between reflectance (R_{675}) and illumination angle showed that coral morphology had some influence on coral reflectance of *P. damicornis* ($F_{2,2} = 31.13$, $P = 0.0311$; Table 4.2) but not the other species (Table 4.2). Since illumination angle had a significant effect on coral reflectance in *P. damicornis*, subsequent analyses used coral reflectance values determined for corals subject to full illumination, i.e. both lamps on. There were significant relationships between coral reflectance and concentration of chlorophyll *a* for all species (Table 4.3). The linear model explained approximately 81% of the variance between coral reflectance and chlorophyll *a* concentration in *S. pistillata*, followed by *P. damicornis* (80%), *A. millepora* (77%), *T. reniformis* (65%) and *P. lobata* (27%) (Table 4.3). ANCOVA showed that reflectance varied inconsistently among species and with concentrations of chlorophyll *a* (Table 4.4a) and that there were differences in the intercepts of the slopes (Table 4.4b, Fig. 4.3).

Table 4.1. Summary of linear models testing relationships between (a) coral reflectance % ($R_{675\ nm}$) and (b) concentrations of chlorophyll *a* (log_2 transformed, μg cm^{-2}), with the colour chart for all species.

Species	r^2	Slope	SE	t	*P*
(a) $R_{675\ nm}$ (%)					
All taxa	0.46	-0.470	0.043	-10.88	<0.0001
Acropora millepora	0.76	-0.448	0.077	-5.83	0.0001
Pocillopora damicornis	0.93	-0.698	0.069	-10.05	<0.0001
Stylophora pistillata	0.93	-0.673	0.055	-12.27	<0.0001
Turbinaria reniformis	0.88	-0.913	0.108	-8.43	<0.0001
Porites lobata	0.24	-0.298	0.056	-5.31	<0.0001
(b) Chlorophyll *a* (μg cm^{-2})					
All taxa	0.58	0.658	0.048	13.74	<0.0001
Acropora millepora	0.89	0.598	0.063	9.50	<0.0001
Pocillopora damicornis	0.93	0.886	0.085	10.42	<0.0001
Stylophora pistillata	0.83	1.030	0.134	7.69	<0.0001
Turbinaria reniformis	0.87	0.870	0.108	8.10	<0.0001
Porites lobata	0.44	0.420	0.050	8.43	<0.0001

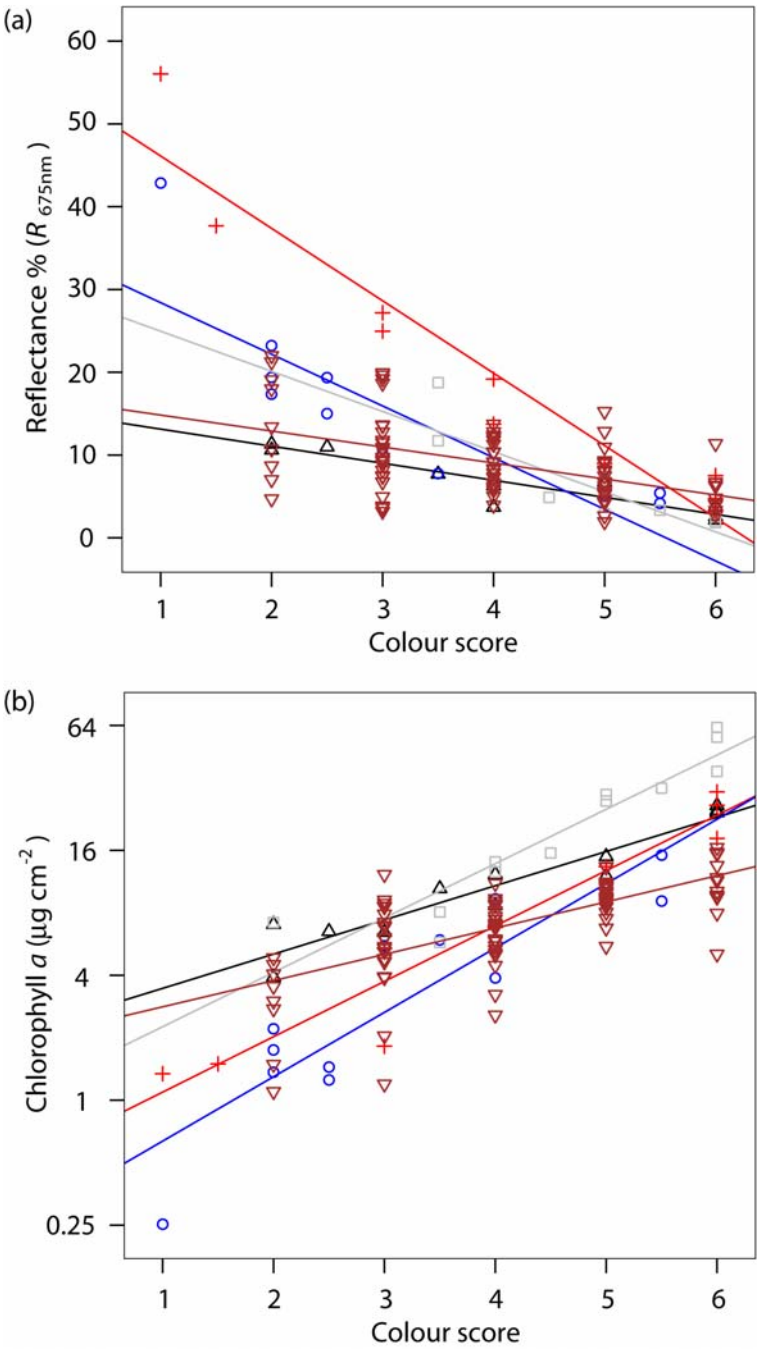

Fig. 4.2. Relationship between (a) coral reflectance % ($R_{675\ nm}$) and (b) the concentration of chlorophyll *a* ($\log_2$ transformed, µg cm^{-2}), and the colour chart for *Acropora millepora* (black △), *Pocillopora damicornis* (red +), *Stylophora pistillata* (blue ○), *Turbinaria reniformis* (grey □) and *Porites lobata* (brown ▽).

Table 4.2. Summary of analyses comparing the influence of shadows due to coral morphology produced by differing illumination angles on coral reflectance.

Variate	Source of variation	df	MS	*F*	*P*
(a) *Acropora millepora*	Chlorophyll *a*	1	0.0302	61.34	<0.0001
	Angle	2	0.0004	13.73	0.0679
	Chl *a* x Angle	2	0.0000	0.05	0.9479
	Residual	33	0.0005		
(b) *Pocillopora damicornis*	Chlorophyll *a*	1	0.4742	33.40	<0.0001
	Angle	2	0.0047	31.13	0.0311
	Chl *a* x Angle	2	0.0002	0.01	0.9893
	Residual	24	0.0142		
(c) *Stylophora pistillata*	Chlorophyll *a*	1	0.1892	33.64	<0.0001
	Angle	2	0.0001	0.14	0.8809
	Chl *a* x Angle	2	0.0011	0.19	0.8283
	Residual	36	0.0056		
(d) *Turbinaria reniformis*	Chlorophyll *a*	1	0.0711	28.59	<0.0001
	Angle	2	0.0001	9.00	0.1000
	Chl *a* x Angle	2	0.0000	0.01	0.9950
	Residual	30	0.0025		
(e) *Porites lobata*	Chlorophyll *a*	1	0.1222	74.53	<0.0001
	Angle	2	0.0001	0.53	0.6552
	Chl *a* x Angle	2	0.0002	0.12	0.8883
	Residual	270	0.0016		

Table 4.3. Summary of linear models testing relationships between coral reflectance % ($R_{675\ nm}$) and concentrations of chlorophyll *a* ($\log_2$ transformed, μg cm^{-2}) among different coral species.

Species	r^2	Slope	SE	t	*P*
Acropora millepora	0.77	-3.756	0.609	-6.17	0.0001
Pocillopora damicornis	0.80	-9.459	1.551	-6.10	0.0003
Stylophora pistillata	0.81	-5.356	0.717	-7.47	<0.0001
Turbinaria reniformis	0.65	-4.787	1.040	-4.61	0.0010
Porites lobata	0.27	-3.208	0.542	-5.92	<0.0001

Table 4.4. Summary of analyses comparing (a) homogeneity of slopes and (b) differences among intercepts of the relationship between coral reflectance % ($R_{675\ nm}$) and concentrations of chlorophyll *a* (log_2 transformed, μg cm^{-2}) among different coral species.

Source of variation	df	MS	*F*	*P*
(a) ANOVA testing for homogeneity of slopes				
Species	4	429.99	24.60	<0.0001
Chlorophyll *a*	1	2587.19	147.99	<0.0001
Species x Chlorophyll *a*	4	172.15	9.85	<0.0001
Residual	130	17.15		
(b) ANCOVA testing for differences among intercepts				
Species	4	3611.82	20.33	<0.0001
Chlorophyll *a*	1	449.26	163.43	<0.0001
Residual	134	22.10		

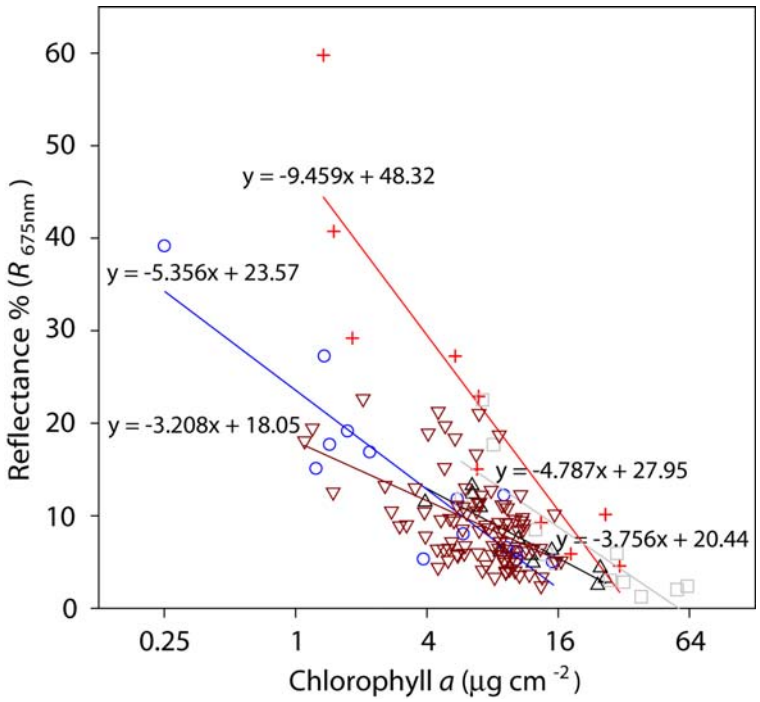

Fig. 4.3. Relationship between coral reflectance % ($R_{675\ nm}$) and concentrations of chlorophyll *a* (log_2 transformed, μg cm^{-2}). Symbols: *Acropora millepora* (black △), *Pocillopora damicornis* (red +), *Stylophora pistillata* (blue ○), *Turbinaria reniformis* (grey □) and *Porites lobata* (brown ▽).

4.4 Discussion

This study has demonstrated that coral brightness can be quantified using reflectance spectrometry and that this relationship can be mostly explained by the concentration of chlorophyll *a* in their symbionts, although differences in coral morphology have some influence on coral reflectance. Corals may change their colour brightness in response to light availability, contaminants, altered regimes of salinity and temperature (reviewed by Hoegh-Guldberg 1999), concentrations of nutrients (Hoegh-Guldberg and Smith 1989; Stambler et al. 1991) and sedimentation (Nugues and Roberts 2003). On this basis, alterations in coral brightness are considered to be symptomatic of changes in the environment. Several studies have investigated the potential of using coral colour as an indicator of coral health. Kizner et al. (1995) analysed photographic slides and found a significant positive relationship between concentrations of chlorophyll *a* and the colour intensity of corals exposed to nutrients. Joyce and Phinn (2003) found a variable relationship between chlorophyll *a* concentration and reflectance in massive *Porites*. Using predominately massive *Porites*, Hochberg et al. (2006) developed models that could be used to predict the concentrations of a range of photopigments in corals from optical reflectance spectra collected via satellite. The results presented here are consistent with those of Hochberg et al. (2004, 2006) and by using a range of coral species with branching, massive and foliaceous morphologies, suggest that reflectance spectrometry has broad applications in experiments and monitoring programmes where colour brightness in corals need to be quantified. Importantly, significant relationships between coral reflectance and concentrations of chlorophyll *a* for all study species in a controlled illumination environment demonstrate the potential of reflectance spectrometry as a new tool for the rapid quantitation of chlorophyll *a* in corals.

Variation of coral reflectance (R_{675}) at different illumination angles showed coral morphology influenced reflectance for one of the species in this study (*P. damicornis*). Joyce and Phinn (2002) found that viewing angle is a significant control on coral reflectance as reported reflectance variance across different viewing angles was lower for corals with a tabular than branching morphology. Thus, understanding BRDF of corals is important as differences in illumination angles (particularly side angles) will have contrasting effects on the distribution of shadows across the surface of the coral that influence measured coral reflectance. *P. damicornis* has a branching growth form that generally forms small clumps (Veron 2000) although the growth form in this species shows great variation depending on physical environmental factors such as wave exposure (Veron 1995). In *P. damicornis*, the reflectance under the side angle illumination was lower than when illuminated from the top, or when both lamps were illuminated, indicating that the side angle was casting shadows over the surface, and/or increasing internal shadowing of the nubbins, and thus decreasing coral reflectance. However, no significant differences due to illumination angle were detected for the other branching corals, which may have been a function of nubbin

morphology. The *A. millepora* and *S. pistillata* nubbins typically had ~6 and ~3 branches, respectively. Thus, the sample nubbins may not have been large enough to significantly alter the degree of internal shadowing in these species. Nevertheless, the result for *P. damicornis* was consistent with Joyce and Phinn (2002) and highlights the importance of accounting for BRDF in studies of reflectance spectrometry to characterise the optical properties of corals.

Heterogeneous distribution of symbionts may also influence coral reflectance. Previous studies have shown that photosynthetic activity may differ between polyp and coenosarc tissue possibly due to greater symbiont densities in polyp tissues (Ulstrup et al. 2006b). *P. lobata* has small, compacted corallites with very little coenosarc tissue (Veron 2000). It is, therefore, unlikely that small-scale spatial differences in the distribution of photosynthetic pigments could explain the variable relationship between chlorophyll *a* concentration and coral reflectance for *P. lobata*. In contrast, *T. reniformis* has large areas of coenosarc tissue (~10 mm) between the widely spaced conical corallites. A heterogeneous distribution of symbionts may have contributed to the variable relationship ($r^2 = 0.65$) between coral reflectance and concentration of chlorophyll *a* observed in *T. reniformis* if the field of view of the detector was occupied by either coenosarc or polyp tissue and not integrating over both tissue types. Further, a heterogeneous distribution of symbionts could also result in a reduction of the light field of certain wavelengths due to a reduction in multiple scattering by the skeleton (Enriquez et al. 2005). As a consequence, coral reflectance would be reduced relative to the amount of chlorophyll *a* occurring in *T. reniformis*. Any heterogeneous distribution of symbionts may thus influence coral reflectance and careful consideration should be given to species selection in studies of coral reflectance.

The recognition that changes in coral brightness can provide an indicator of environmental conditions highlights the potential use of remote sensing to monitor the status of coral reefs (Myers et al. 1999). An understanding of the relationships between coral reef reflectance and the factors influencing light absorption is required for the successful application of remote sensing tools to monitor the condition of coral reefs (Joyce and Phinn 2003). Recent studies have highlighted inherent problems of measuring coral reflectance. For example, Joyce and Phinn (2003) found a variable relationship (r^2=0.10) between *in situ* reflectance measurements and chlorophyll *a* concentration in *Porites.* Here, there were significant relationships between concentrations of chlorophyll *a* and coral reflectance for all species when placed in an environment with a controlled light field: *S. pistillata* ($r^2 = 0.81$), *P. damicornis* ($r^2 = 0.80$), *A. millepora* ($R^2 = 0.77$), *T. reniformis* ($r^2 = 0.65$) but also a variable relationship ($r^2 = 0.27$) for measurements on *P. lobata.* Interestingly, the correlations were strong for those species where morphology was expected to have some influence on coral reflectance (i.e. the branching corals), while in the massive coral, where reflectance was expected to be less influenced by factors such as

BRDF, the correlation between coral reflectance and chlorophyll *a* concentration was poor (*sensu* Joyce and Phinn 2003). The consistency between the results of this study and those of Joyce and Phinn (2003) suggest the poor correlation between these factors for massive *Porites* may be due to some feature of the study species and not the measurement technique. A possible explanation for this may have been due to a 'packaging effect' of the symbionts, which occurs when the amount of light reflected (and re-emitted) decreases for symbionts packed into multiple layers beneath the coral surface (Stambler and Dubinsky 2005). Based on a symbiont diameter of 10 µm, approximately 1.0 x 10^6 symbionts could theoretically occur as a single layer per cm^2 of coral surface. The density of symbionts in massive *Porites* can range from approximately 0.9 x 10^6 cells cm^{-2} (pale colonies) to 3.4 x 10^6 cells cm^{-2} (dark colonies) (Chapter 5). Assuming a homogeneous distribution of chlorophyll *a* content throughout the symbiont layer, more chlorophyll *a* would be extracted from the coral than expected from reflectance spectrometry for corals where symbionts are stacked into multiple layers. Thus, a packaging effect of the symbionts may in part explain the variable relationship between chlorophyll *a* concentration and coral reflectance observed here for *P. lobata* and previous studies (e.g. Joyce and Phinn 2003).

Through the use of reflectance spectrometry, this study has provided further validation of a colour chart as a monitoring tool (Siebeck et al. 2006) by demonstrating significant relationships exist between coral reflectance and the colour score for a range of coral species. Interestingly, there were differences in the chlorophyll *a* concentration and colour score relationship between the two studies. Siebeck et al. (2006) found a significant, but variable ($r^2 = 0.39$), linear relationship between concentrations of chlorophyll *a* and the colour scores of *Acropora* spp. In contrast, the relationship between chlorophyll *a* concentration and the colour score was strong for all species examined in this study (with the exception of *P. lobata*), while the analyses suggested a logarithmic relationship exists between these parameters. Saturation of the colour score relationship at high concentrations of chlorophyll *a* (Siebeck et al. 2006), or a heterogeneous distribution of symbionts (Ralph et al. 2005), may explain this is discrepancy. For example, photo-acclimatisation of symbionts occurring deep in the tissue layer to sub-saturation irradiances (Ralph et al. 2005) by increases in concentrations of chlorophyll *a* would contribute to variation between these parameters particularly among the darker categories on the colour chart. Whilst patterns of spatial heterogeneity of photosynthetic pigments between coenosarc and polyp tissue horizontally across the coral surface have been reported (e.g. Ralph et al. 2005; Ulstrup et al. 2006b), the possibility that photosynthetic pigments vary spatially in a vertical distribution though the tissue layer requires further investigation.

In conclusion, the ability to quantify the brightness of coral colour represents a step forward in the search for 'early warning' bioindicators for use in monitoring programmes aiming to assess the

condition of coral reefs. Coral brightness can be quantified through the use of colour charts developed by Siebeck et al. (2006) as well as reflectance spectrometry. The colour charts are appealing as monitoring tools as they can be used by a range of personnel (including non-specialists), they are non-invasive and cost effective. Given that nutrient enrichment and light limitation also result in the change of chlorophyll *a* concentration (e.g. Falkowski and Dubinsky 1981; Dubinsky et al. 1984; Porter et al. 1984; Hoegh-Guldberg and Smith 1989) and thus likely also of coral reflectance, the colour chart may have applications beyond monitoring the effects of bleaching events (e.g. Fabricius 2006; Frisch et al. 2007). Reflectance spectrometry represents a potential new tool for the rapid and non-destructive quantitation of chlorophyll *a* in corals. Significant relationships occurred between coral reflectance and concentrations of chlorophyll *a* for corals sampled in a controlled illumination field, i.e. a purpose built chamber, and it should be possible to achieve comparable results with reflectance spectrometry *in situ* once issues associated with the variable illumination conditions have been addressed. The consequences of bidirectional reflectance distribution (BRDF), heterogeneous distribution of symbionts and packaging effects on coral reflectance suggests that consideration should be given to species selection in studies of coral reflectance.

Chapter 5.0 Spatial variation of coral bioindicators along an environmental gradient of the Great Barrier Reef

5.1 Introduction

It is now generally accepted that changes in water quality due to terrestrial runoff are a significant threat to coral reefs in the coastal zone (Bell and Elmetri 1995; Haynes and Michalek-Wagner 2000; Alongi and McKinnon 2005; Fabricius 2005). Increasingly, changes at the colony, population and/or community level are being used as indicators to detect the effects of stressors such as changes in water quality on coral reefs (e.g. Jameson et al. 2001; Risk et al. 2001). This is because biological indicators can provide a time-integrated estimate of past environmental conditions whereas direct sampling provides information about the conditions at the time of sampling only. Given the range of natural and anthropogenic influences affecting coral reefs at different spatial and temporal scales, it is unlikely that a single indicator exists that can sufficiently describe the overall condition of coral reefs (Jameson et al. 1998). Rather, a composite of indicators combining a range of biological responses from different ecological levels of organisation (i.e. colony to communities) has greater potential for success in assessments of coral health. Indeed, Risk et al. (2001) highlighted the need for early warning and cost-effective indicators incorporated into a monitoring toolbox that could be used at large spatial scales in the conservation of the world's coral reefs.

There are a range of coral indicators that could be used to assess changes in water quality. At the colony level, variables such as tissue thickness, surface rugosity and growth rates of the massive coral *Porites* have been suggested as proxies of environmental conditions along cross-shelf and water-quality gradients on the Great Barrier Reef (GBR) (Risk and Sammarco 1991; Barnes and Lough 1992; Lough and Barnes 2000). Other colony measures related to changes in water quality include the determination of chlorophyll *a* and symbiont densities (Falkowski and Dubinsky 1981; Dubinsky et al. 1984; Hoegh-Guldberg and Smith 1989), as well as symbiont and host lipid and protein content (Harland et al. 1992; Anthony and Fabricius 2000; Grover et al. 2002). Siebeck et al. (2006) proposed that the brightness of coral colour, which is correlated to the density and pigmentation of the symbionts, is a simple and appropriate indicator of coral health that can be measured using a colour chart. At the population level, densities of bioeroders have been used to examine the effects of water-quality on coral reefs (Sammarco and Risk 1990; Risk et al. 1995; Koop et al. 2001; Hutchings and Peyrot-Clausade 2002) and estimates of partial mortality and coral demography are useful indicators of coral condition (Ginsburg et al. 2001; Nugues and Roberts 2003). The development of integrated monitoring programmes to examine the condition of coastal reefs of the GBR has commenced (Queensland Government and Commonwealth of Australia 2003) but the patterns of spatial variation of candidate indicators are not well understood.

The aim of the study was to examine the spatial variation of candidate indicators suitable for inclusion into a monitoring toolbox for coastal reefs of the GBR (*sensu* Risk et al. 2001) and was divided into three components. First, a field study was carried out to investigate the spatial variability of selected indicators of two ubiquitous scleractinian corals *Pocillopora damicornis* and massive *Porites* along an environmental gradient in the Whitsunday Islands. This component aimed at understanding the patterns of variation in the indicators for the study species and whether any of these patterns were related to spatial differences in water quality. The indicators examined were concentrations of the pigment chlorophyll *a*, symbiont density, protein content and skeletal density in *P. damicornis*, and colony brightness, tissue thickness, density of bioeroders, partial mortality and surface rugosity in populations of massive *Porites*. Second, the causal effects of increased nutrient supply and decreased irradiance from suspended particulate matter on colony indicators were tested experimentally under controlled conditions. Finally, a manipulative experiment involving the relocation of corals to different conditions of water quality along an environmental gradient in the Whitsunday Islands was performed to determine if the responses measured in the laboratory could be detected under field conditions.

5.2 Materials and methods

5.2.1 Field study area and sampling design

The study was conducted in the Whitsunday Islands (20° 00'–30'S; 148° 45'–149° 15'E) as existing water quality data indicated the persistence of an environmental gradient where levels of water column nutrients increase and irradiance decreases, from the outer islands toward the inshore reefs near the Australian coast (Brodie et al. 2007; Chapter 2; Fig. 5.1). The gradient was quantified by a water quality index (WQI) calculated from thirteen irradiance and water-column nutrient variables. These included Secchi- and optical depth, water chlorophyll *a*, particulate nitrogen, particulate phosphorus, particulate organic carbon, dissolved organic and inorganic nitrogen and phosphorus, dissolved silicate and total suspended solids (further details provided in Chapter 2). The fringing reefs sampled were Repulse, Lindeman, Long, Dent, Whitsunday, Hook, Border and Deloraine Islands; the mid-shelf reefs were Bait and Charity Reefs (Fig. 5.1).

Apical branches (~6 cm long) of *Pocillopora damicornis* were collected from the centre of each of four colonies (n=4) at each of two sites and depths (shallow 1 – 3 m; deep 8 – 10 m below lowest astronomical tide) per reef for analysis of physiological parameters. These included concentration of chlorophyll *a*, the density of symbiotic dinoflagellates, protein content and skeletal density (described below). Colony brightness, density of macro-bioeroders, surface rugosity and partial mortality were recorded for every massive *Porites* occurring in each of two belt transects (10 m long x 3 m wide) placed parallel to the depth contour at each of the two sites and depths per reef. Colony brightness was estimated using a colour chart (Siebeck et al. 2006). The density of macro-

boring bioeroders was counted within 3 replicate 25 x 25 cm quadrats placed randomly on living surfaces of massive *Porites* (adapted from Hutchings and Peyrot-Clausade 2002) and the surface rugosity estimated as the difference between the vertical and lineal distance of a piece of small-gauge chain positioned across each colony (Darke 1991). For tissue thickness, a small core approximately 21 mm diameter x 30 mm length were sampled using a drill with a 25 mm hole-saw attachment (following Barnes and Lough 1992) from the upper surfaces of five replicate colonies (n=5) 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. Sampling was done from 8th – 16th August 2004.

5.2.2 Laboratory experiments

Two tanks experiments were carried out to examine the response of colony brightness, tissue thickness, chlorophyll *a* content and the density of symbionts in a scleractinian coral. The aim of Experiment 1 was to test causal effects of increased nutrient supply and decreased irradiance from suspended particulate matter (SPM) on these indicators using small cores from the massive coral *Porites lobata*. Experiment 1 ran for a total of 56 d commencing in November, 2004. The aim of Experiment 2 was to examine the recovery of colony brightness following exposure to SPM, which ran for a further 36 d following a 56 d exposure to SPM commencing in August 2005.

Small nubbins of *P. lobata* were collected from large colonies (>2 m diameter) using a hole-saw (25 mm diameter) attached to a pneumatic drill. A drilling guide was used to minimise damage to the tissue layer of the source colonies and the nubbins. The sediments used in the experiment were collected *in situ* from around the base of coral heads on a fringing reef of nearshore island on the GBR (High Island; 17˚ 10.0'S, 146˚ 00.0'E). These sediments were sieved and the fine fraction (<63 μm) retained and used as SPM for the experiment.

The aquarium 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 adjusted 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. Irradiance was provided for 12 h d^{-1} (12:12 dark:light cycle) using 400W metal halide lamps. Shade cloth was used to produce two experimental treatments: Shaded and Unshaded. The irradiance within the tanks was further characterised with replicate Odyssey light loggers (cosine-corrected photosynthetic irradiance sensor PAR 400-700 nm; Dataflow systems, Christchurch, NZ) deployed in the experimental treatments. The Odyssey loggers were calibrated against at manufacturer calibrated LI-192 light sensor (LI-COR, Nebraska, USA). A dosing system comprising a peristaltic pump (Masterflex L/S digital variable drive, Cole-Palmer, Illinois, USA) was used to deliver a continuous flow of SPM at a concentration of

approximately 20 mg L^{-1} resulting in two experimental treatments: SPM (20 mg L^{-1}) and filtered (500 μm filter) seawater. The water temperature was set to 25°C and each tank was cleaned once a week to minimise algal growth within the tanks. Samples for analysis of water quality parameters including dissolved inorganic and organic nutrients, and particulate nutrients were collected at 14 d intervals, although for total suspended solids, samples were collected at 4 d intervals to ensure the dosing system was maintaining concentrations of SPM at 20 mg L^{-1}. All water quality samples were processed using standard analytical techniques (further details provided in Chapter 2).

5.2.3 Field manipulative experiment

A manipulative experiment along an environmental gradient in the Whitsunday Islands was carried out 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) at each of 2 reefs within 2 cross-shelf positions along the gradient (Fig. 5.1): the inner zone (Lindeman and Long Island) with elevated levels of nutrients and low irradiance, and the outer zone (Edward and Deloraine Island) distant from terrestrial influences with low levels of nutrients and higher irradiance (Chapter 2). In total, 20 replicate nubbins were sampled from each of three source colonies at each of the depths and reefs described above and assigned randomly to each of 10 experimental treatments (Table 5.1). These included procedural controls and experimental treatments to test hypotheses about the effects of irradiance and water quality on colony brightness. The nubbins were collected using the drilling process described in Section 5.2.1.

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

Treatment	Action
UN	Control, sample undisturbed colonies
CO	Coring control, nubbin cored and placed back into colony
MO	Movement control, nubbins moved (with others) but returned to source reef
TLS	Translocate nubbins 25 m on source reef to examine effects of site
TLR	Translocate nubbins to nearby reef in the same zone to examine reef effects
DS/SD	Transplant nubbins between depths: SD = shallow to deep; DS = deep to shallow to examine effects of depth
RSD/RDS	Transplant nubbins between depths to a nearby reef to examine effects of depth and reef at larger scale
IO/OI	Transplant nubbins to new reef in a different water quality zone: IO = inner to outer, OI = Outer to Inner
IDOS/ISOD	Transplant nubbins to new reef and depth in a different water quality zone: IDOS = inner deep to outer shallow; ISOD = inner shallow to outer deep
ODIS/OSID	Transplant nubbins to new reef and depth in a different water quality zone: ODIS = outer deep to inner shallow; OSID = outer shallow to inner deep

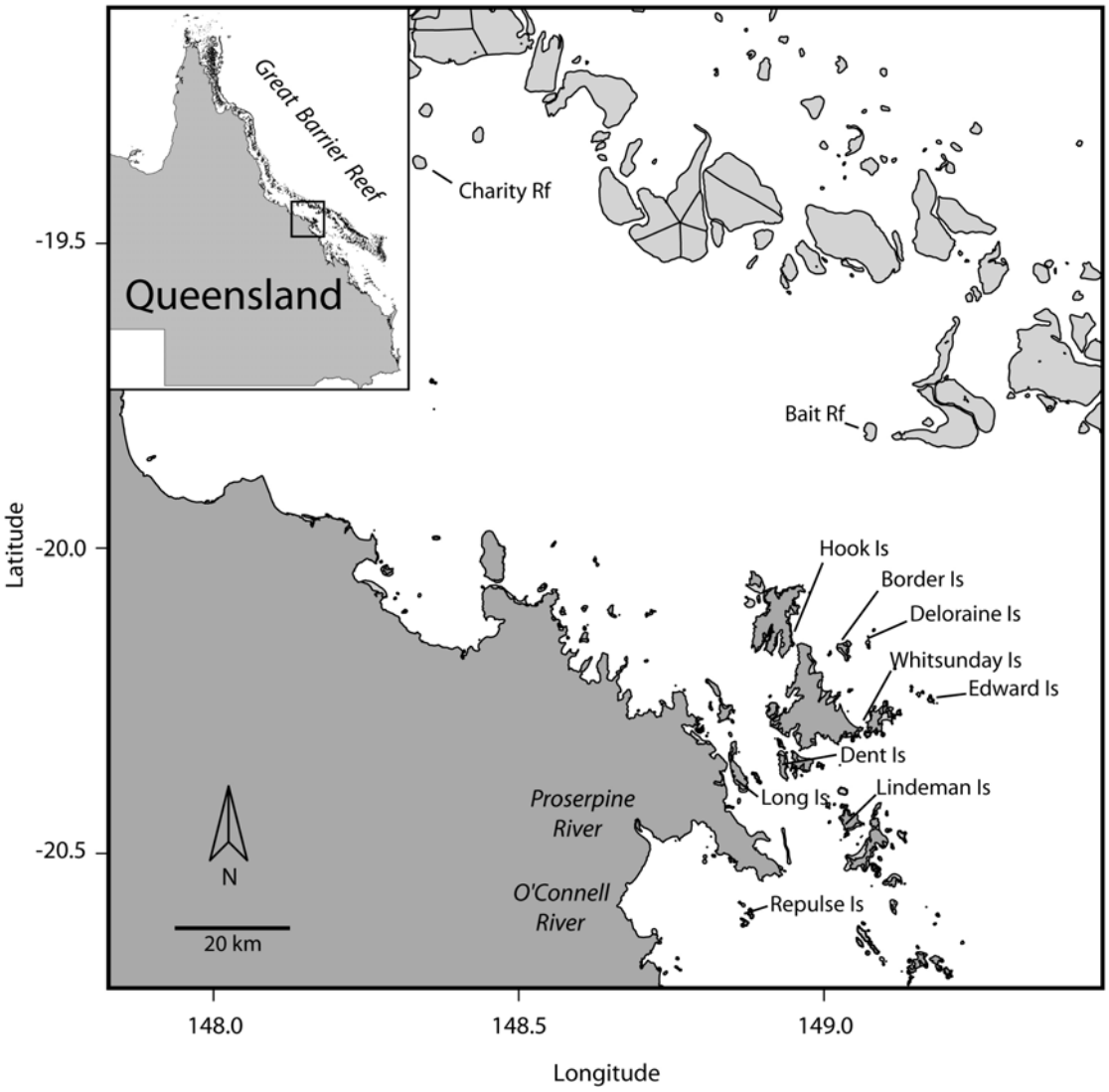

Fig. 5.1. Map of study locations to examine spatial variation of colony indicators of *Pocillopora damicornis* and massive *Porites* in the Whitsunday Islands. Manipulative experiment involved transplanting small nubbins of *Porites* among Long and Lindeman Islands (inner), and Deloraine and Edward Islands (outer).

For each nubbin, colour scores were determined using a colour chart following the procedures described by Siebeck et al. (2006) and colour brightness was quantified by reflectance spectrometry on board a research vessel. Reflectance measurements were conducted using a USB 2000 fibre optic spectrometer (Ocean Optics Inc. Florida, USA) in a purpose built chamber (full details in Chapter 4). Following these measurements, each nubbin had a small hole drilled transversely through the dead portion of the core and attached into holders on 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. Two replicate transplant units were then deployed at tide-corrected depths adjacent to the source colonies on the back-reef (leeward side) at each of the four islands. Transplanting was done from 8^{th} – 12^{th} August 2005 and all units were retrieved 4 months later on 14^{th} – 18^{th} January 2006.

5.2.4 Physiological analyses

For all physiological analyses, each coral sample was placed into a plastic bag with filtered (0.2 μm) seawater and blasted with an air gun until the tissue was removed from the skeleton. The resulting tissue slurry was then homogenised for 30 s using a tissue grinder and divided into sub-samples for determinations of chlorophyll *a*, density of symbionts and protein content. A double extraction of chlorophyll was done in darkness using 100% acetone as the solvent for 24 h at 4°C. The optical properties of the combined extracts were measured using a Shimadzu UV-1700 Spectrophotometer (Shimadzu Corporation, Kyoto, Japan). Levels of chlorophyll *a* were determined using the formula from Jeffrey and Humphrey (1975) after correction for the volume of the homogenate and solvent. The density of symbiont cells was determined with eight replicate counts in a Neubauer Improved haemocytometer (Brand, Wertheim, Germany). 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. Absorbances were measured at 690 nm using a Perkin Elmer spectrophotometer (Wallac Victor^2, 1420 Multilabel Counter). The determinations of chlorophyll *a*, density of symbionts and protein content, were normalised to surface area of the coral branch determined by wax dipping (Stimson and Kinzie 1991). Skeletal density (ρ_s) of *P. damicornis* was determined using the procedures described by Anthony et al. (2002).

5.2.5 Statistical analyses

For the field gradient study, linear models were used to examine relationships between the coral indicators (response) and the WQI (explanatory) derived for the Whitsunday Islands. For the exposure experiments, colony parameters in *Porites* were analysed with two factor ANOVAs. The factors were Irradiance (2 levels: Shaded and Unshaded, fixed) and SPM (2 levels: 20 mg L^{-1} and filtered seawater [FSW], random and orthogonal). Concentrations of dissolved (inorganic and organic) and particulate nutrients were analysed with a one factor ANOVA. The aim of the field manipulative experiment was to examine the response of the indicators under different regimes of irradiance and water quality *in situ* in the Whitsunday Islands. Due to mortality among some of the nubbins, differences among the experimental treatments were examined using a one factor ANOVA. For all ANOVAs, data were tested for deviations from the assumption of homogeneity of variances and data were transformed if necessary. Pooling procedures involving elimination of terms from the mean square estimates were done if a term was non-significant at $P > 0.25$

(Underwood 1997). 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

5.3.1 Field study

Most of the potential measures in *P. damicornis* and massive *Porites* were related significantly to the WQI in the Whitsunday Islands (low WQI indicates clear water, high WQI indicates turbid conditions; Table 5.2). In *P. damicornis*, concentrations of chlorophyll *a* and symbiont density increased approximately 2.5-fold, but the density of the skeleton decreased 1.2-fold, along the gradient as nutrient and sediment levels increased from outer islands toward the nearshore reefs (Fig. 5.2a, b, d). There was no relationship between the protein content of *P. damicornis* and the WQI (Table 5.2). For the massive *Porites*, there was a 1.4-fold increase in colony brightness, but a 0.6-fold decrease in tissue thickness, of massive *Porites* as nutrient and sediment levels increased from outer islands toward the nearshore reefs (Fig. 5.2e, f). Similarly, there was a 50-fold increase in the abundance of bioeroders at the deep depth (but no change at the shallow depth), and a 3.5-fold increase in surface rugosity at the shallow depth, of massive *Porites* along the gradient from outer islands toward the nearshore reefs (Fig. 5.2g, h). There was no relationship between partial mortality of massive *Porites* and the WQI (Table 5.2).

Table 5.2. Summary of linear models comparing indicators in (a–d) *Pocillopora damicornis* and (e–i) massive *Porites* with the Water Quality Index between two depths (shallow and deep) in the Whitsunday Islands.

Variate	Slope	SE	t	*P*
(a) Chlorophyll *a* (μg cm^{-2})				
Shallow	0.093	0.026	3.620	0.0028
Deep	0.147	0.100	1.464	0.1670
(b) Symbiont density (cells cm^{-2})				
Shallow	0.042	0.006	7.270	<0.0001
Deep	0.052	0.023	2.283	0.0399
(c) Protein content (μg cm^{-2})				
Shallow	-0.009	0.005	-1.640	0.1233
Deep	-0.005	0.020	-0.257	0.8010
(d) Skeletal density (g cm^{-3})				
Shallow	-0.010	0.001	-6.639	<0.0001
Deep	-0.007	0.006	-1.276	0.2240
(e) Colony brightness (colour score)				
Shallow	0.022	0.005	4.257	0.0008
Deep	0.042	0.013	3.295	0.0053
(f) Tissue thickness (mm)				
Shallow	-0.070	0.011	-6.600	<0.0001
Deep	-0.119	0.026	-4.616	0.0004
(g) Density of bioeroders (m^{-2})				
Shallow	3.025	1.545	1.958	0.0705
Deep	10.466	3.731	2.805	0.0140
(h) Surface rugosity				
Shallow	0.017	0.003	6.767	<0.0001
Deep	0.014	0.006	2.321	0.0359
(i) Partial mortality (%)				
Shallow	-0.046	0.065	-0.704	0.4932
Deep	0.263	0.156	1.680	0.1150

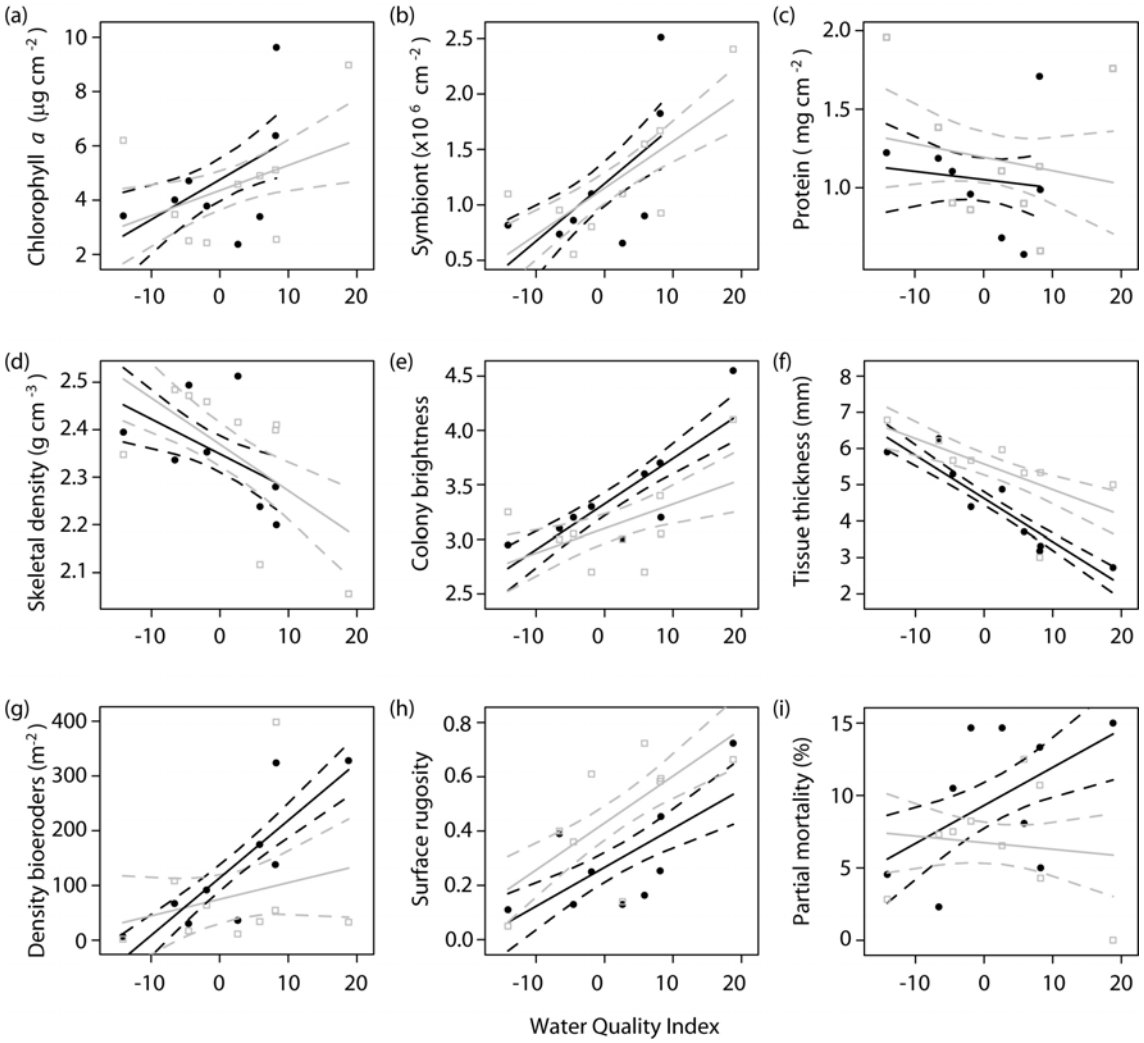

Fig. 5.2. Relationships between indicators in (a–d) *Pocillopora damicornis*, (e–i) massive *Porites* spp. between shallow (□) and deep (●) with a water quality index (WQI) for the Whitsunday Islands. Dashed lines ± standard error (SE). WQI derived from five surveys between August 2004 and August 2006; large positive numbers correspond to elevated water column nutrients and low irradiance on nearshore reefs, negative numbers correspond to low water column nutrients and high irradiance on outer islands and mid-shelf reefs.

5.3.2 Laboratory experiments

The *P. lobata* nubbins were maintained successfully in the experimental set-up with no mortality. Interestingly, some nubbins appeared to be less efficient at rejecting sediment than others. 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.

5.3.2.1 Experiment 1

Downward irradiance differed between the experimental treatments in Experiment 1. Mean daytime irradiance (± SE, *n*=2) was greatest in filtered seawater (FSW) and unshaded (835 ± 4 µmol photons m^{-2} s^{-1}), followed by suspended particulate matter (SPM) and unshaded (598 ± 2 µmol photons m^{-2} s^{-1}), FSW and shaded (56 ± 0.3 µmol photons m^{-2} s^{-1}), with the lowest levels recorded in the SPM and shaded treatment (32 ± 0.2 µmol photons m^{-2} s^{-1}). In general, shading and SPM resulted in a 93% and 94% reduction in the downward irradiance, respectively.

Water quality varied between the experimental treatments in Experiment 1. There were few differences between treatments for levels of dissolved inorganic and organic nutrients in the water column. Levels of nitrate (NO_3, $F_{1,38} = 34.1$, $P < 0.0001$), nitrite (NO_2, $F_{1,38} = 21.2$, $P < 0.0001$) and dissolved inorganic nitrogen (DIN, $F_{1,38} = 33.7$, $P < 0.0001$) were, however, generally 2-fold greater in the SPM compared with filtered-seawater treatment (Fig. 5.3). Similarly, concentrations of particulate nitrogen ($F_{1,78} = 295.7$, $P < 0.0001$), particulate phosphorus ($F_{1,78} = 222.2$, $P < 0.0001$) and particulate organic carbon ($F_{1,78} = 218.4$, $P < 0.0001$) differed 2- to 3-fold between the water quality treatments (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 ($F_{1,78} = 427.7$, $P < 0.0001$; Fig. 5.3).

The colony brightness of the *P. lobata* differed significantly among treatments (Table 5.3). The nubbins commenced the experiment with a colour brightness of approximately 4.0 colour chart units. By Day 10 of the experiment nubbins in the FSW, unshaded treatment (i.e. control) had maintained a colour of 3.7 ± 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, unshaded treatment were still within the colour brightness range that they started the experiment with (3.9 ± 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, unshaded treatment appeared to stabilise in colour brightness 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 brightness within approximately 20 d and they maintained the values recorded at Day 20 until the exposure was stopped on Day 56 (Fig. 5.5a).

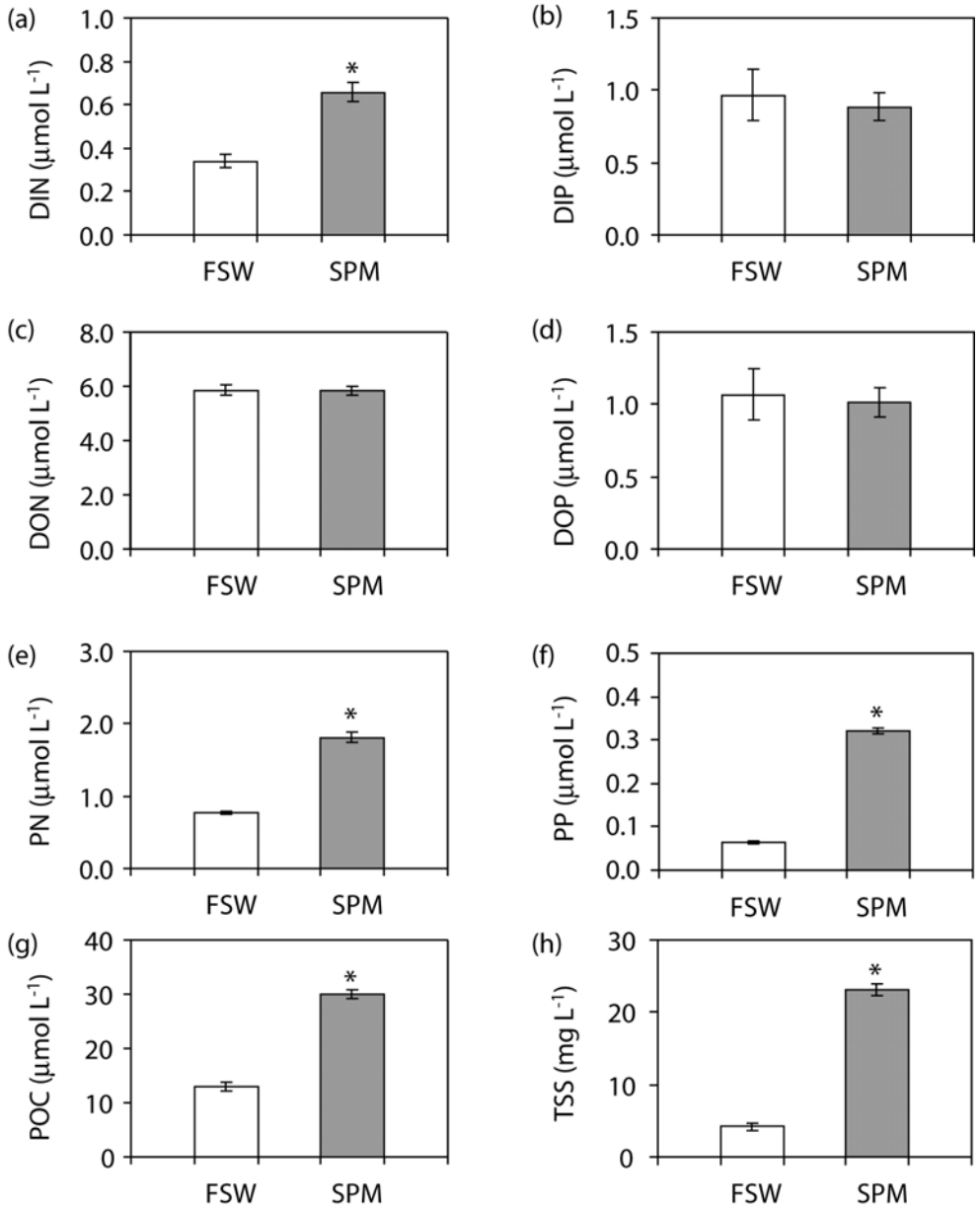

Fig. 5.3. Mean concentration (± SE) of water column parameters in Experiment 1 to examine response of *Porites lobata* nubbins exposed to suspended particulate matter (values averaged over 56 d). (a – d) dissolved nutrients (n=20) and (e – f) particulate nutrients and suspended solids (n=40). Treatments: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

The thickness of the tissue layer of the nubbins varied significantly between SPM treatments (Table 5.3). The tissue layer of the nubbins in the SPM treatment was thicker (5.52 ± 0.31 mm) than in the FSW treatment (4.69 ± 0.21 mm) (Fig. 5.6a). The concentration of chlorophyll *a* cm^{-2}

varied inconsistently between the irradiance and water quality treatments (Table 5.3). Under high irradiance, 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 under low irradiance (Fig. 5.6b). The density of symbionts also varied significantly between SPM treatments (Table 5.3). The density of symbionts was greater for nubbins in the SPM treatment (3.13 ± 0.28 x10^6 cm^{-2}) than in the FSW treatment (2.12 ± 0.30 x10^6 cm^{-2}) (Fig. 5.6c).

5.3.2.2 Experiment 2

Water quality varied inconsistently among times of sampling and between the experimental treatments (Time x Treatment interaction) in Experiment 2. When differences occurred among times and between treatments, it was common for the magnitude of the change between the dosing and recovery periods for the water quality variables of the SPM treatment to be much greater than any small temporal differences in the FSW treatment (Fig. 5.4). For example, concentrations of particulate phosphorus were significantly lower during the recovery period (i.e. post Day 56) compared with the first 3 times of sampling the dosing period, but there were no differences among any times in the FSW treatment ($F_{6,42} = 146.03$, $P < 0.0001$; Fig. 5.4). Differences among times and between treatments for levels of dissolved inorganic phosphorus ($F_{6,42} = 3.80$, $P = 0.0041$) were not consistent with the addition of SPM but seemed to reflect some external influence on the seawater system of the aquarium facility (Fig. 5.4)

Patterns of variation for colony brightness in Experiment 2 were similar to those of Experiment 1. Nubbins in the FSW and Unshaded treatment maintained consistent colour brightness while all other nubbins became darker following exposure to SPM or Shaded conditions (Fig. 5.5b). At Day 56, nubbins in the FSW and Unshaded treatment had maintained a colour of 2.8 ± 0.1 colour chart units, but corals in all the other treatments were noticeably darker and had increased by approximately 1.5 – 2 colour scores. Dosing with SPM ceased at Day 56. From Day 56 until the completion of the experiment, nubbins in the shaded treatments maintained a colour score of approximately 5.0 colour chart units. However, the colour brightness decreased for nubbins in the Unshaded treatment but exposed previously to SPM and the brightness of these nubbins was comparable to the controls at the completion of the experiment (Fig. 5.5b).

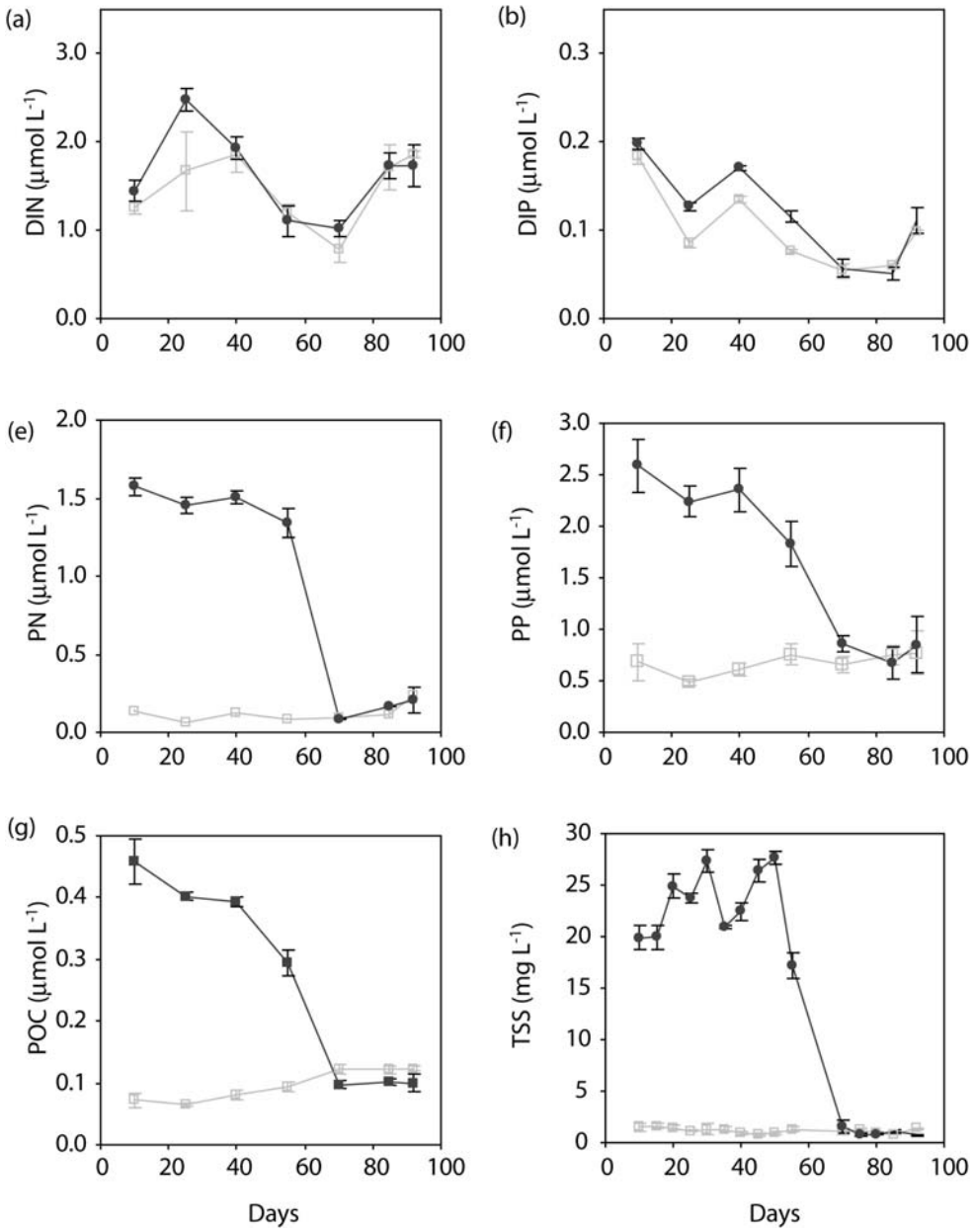

Fig. 5.4. Time series of mean concentration (± SE, *n*=8) of water column parameters in Experiment 2 to examine response of *Porites lobata* nubbins exposed to suspended particulate matter. Treatments: FSW = filtered seawater (grey lines) and SPM = suspended particulate matter (black lines). Abbreviations: DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; PN, particulate nitrogen; PP, particulate phosphorus; POC, particulate organic carbon, TSS, total suspended solids.

Table 5.3. Summary of ANOVAs comparing colony parameters in *Porites lobata* nubbins after 56 d exposure to different treatments of nutrients and irradiance (Tank Experiment 1). * denotes term eliminated at $P > 0.25$. For *post hoc* tests, means (± SE) are untransformed and in ascending order. Underlined terms were not significantly different from each other. Abbreviations: FSW = filtered seawater, SPM = suspended particulate matter.

Variate	Source of variation	df	MS	*F*	*P*	*Post hoc* tests			
(a) Colony brightness	Irradiance	1	30.88	1.70	0.4162	Shaded		Unshaded	
transform: none	SPM	1	8.76	0.48	0.6134	SPM FSW		FSW < SPM	
	Irradiance x SPM	1	18.13	64.14	<0.0001	5.58	5.96	3.13	5.21
	Residual	44	0.283			(0.26)	(0.04)	(0.07)	(0.14)
(b) Tissue thickness (mm)	Irradiance	1	0.864	0.50	0.4831	SPM			
transform: none	SPM	1	8.411	4.87	0.0326	FSW<SPM			
	Irradiance x SPM	1	1.768	1.02	0.3171*	4.69	5.53		
	Residual	44	1.727			(0.21)	(0.31)		
(c) Chlorophyll *a* (μg cm^{-2})	Irradiance	1	29.01	1.03	0.4956	Shaded		Unshaded	
transform: none	SPM	1	15.75	0.56	0.5916	SPM FSW		FSW < SPM	
	Irradiance x SPM	1	28.22	4.68	0.0360	6.77	7.16	4.07	6.75
	Residual	44	6.03			(0.68)	(0.95)	(0.32)	(0.75)
(d) Symbionts (x10^6 cells cm^{-2})	Irradiance	1	1.48x10^{13}	4.4	0.2831	SPM			
transform: none	SPM	1	1.24 x10^{13}	7.24	0.0100	FSW<SPM			
	Irradiance x SPM	1	3.37 x10^{12}	1.97	0.1671	2.12x10^6	3.13x10^6		
	Residual	44	1.71 x10^{12}			(0.30x10^6)	(0.28x10^6)		

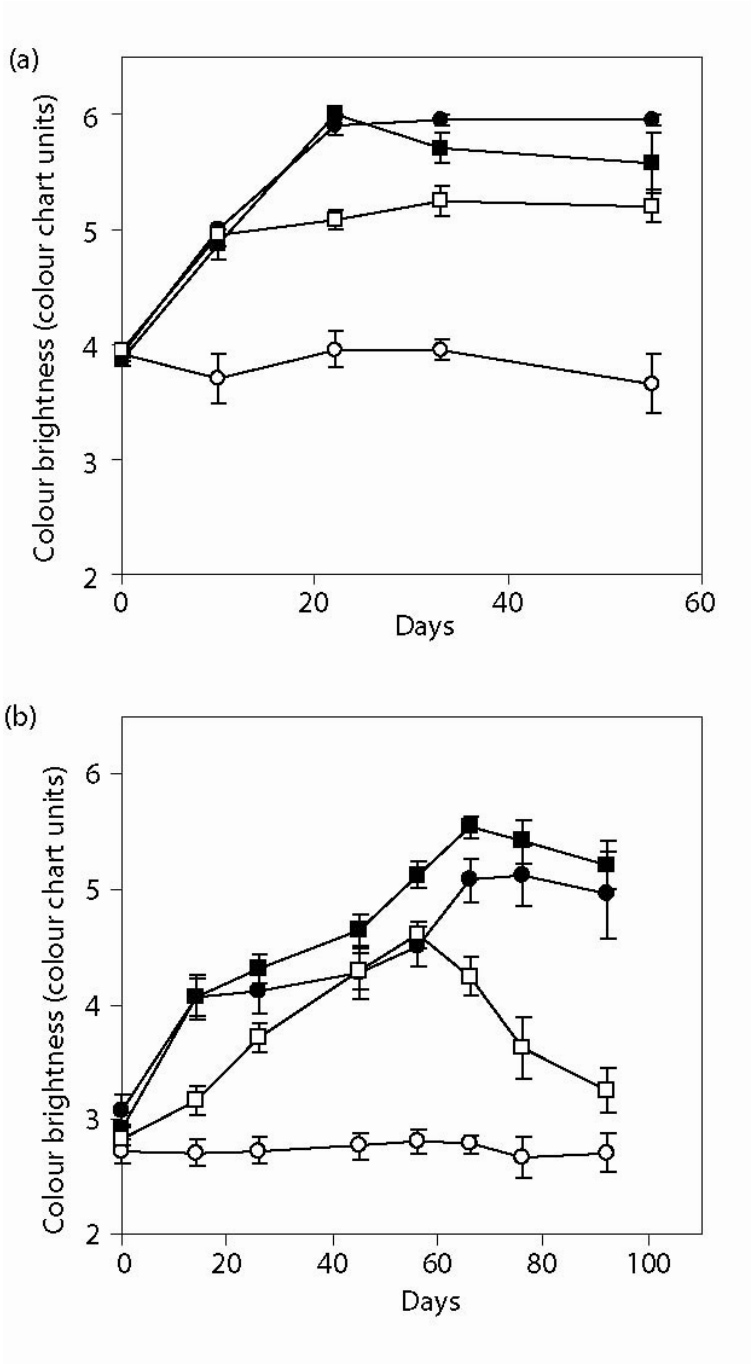

Fig. 5.5. (a) Tank Experiment 1: Response of mean coral brightness (± SE, *n*=12) of *Porites lobata* nubbins exposed to different treatments of SPM and irradiance. (b) Tank Experiment 2: Recovery of colony brightness (± SE, *n*=12) of *Porites lobata* nubbins following exposure to different treatments of nutrient and SPM. Symbols: circles = filtered seawater; squares = SPM; open symbols = unshaded; dark symbols = shaded.

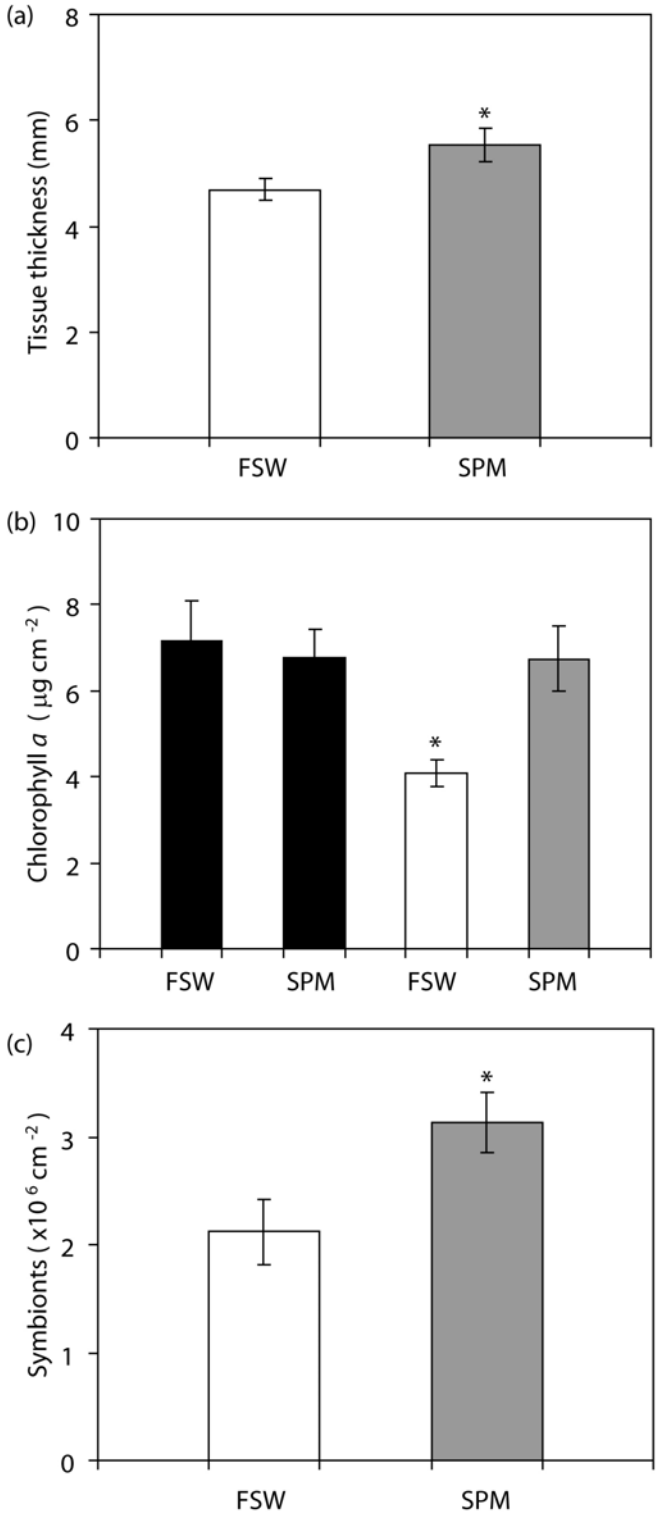

Fig. 5.6. Mean values (± SE, *n*=12) of (a) tissue thickness, (b) concentration of chlorophyll *a* and (c) density of symbionts in *Porites lobata* nubbins exposed to different treatments of SPM and irradiance (Tank Experiment 1). FSW = filtered seawater; SPM = suspended particulate matter. Symbols: black bars = shaded; white bars = unshaded; grey bars = unshaded + SPM. * denotes statistical significance at $P < 0.05$.

5.3.3 Field manipulative experiment

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 brightness, 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 brightness of colour, was not included in the analyses due to a high level of mortality.

In general, there was a decrease in the darkness of colour for nubbins in all experimental treatments sourced from the inner zone (Fig. 5.7a). This included treatments that were transplanted to a new water quality zone, i.e. from the inner (elevated nutrients, low irradiance) to the outer zone (low nutrients, high irradiance), 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 darkness of colour (Fig. 5.7b). These patterns were expected as the study was done when conditions were changing toward summer with increasing temperatures and irradiance. There were, however, two treatments where the darkness 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 ± 0.1 colour chart units increasing to 4.5 ± 0.2 colour chart units at the completion of the experiment. The greatest increase in darkness occurred for nubbins moved from the outer shallow to the inner deep (OSID treatment) that commenced with a colour score of 3.5 ± 0.1 colour chart units and increased to 4.6 ± 0.2 colour chart units by the end of the deployment (Fig. 5.7b).

Analysis of chlorophyll *a* content 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 5.4). There was more chlorophyll *a* 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. 5.8). 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 5.4). Nubbins transplanted from the outer shallow to the inner deep depth (OSID treatment) reflected less light compared with nubbins in the other treatments, but no differences occurred among the other experimental treatments (Fig. 5.9).

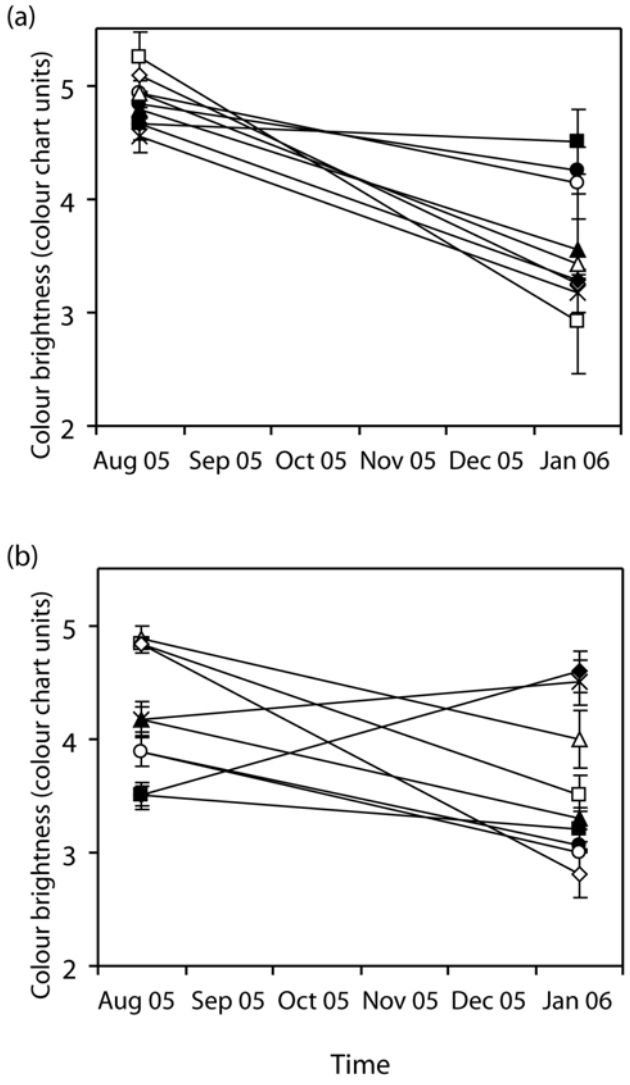

Fig. 5.7. Mean brightness of colour (± SE) of coral nubbins sourced from (a) inner zone, and (b) outer zone, and transplanted along an environmental gradient in the Whitsunday Islands. Colour brightness measured with a Coral Health Monitoring Chart (Siebeck et al. 2006). Symbols: ● undisturbed; ○ cored; ▲ moved; □ translocated deep to shallow; ■ translocated shallow to deep; △ translocated 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.

Table 5.4. Summary of ANOVAs comparing concentrations of chlorophyll *a* and spectral reflectance among experimental treatments for coral nubbins transplanted along an environmental gradient in the Whitsunday Islands. Inner nubbins refers to nubbins sourced from the nearshore islands (Long and Lindeman Islands); outer nubbins refers to nubbins sourced from the outer islands (Deloraine and Edward Islands) of the Whitsunday Islands.

Variate	Source of variation	df	MS	*F*	*P*
(a) Chlorophyll *a*: inner nubbins	Treatment	5	24.10	1.54	0.1824
transform: none	Residual	111	132.30		
(b) Chlorophyll *a*: outer nubbins	Treatment	5	119.27	3.22	0.0121
transform: none	Residual	62	37.09		
(c) Reflectance: inner nubbins	Treatment	5	0.0042	1.25	0.2927
transform: none	Residual	112	0.0034		
(d) Reflectance: outer nubbins	Treatment	5	0.0073	2.69	0.0289
transform: none	Residual	63	0.0027		

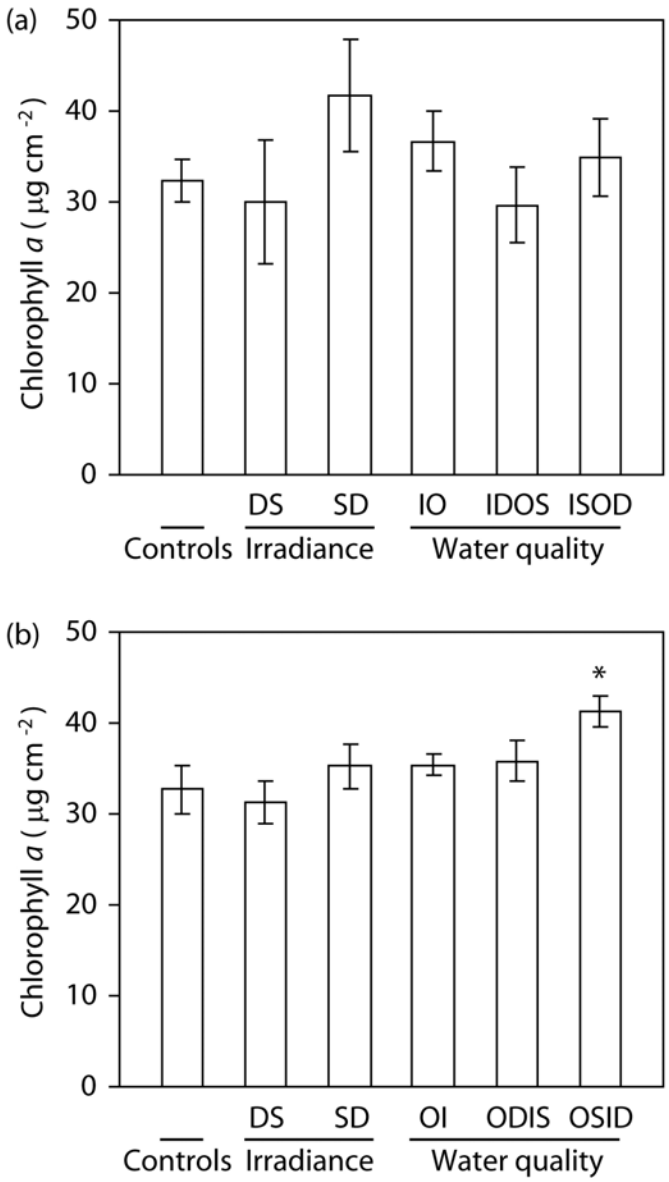

Fig. 5.8. Mean concentration of chlorophyll *a* (µg cm^{-2}, ± SE) for coral nubbins sourced from (a) inner zone, and (b) outer zone, and transplanted along an environmental gradient in the Whitsunday Islands. Abbreviations: DS = deep to shallow; SD = shallow to deep; IO = inner to outer; OI = outer to inner; transplant treatments are combinations of these. * denotes statistical significance at $P < 0.05$.

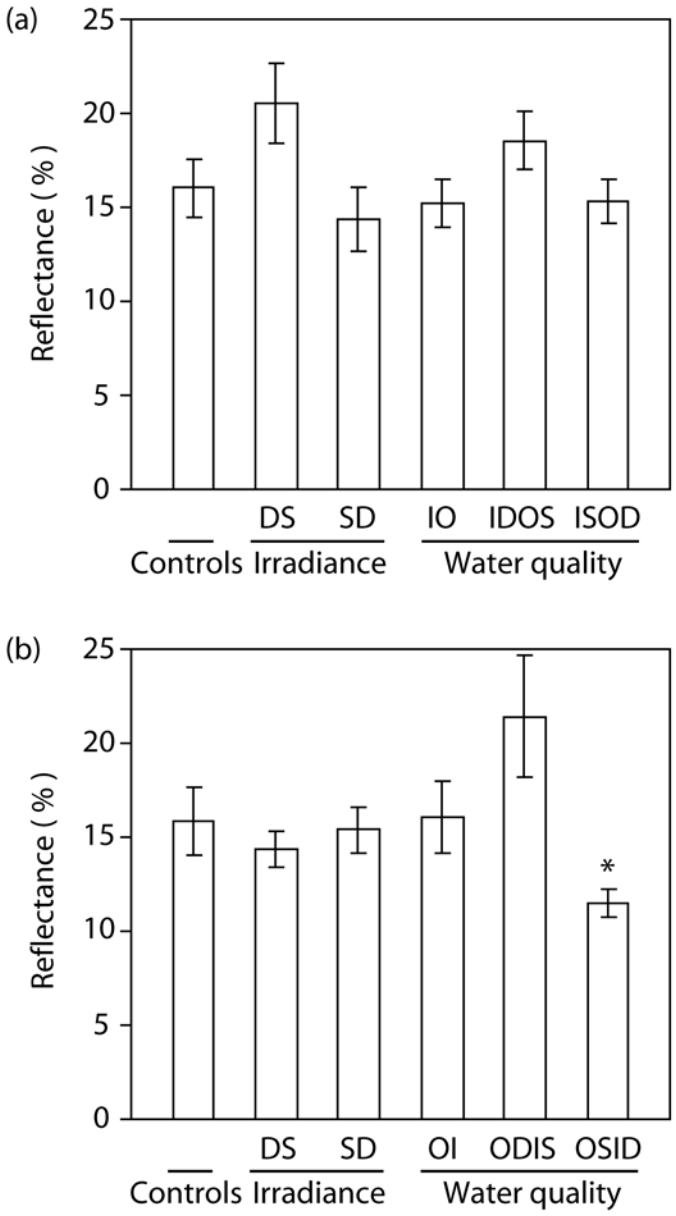

Fig. 5.9. Mean reflectance (± SE) of coral nubbins sourced from (a) inner zone, and (b) outer zone, and transplanted along an environmental gradient in the Whitsunday Islands. Abbreviations: DS = deep to shallow; SD = shallow to deep; IO = inner to outer; OI = outer to inner; transplant treatments are combinations of these. * denotes statistical significance at $P < 0.05$.

5.4 Discussion

This study has demonstrated that some biological responses in two scleractinian corals can be used as indicators of changes in water quality on coastal coral reefs of the GBR. In the field study, most of the indicators examined showed significant relationships with water quality in both *P. damicornis* and massive *Porites*. These patterns are consistent with other studies that have found physiological differences including increased symbiont density and chlorophyll *a*

concentration 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 photosynthesising pigments under low irradiance (Falkowski and Dubinsky 1981; Anthony and Hoegh-Guldberg 2003a). There are clear differences in the water column characteristics between inner and outer conditions in the Whitsunday Islands. For example, there was a 2- to 3-fold increase in 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). An important finding of the field study was that the physiological differences in two coral species were related to a WQI spanning a relatively small spatial scale (i.e. ~50 km) suggesting that there are physiological features in corals that are sensitive to differences in water quality. Other studies have identified population and community level responses along water quality gradients and the results presented here add evidence at a colony level, to the population and community-level responses reported elsewhere (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.

Changes in the density and species composition of bioeroders have been suggested previously as a potential indicator of changes in water quality (e.g. Risk et al. 2001), the rationale being that macro-bioeroders (especially sponges, polychaetes, bivalvia and barnacles) are filter feeders that flourish at high particle loads. For example, Rose and Risk (1985) found increased abundances of the boring sponge *Cliona delitrix* were associated with the discharge of untreated sewage on reefs in the Caymans Islands. In French Polynesia, there were more deposit-feeding polychaetes in experimental units deployed on eutrophic fringing reefs, which were subject to terrestrial runoff, compared with oligotrophic atolls suggesting changes in feeding-guilds of macro-boring polychaetes may provide an indicator of particulate food availability in the water column. In Indonesia, rates of bioerosion were greater on eutrophic reefs in both live colonies of massive corals and in the rubble fragments of branching coral (Holmes et al. 2000). In this study, there was a 50-fold increase in the density of boring macro-bioeroders at the deep depth (~6 m) along an environmental gradient from mid-shelf to nearshore reefs in the Whitsunday Islands. The lack of any correlation at the shallow depth was intriguing and may be due to greater rates of sedimentation at deeper depths on inshore islands (Wolanski et al. 2005) possibly providing a greater potential for particulate feeding by macroborers at deeper depths along the gradient from nearshore to outer islands in the Whitsunday Islands. Notwithstanding this, the correlation between bioeroder density at the deep depth and the water quality index was consistent with other studies of bioerosion on the GBR (Sammarco and Risk 1990; Risk et al. 1995; Hutchings et al. 2005). However, further work is required to test causality between the density of macro-

bioeroders and changes in water quality before it can be used as an indicator on the GBR. Several previous studies have attempted this with limited success. The ENCORE experiment found no effect for rates of bioerosion demonstrating that bioeroding fauna were not influenced by dissolved nutrients at the study concentrations (Koop et al. 2001). Hutchings et al. (2005) deployed dead-coral blocks along a water quality gradient on the GBR and found rates of bioerosion were greater at offshore sites than those with greater exposure to terrestrial runoff, although this finding is complicated as the nearshore blocks were covered in fine sediment throughout the experiment thus potentially limiting colonisation by bioeroders. Currently, estimates of bioerosion are not a component of monitoring programmes on the GBR, which is surprising given the data can be collected economically (here counts were done using small quadrats) and it that it has a high specificity to changes in water quality (e.g. Holmes et al. 2000). Indeed, the coral rubble technique described by Holmes et al. (2000) is meritorious and should be assessed for its applicability to the GBR.

In two tank exposure experiments, *P. lobata* showed several responses to differences in water quality. A change in colour brightness occurred within ~20 d of both exposure, and recovery from, exposure to SPM. Hoegh-Guldberg and Smith (1989) used a similar experimental approach to examine the effects of ammonium on coral symbionts and reported that corals in nutrient enriched treatments were 'darker' compared with those in the controls. Using a simple colour chart (Siebeck et al. 2006), it has been possible to quantify the colour brightness in corals exposed to differing concentrations of nutrient and light limitation in the laboratory. Moreover, the colour difference among the treatments was detectable as a difference in concentrations of pigment chlorophyll *a*. Corals exposed to elevated levels of SPM at levels that simulated turbidity events on a coral reef such as those that might occur during resuspension events (Larcombe et al. 1995; Orpin et al. 2004) or flood plumes (Devlin et al. 2001), contained concentrations of chlorophyll *a* that were comparable to corals placed in both the shaded treatments. Further experiments are required to determine if this was a photo-acclimatory response to the reduced irradiance owing to absorption and dispersion of incident light by the suspended particles, or whether it was a symbiont population response to increased nutrient availability associated with the sediments (Falkowski and Dubinsky 1981; Dubinsky and Jokiel 1994; Anthony and Hoegh-Guldberg 2003a). Also, the thickness of the tissue layer, which has been reported to decrease in response to high levels of sedimentation (Barnes and Lough 1999), increased when exposed to suspended particulates, which may have been due to increased particle feeding (Anthony 1999; Anthony and Fabricius 2000). This finding validates earlier assertions of the potential of tissue thickness as an indicator of water quality by Barnes and Lough (1992) and Lough and Barnes (2000), who found a thicker tissue layer in *Porites* from nearshore compared with outer reefs of the GBR and suggested this may have been a growth response due to increased availability of nutrients on the

nearshore reefs. The discrepancy between the SPM exposure experiment and the field study for tissue thickness (i.e. tissue thickness was lowest on nearshore locations corresponding to elevated nutrients and sediments) suggests that the effects of light limitation on coral growth (e.g. Anthony and Fabricius 2000) may be a greater influence on corals in the nearshore Whitsunday Islands than nutrient availability, although this remains to be determined.

Using an experimental design for a manipulative experiment that incorporated appropriate procedural controls, the results of the exposure experiments were validated under field conditions and confirmed that coral brightness responds to changes in water quality. Nubbins of *P. lobata* transplanted from outer, shallow locations (low nutrients, high irradiance) to inner, deep locations (elevated nutrients, low irradiance) were noticeably darker as measured by colour chart and spectral reflectance, and had higher concentrations of chlorophyll *a*. This result was consistent with other studies of photo-acclimatisation to enhanced nutrients (Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989) and light limitation (Falkowski and Dubinsky 1981; Dubinsky et al. 1984) suggesting that the transplanted corals had acclimated to different environmental conditions. The limitation to this finding was that a low-level bleaching event (i.e. <10% live coral cover) occurred in the Whitsunday region during 2005/06 (Great Barrier Reef Marine Park Authority 2006) confounding results that could be attributed to a change in water quality. 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 transplanted from the shallow depth of outer islands (low nutrients, high irradiance) to the deep depth of inner islands (elevated nutrients, low irradiance; Chapter 2) went against this overall trend with an increase in colour brightness. Thus, the transplantation of coral nubbins from an outer to a nearshore zone in the Whitsunday Islands resulting in a darkening of colour, and measured with three different methods, indicates that coral brightness could be used as a valid indicator of the effects of water quality. This finding will be further tested in Chapter 6. Changes in coral colour due to acclimation to altered irradiance or nutrient availability also occurred under experimental conditions within a period of several weeks. However, as was shown in the transplantation experiment, coral colour can vary naturally in response to the physical environment (e.g. light and temperature; Hoegh-Guldberg 1999) and seasonally (Brown et al. 1999b; Fitt et al. 2000), and these factors have to be controlled for when using colony brightness as an indicator of changing water quality on coral reefs.

Of the measures used to record a response in corals to differences in water quality, the colour chart developed by Siebeck et al. (2006) to quantify a change in colony brightness is arguably the simplest to use. The chart was developed as a tool for assessing bleaching events and based on the

principle 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 colour chart for assessing the effects of water quality on coral reefs, although Fabricius (2006) showed that corals on nutrient-exposed nearshore reefs were darker compared with those on offshore reefs of the GBR. Indeed, the results of this study support the hypothesis that colony brightness and tissue thickness in massive *Porites* respond to changes in water quality and they could be used as early warning indicators in a monitoring toolbox. Further, the relationship between the density of macro-bioeroders and water quality in the Whitsunday Islands, coupled with evidence from previous studies (e.g. Rose and Risk 1985; Holmes et al. 2000), suggests further work incorporating *in situ* manipulative experiments to examine causality with changes in water quality are warranted on the GBR.

Chapter 6.0 Temporal dynamics in coral bioindicators for water quality on a coastal coral reef of the Great Barrier Reef

6.1 Introduction

Responses of reef building corals and their endosymbiotic dinoflagellates (*Symbiodinium*) to changes in environmental conditions can be used as bioindicators in monitoring programmes of coral reefs. These responses range from the genetic- to the community-level of organisation and include variation in parameters such as RNA/DNA ratio, symbiont density, photo-physiology and coral growth rates, through to rates of bioerosion in massive corals (e.g. Hoegh-Guldberg and Smith 1989; Lough and Barnes 2000; Risk et al. 2001; Hutchings and Peyrot-Clausade 2002; Meesters et al. 2002). For example, the photo-physiology of *Symbiodinium* has received attention as a proxy of coral health (e.g. Jones et al. 1998; Jones and Hoegh-Guldberg 2001; Lesser and Gorbunov 2001) because the physiological performance of the symbionts is governed by a suite of environmental factors, with light considered one of the key environmental resources as it drives photosynthesis. Symbiotic photosynthesis in corals results in the translocation of photosynthates to the coral host, which is essential to maintain high rates of calcification, and hence growth, of coral reefs (Barnes and Chalker 1990; Muscatine 1990). Other factors that influence the physiological performance of corals are sea surface temperature (SST) and water quality such as exposure to nutrients, suspended particulate matter and pesticides (see reviews by Hoegh-Guldberg 1999; Fabricius 2005). Environmental conditions that maintain light, SST and water quality within tolerance thresholds are, therefore, vital to the physiological and ecological success of coastal coral reefs.

Environmental conditions on coastal coral reefs are influenced by a range of natural and anthropogenic factors that vary in time and space. On short time-scales (hours to weeks), corals on coastal reefs are exposed to variable regimes of hydrodynamics, meteorological patterns and turbidity that influence the amount of light reaching the benthic assemblage (Anthony et al. 2004) and alter the energy balance of corals (Anthony and Fabricius 2000). Weather-dependent resuspension of sediments that lead to so-called turbidity events are a natural feature of coastal coral reefs (Orpin et al. 2004). These events may result in sudden changes in irradiance as well as the remobilisation of particulate nutrients into the water column (Alongi and McKinnon 2005). Comparisons of benthic irradiance (E_z) with the minimum saturating irradiance (E_k) showed that corals may switch between periods of light limitation ($E_z < E_k$) and light stress ($E_z > E_k$) on time-scales of days to weeks in response to changing turbidity (Anthony et al. 2004). The extent of these turbidity events on the Great Barrier Reef (GBR) is currently poorly understood.

Super-imposed on these short-term events are seasonal changes in daily insolation (Kirk 1994), SST and terrestrial runoff (Wolanski et al. 2008) that alter environmental conditions on coral reefs. Studies from the Indo-Pacific and Caribbean have shown that the density and pigment content of *Symbiodinium* are regulated by seasonal variations in SST (Brown et al. 1999b;

Fagoonee et al. 1999; Fitt et al. 2000), irradiance (Stimson 1997; Brown et al. 1999b) and water quality (Stimson 1997; Fagoonee et al. 1999). Seasonal differences in photo-physiology have also been reported for corals in the Caribbean and Red Sea (Warner et al. 2002; Winters et al. 2006). Studies from the GBR have shown that the tissue layer of colonies of *Porites* is significantly thicker in summer than in winter (Barnes and Lough 1992) and that lipid content varies seasonally in relation to spawning cycles in seven coral species (Leuzinger et al. 2003). Pillay et al. (2005) reported that symbiont density increases 2-fold with the onset of winter in *Acropora millepora* from the central GBR while Hill and Ralph (2005) showed that daily diel changes in irradiance has a greater influence on photo-physiology than seasonal variation for three coral species from the southern GBR. Recently, Ulstrup et al. (2008) demonstrated seasonal regulation of coral photo-physiology, with non-photochemical quenching being higher in summer than in winter. To date, no studies have examined seasonal variation in coral bioindicators within the context of temporal variation in water quality on the GBR.

To use coral bioindicators as response measures of the effects of changes in water quality requires an understanding of both spatial and temporal patterns of variation of such measures. The aim of this study was to obtain estimates of the seasonal and temporal variability of a range of bioindicators in coastal corals on the GBR including symbiont density, concentrations of chlorophyll *a*, skeletal density and colony brightness of *Pocillopora damicornis*, as well as colony brightness and density of macro-bioeroders in colonies of massive *Porites*. Specifically, the objectives of this study were to (1) quantify temporal changes in environmental parameters such as turbidity, benthic irradiance, SST and water column nutrients, and develop potential stress thresholds for turbidity; (2) test the hypothesis that variations in environmental conditions can be measured as a response in coral bioindicators at a coastal coral reef of the GBR; and (3) investigate the significance of the relationships between bioindicators and environmental parameters to assess their specificity to changes in water quality.

6.2 Materials and methods

6.2.1 Study area and sampling design

To quantify temporal variation in coral bioindicators and environmental parameters, a study location was selected in the coastal zone of the GBR, i.e. within the 20 m isobath (Alongi and McKinnon 2005), while two reference locations were selected at nearby mid-shelf reefs. Sampling at the coastal location was undertaken at Horseshoe Bay (19° 06.5'S, 146° 50.2'E) on the northern side of Magnetic Island, a continental island located in the northward-facing Cleveland Bay approximately 7 km from the city of Townsville (Queensland, Australia; Fig. 6.1). The main influences on water quality in Cleveland Bay are wind-driven resuspension of sediments (Larcombe et al. 1995; Orpin et al. 2004), although three rivers may also influence water quality

in the bay. These are the Ross River that flows through Townsville, and the Haughton and Burdekin Rivers located ~40 km and ~90 km, respectively, to the south. The rivers differ markedly in catchment size: ~1,700 km^2, 4,000 km^2 and ~130,000 km^2, and estimated annual runoff: 0.49 km^3, 0.74 km^3 and 10.49 km^3 for the Ross, Haughton and Burdekin Rivers, respectively (Furnas 2003). The Burdekin River is likely to have a greater influence on water quality during episodic runoff events than the smaller Ross and Haughton Rivers. In addition to these rivers, there are several small creeks, e.g. Endeavour Creek and Gorge Creek, with catchments dominated by natural vegetation and low-scale urbanisation that flow into Horseshoe Bay. These small creeks are likely to have localised effects on water quality in Horseshoe Bay. The reference locations were Davies (18° 49.6'S, 147° 37.8'E) and Broadhurst Reefs (18° 52.3'S, 147° 42.4'E), which are both located ~60 km from the Australian mainland and thus distant from most terrestrial influences (Fig. 6.1). The general sampling design used for the study comprised each of three sampling events within each of 2 seasons: dry (June to November inclusive) and wet (December to May inclusive) over a 2-year period from 2005 to 2007 at each of the three locations. Coral and water samples were collected in June, September and October 2005 (Year 1, Dry Season); February, March and April 2006 (Year 1, Wet Season); July, September and October 2006 Year 2, Dry Season); and March, April and May 2007 (Year 2, Wet Season).

6.2.2 Weather data

Total monthly rainfall for Townsville region during the study period was obtained from the Bureau of Meteorology (www.bom.gov.au/weather/qld/townsville/observations.shtml). SST, surface irradiance (µmol photons m^{-2} s^{-1}) and wind speed (m s^{-1}) recorded at 30 min intervals for Cleveland Bay and Davies Reef were obtained from automatic weather stations (AWS) operated by the Australian Institute of Marine Science (www.aims.gov.au/pages/facilities/weather-stations/weather-data.html). The Cleveland Bay AWS (19° 09'S, 147° 53'E) is located ~6 km from the Horseshoe Bay study site off the south-eastern side of Magnetic Island, while the Davies Reef AWS (18° 50'S, 147° 41'E) is ~500 m from the study site. Weather conditions were assumed to be comparable at Broadhurst Reef, situated ~10 km south of Davies Reef, hence weather data from the Davies Reef AWS were used as explanatory variables for Broadhurst Reef. From the weather data, mean SST, mean total daily surface irradiance (mol photons m^{-2} d^{-1}) and mean wind speed (m s^{-1}) were calculated for the 14 d preceding each sampling event as per Brown et al. (1999b). Mean wind speed from the Cleveland Bay AWS was used to provide an indication of the effects of wave height, and hence resuspension of sediments within Cleveland Bay (as described by Anthony et al. 2004), which was considered to be representative of conditions in nearby Horseshoe Bay.

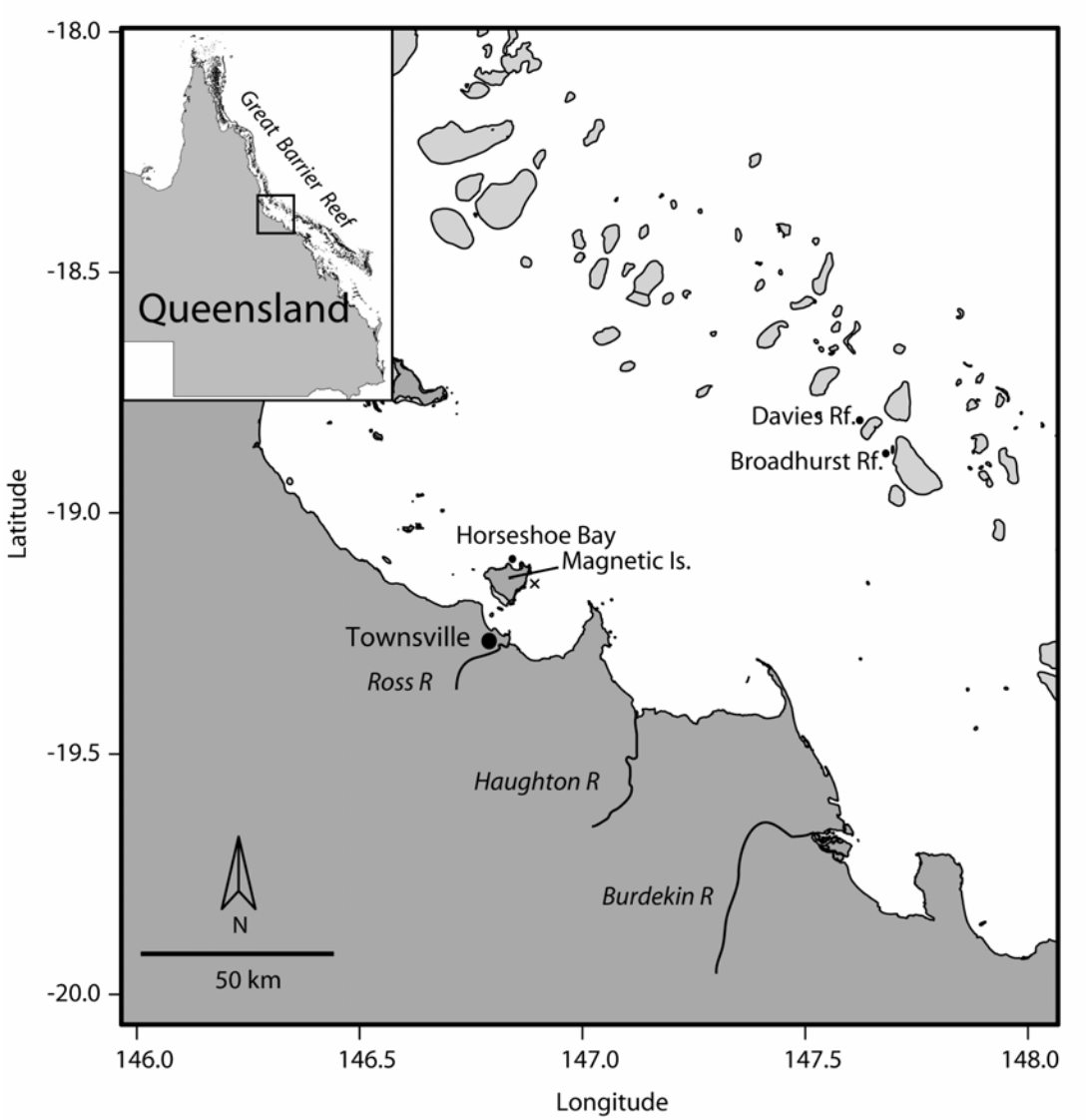

Fig. 6.1. Map of study locations at Horseshoe Bay on Magnetic Island (coastal) and Davies and Broadhurst Reefs (mid-shelf). ✕ Cleveland Bay AWS.

6.2.3 Turbidity and benthic irradiance

Turbidity and benthic irradiance loggers (JCU MK8, James Cook University, Townsville) were deployed at Horseshoe Bay (2.0 m below lowest astronomical tide, LAT) and Davies Reef (2.8 m below LAT) during the study. Turbidity was measured as nephelometric turbidity units (NTU) with optical backscatter sensors (Ridd and Larcombe 1994). Benthic irradiance was measured with a cosine-corrected light sensor measuring photosynthetically active radiation (PAR) between 400 to 700 nm. Both sensors were housed in the same unit. The light sensor was calibrated in water against a LI-192 light sensor (LI-COR, Nebraska, USA). The loggers measured turbidity and benthic irradiance every ten minutes (comprising 20 measurements integrated over 10 s).

Each logger had a cleaning mechanism to maintain the surface of the sensors free of bio-fouling (Ridd and Larcombe 1994).

The relationship between turbidity and attenuation coefficient for downward irradiance K_d (PAR) for the coastal location was examined using data recorded at noon by the turbidity and irradiance logger at Horseshoe Bay and the Cleveland Bay AWS. The noon K_d values were determined following rearrangement of Beer-Lambert's Law:

$$K_d = \ln(E_z/E_0)/z \qquad (1)$$

where E_z is noon benthic irradiance recorded by the logger, E_0 is irradiance beneath the surface determined from the surface irradiance at the Cleveland Bay weather station and corrected for 5% surface reflectance (Kirk 1994) and z is water depth above the logger in metres determined as the sum of the logger depth below LAT and the corresponding noon tide height. As data were being compared from a time series spanning a 2-year period, it was necessary to normalise each K_d value for changes in solar zenith angle following Mobley (1994) using:

$$S_{ZAuw} = \arcsin(\sin(S_{ZA})/1.34) \qquad (2)$$

where S_{ZA} is the solar zenith angle above the water, 1.34 is the refractive index of seawater and S_{ZAuw} is the solar zenith angle underwater. The noon K_d values for each day were then normalised by:

$$K_{dn} = K_{dm}\cos(S_{ZAuw}) \qquad (3)$$

where K_{dn} is the normalised value and K_{dm} is the measured value.

6.2.4 Water column nutrients

Surface water was sampled at each of two sites (separated by ~200 m) within each location during each sampling event to measure chlorophyll *a*, phaeophytin, particulate nitrogen (PN), particulate phosphorus (PP), particulate organic carbon (POC), dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), dissolved organic nutrients (DON and DOP) and total suspended solids (TSS). Analysis of the water samples followed standard analytical procedures described in Chapter 2. A water quality index (WQI) was calculated for each season using sites and sampling events as replicates and derived from the sum of z-score transformations for the water column nutrient variables measured at each of the sampling locations (further details in Fabricius and De'ath (2004) and Fabricius et al. (2005). The parameters used to calculate the WQI included chlorophyll *a*, phaeophytin, PN, PP, POC, DIN, DIP, DON, DOP and TSS.

6.2.5 Coral indicators

Apical branches (~6 cm long) of *Pocillopora damicornis* were collected from the centre of each of six colonies at 1 – 3 m below LAT during each sampling event at sites within each of the three locations and frozen at -20°C pending further analysis. Physiological parameters analysed included determinations of symbiont density, chlorophyll *a* and skeletal density. Each coral sample was placed into a plastic bag with filtered (0.2 μm) seawater and the tissue stripped from the skeleton using an air gun. The resulting tissue slurry was then homogenised for 30 s using a tissue grinder and divided into sub-samples of known volume for determinations of density of symbionts and chlorophyll *a*. The density of symbiont cells was determined with eight replicate counts in a Neubauer Improved haemocytometer (Brand, Wertheim, Germany). The determination of chlorophyll *a* comprised a double extraction using acetone (100%) for 24 h in darkness at 4°C. The optical properties of the combined extracts were measured using a Shimadzu UV-1700 Spectrophotometer (Shimadzu Corporation, Kyoto, Japan). Levels of chlorophyll *a* were determined using the formula from Jeffrey and Humphrey (1975) after correction for the volume of the homogenate and solvent. The density of symbionts and concentrations of chlorophyll *a* were normalised to surface area of the coral branch determined by wax dipping (Stimson and Kinzie 1991). Skeletal density (ρ_s) of *P. damicornis* was determined as the ratio between dry weight and buoyant weight following the procedures described by Anthony et al. (2002).

Colony brightness and density of macro-bioeroders were recorded for colonies of massive *Porites* occurring in belt transects (100 m long x 3 m wide) during each sampling event at each of the three locations described above. Colony brightness was estimated visually using a colour chart (Siebeck et al. 2006). Macro-bioeroders on each colony were counted on small colonies, but sub-sampled with three replicate 25 x 25 cm quadrats for larger (i.e. >1 m diameter) colonies.

6.2.6 Statistical analyses

Principal Components Analysis (PCA) was used to examine the relationships of the physiological variables of *P. damicornis* among the study locations and times of sampling with the environmental variables. Data were log-transformed prior to the PCA. Differences in the concentrations of water quality parameters and the bioindicators between years (2 levels: random) and seasons (2 levels: fixed, orthogonal), and among locations (3 levels: random, orthogonal) at each of three times (3 levels: random, nested) were analysed with a four factor analysis of variance (ANOVA). Data were tested for deviations from the assumption of homogeneity of variances and transformed if necessary. Untransformed data were used if transformations failed to stabilise heterogeneous variances but the level of significance, α, was reduced from 0.05 to 0.01 to reduce the chance of making a Type I error (Underwood 1981). Pooling procedures involving

elimination of terms from the mean square estimates were done if a term was non-significant at $P > 0.25$ (Underwood 1997). Means for significant factors in the ANOVA were compared using Student Newman Keuls (SNK) tests.

Predictive models were used to determine which environmental variables best explained the patterns of variation of the response variables of *P. damicornis* and *Porites*. These analyses involved fitting a full linear model using all of the predictors (environmental variables) with terms dropped one at a time from the overall model. The best models were then selected based on the Akaike Information Criterion (AIC) (Akaike 1974; Burnham and Anderson 2002), which is a measure of the goodness of fit of the estimated model to the data. Once the models were selected, comparisons of indicators in *P. damicornis* and *Porites* were done using ANOVA. The model selection was done using the statistical software R (R Development Core Team 2006).

6.3 Results

6.3.1 Weather data

There were several weather events that influenced water quality at the study locations during the 2-year study period. Severe Tropical Cyclone (TC) Larry was classed a Category 4 storm (maximum wind gusts to 240 km h^{-1}) when it crossed the North Queensland coast ~250 km north of the study area on 20th March 2006. The main influence of the cyclone on the Horseshoe Bay location was strong winds generating swells that resuspended bottom sediments.

The monthly rainfall record for the Townsville region was consistent with a monsoonal influence with greatest rainfall occurring between January and April compared with June to November for both years. In early February 2007, intense rainfall resulted in major flooding to North Queensland catchments between Cairns and Mackay. In the Townsville region, total rainfall for the period between 30th January and 8th February 2007 was approximately 700 mm and major flooding was reported for several rivers in the region including the Ross, Haughton and Burdekin Rivers (Bureau of Meteorology 2007). A satellite image taken on 10th February 2007 clearly shows flood plumes emerging from rivers along the North Queensland coast (Fig. 6.2). Upon reaching the coastal zone, the flood plumes formed a continuous, northward moving plume with an exit point from the GBR lagoon at the Grafton Passage, which is consistent with a recent study that suggested siliciclastic material is transported along the shelf leaving the GBR through interreef passages in the Cairns region and ultimately deposited in the Queensland Trough (Francis et al. 2007). Records maintained by the Bureau of Meteorology indicate that this was a ‘1 in 5 year’ flood event for the Burdekin River (P. Baddiley, Hydrologist, Bureau of Meteorology, pers. comm., 2007).

Data of SST and irradiance during the study period are shown in Fig. 6.3. Sea surface temperatures at Magnetic Island reached a maximum of 31.43°C (December 2005) and 30.45°C (March 2007) and a minimum of 20.70°C (July 2005) and 20.33°C (July 2006) in Year 1 and 2, respectively. The mean summer SST at Magnetic Island in Year 1 was 29.82 ± 0.01°C whereas the summer of Year 2 was cooler with mean SST of 28.10 ± 0.01°C. At Davies Reef, the modulation of SST was not as great as at Magnetic Island reaching a maximum of 29.75°C (January 2006) and 29.12°C (March 2007) and a minimum of 22.72°C (July 2005) and 22.54°C (August 2006) in Year 1 and 2, respectively. The mean summer SST at Davies Reef in Year 1 was 28.64 ± 0.01°C whereas the summer of Year 2 was cooler with a mean SST of 27.55 ± 0.01°C. In general, SST oscillated within a range of ~10°C between seasons at Magnetic Island and ~7°C at Davies Reef during both years (Fig. 6.3).

Surface irradiance showed seasonally determined variation at both locations. At Magnetic Island, mean total daily surface irradiance (28 d mean ± SE) reached a maximum during the summer months at 55.6 ± 1.2 mol photons m^{-2} d^{-1} (February 2006) and 55.6 ± 2.0 mol photons m^{-2} d^{-1} (December 2006) with a minimum of 28.2 ± 1.5 mol photons m^{-2} d^{-1} (June 2005) and 27.7 ± 1.4 mol photons m^{-2} d^{-1} (June 2006) in Year 1 and 2, respectively. Similarly, at Davies Reef, mean total daily surface irradiance reached a maximum of 50.0 ± 1.0 mol photons m^{-2} d^{-1} (October 2005) and 51.1 ± 2.5 mol photons m^{-2} d^{-1} (November 2006) with a minimum of 30.9 ± 1.5 mol photons m^{-2} d^{-1} (June 2005) and 24.6 ± 1.4 mol photons m^{-2} d^{-1} (June 2006) in Year 1 and 2, respectively (Fig. 6.3).

The mean wind speed for the study period at Magnetic Island was 5.53 ± 0.01 m s^{-1} and only exceeded 15 m s^{-1} when TC Larry passed to the north of the study area in March 2006 and during the flood event in February 2007 (Fig. 6.4). At Davies Reef, the mean wind speed for the study period was 7.40 ± 0.02 m s^{-1} with winds greater than 20 m s^{-1} recorded in July 2006 and February 2007.

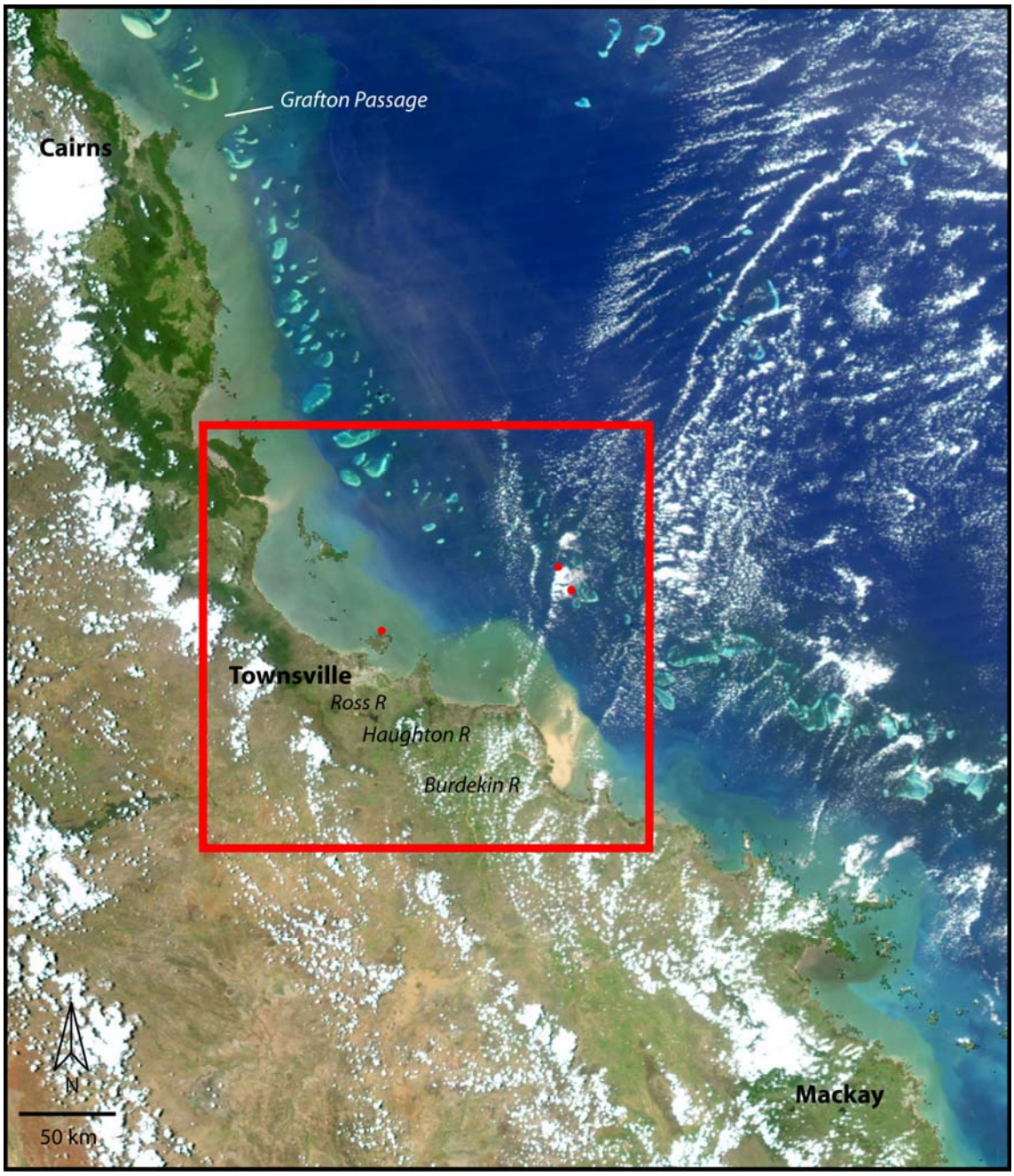

Fig. 6.2. MODIS-aqua satellite image of a flood event on the Great Barrier Reef taken 10th February 2007. Red line shows study area in Fig.1, red dots indicate study locations. Image downloaded from Ocean Colour Web (Feldman and McClain 2007) and processed by SeaDAS (Baith et al. 2001). Image courtesy M Slivkoff.

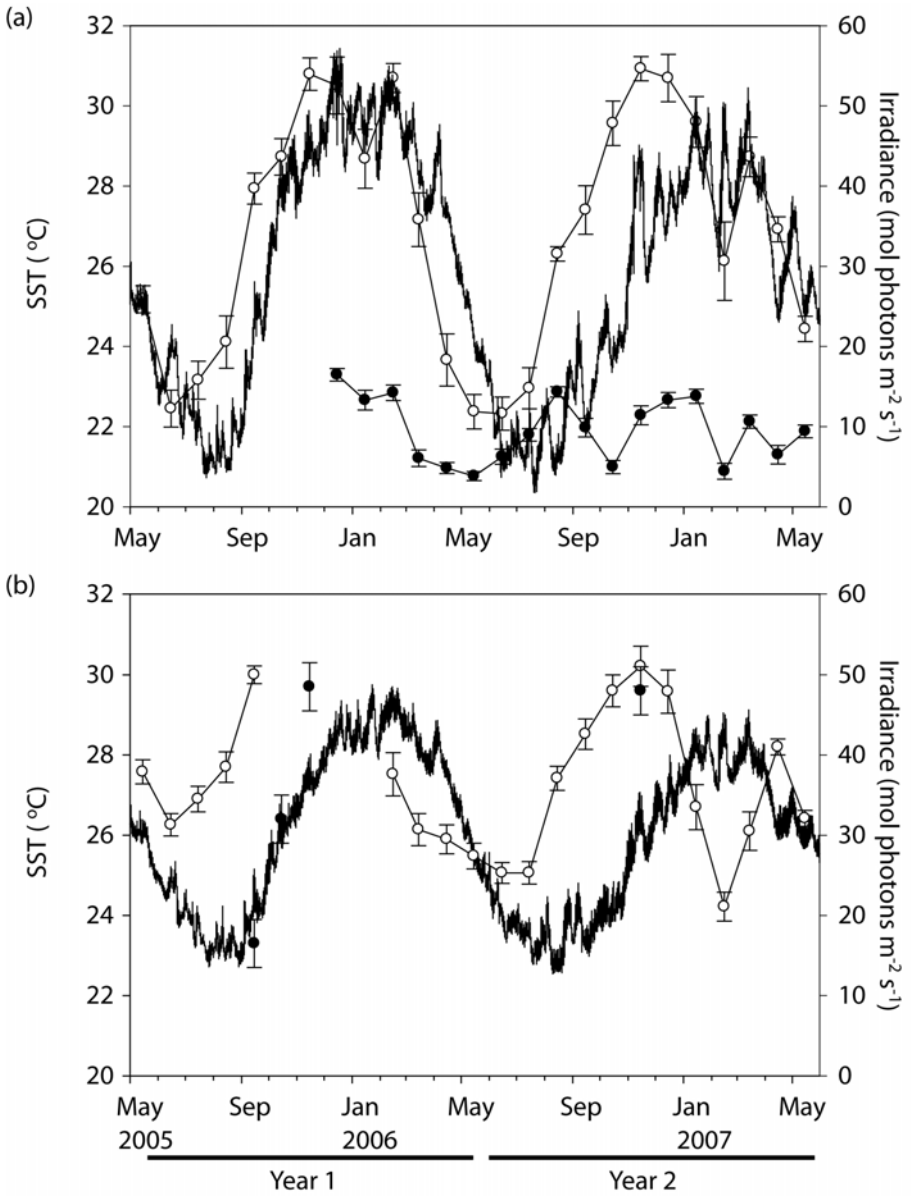

Fig. 6.3. Sea surface temperature (°C, solid line) and monthly mean (28 d ± SE) total daily irradiance (mol photons m^{-2} d^{-1}) at the surface (○) recorded by an automated weather station, and benthic irradiance (●), recorded at (a) Horseshoe Bay and (b) Davies Reef. Gaps in the time-series are missing data due to instrument malfunction.

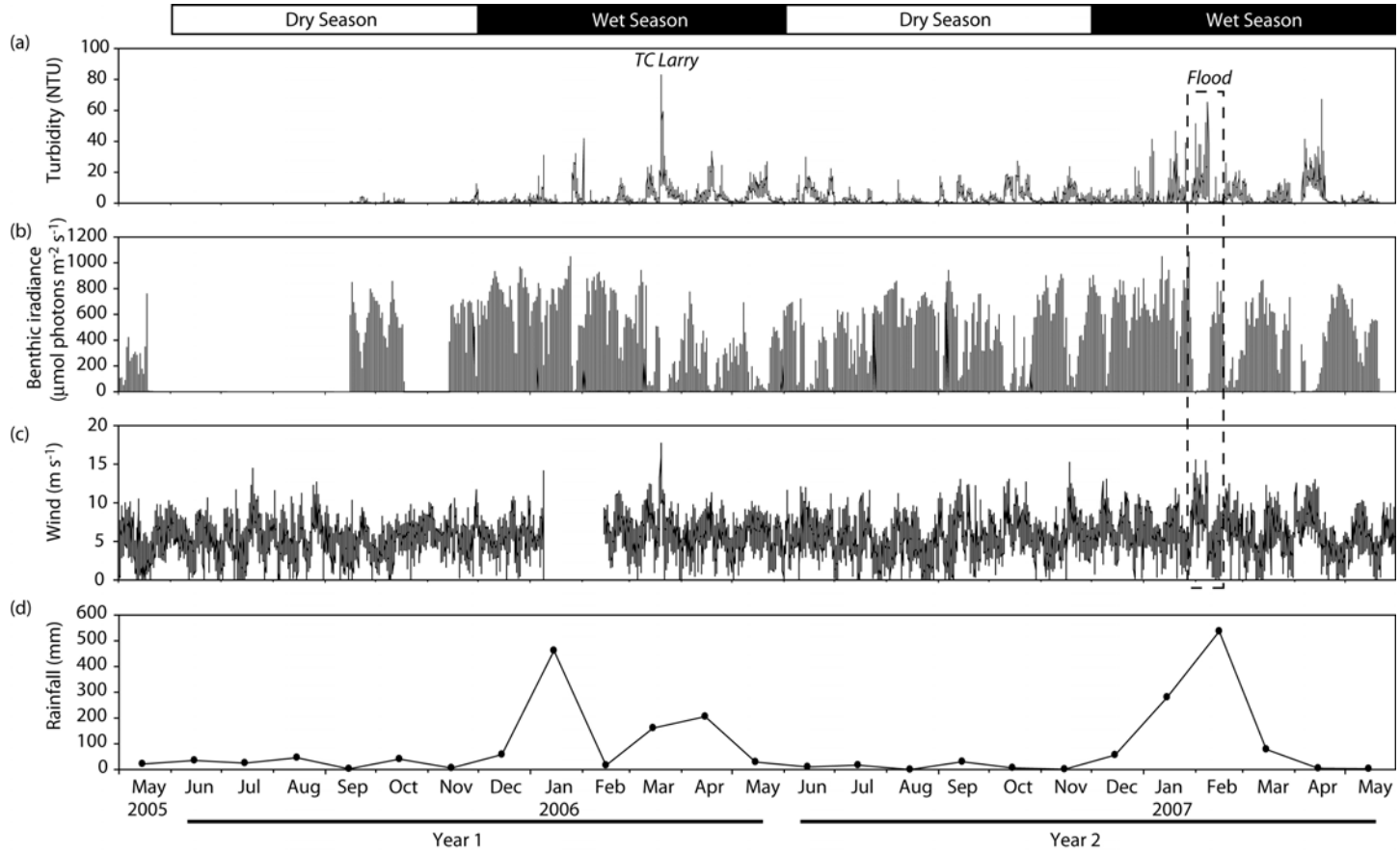

Fig. 6.4. (a) Turbidity (NTU), (b) benthic irradiance (µmol photons m^{-2} s^{-1}), (c) wind speed (m s^{-1}) and (d) total monthly rainfall during study. (a) and (b) recorded by a logger at a shallow depth (2 m below LAT) on the fringing reef at Horseshoe Bay, (c) recorded at by Cleveland Bay AWS. Gaps in the time-series during Dry Season of Year 1 for (a) and (b), and Wet Season of Year 1 for (c), are missing data due to instrument malfunction. Dashed line denotes time series shown in Fig. 6.5.

6.3.2 Turbidity and benthic irradiance

The maximum hourly turbidity recorded during the study was ~83 NTU when TC Larry passed to the north of the study site at Horseshoe Bay. Turbidity remained above ~5 NTU and mean wind speed was 7.03 ± 0.65 m s^{-1} at this location for a period of approximately 10 d following the cyclone in March 2006 (Fig. 6.4). There were another three weather-dependent turbidity events at Horseshoe Bay where levels remained elevated around 5 NTU for periods of ≥ 5 d in March, April and May of Year 1. Turbidity at Davies Reef changed very little during these turbidity events in Year 1 and rarely exceeded 1 – 2 NTU. In Year 2, there were at least six weather-dependent turbidity events where levels remained elevated around 5 NTU for periods of ≥ 5 d in June, September, October and November 2006 and January and March/April 2007 (Fig. 6.4). Interestingly, for a four week period in March/April 2007 following the flood event in February 2007, turbidity at Horseshoe Bay averaged 9.2 ± 0.2 NTU reaching a maximum hourly turbidity of 67 NTU on 17th April 2007 (Fig. 6.4). This turbidity event coincided with a mean wind speed over the four weeks of 6.86 ± 0.37 m s^{-1}.

Changes in benthic irradiance at Horseshoe Bay related inversely to turbidity (Fig. 6.4). The mean total daily benthic irradiance recorded at this location for a 10 d period after TC Larry was 1.3 ± 0.5 mol photons m^{-2} d^{-1}. There were similar decreases in irradiance during the turbidity events in both years (Fig. 6.4). For example, during the 4 week turbidity event in March/April 2007 (Year 2), the mean total daily benthic irradiance recorded at Horseshoe Bay was 5.8 ± 0.9 mol photons m^{-2} d^{-1} (Fig. 6.4).

During the flood event in February 2007, the mean turbidity and total daily benthic irradiance (10 d mean ± SE) were 13.0 ± 0.7 NTU and 0.7 ± 0.5 mol photons m^{-2} d^{-1}, respectively (Fig. 6.5). Strong winds coincided with the commencement of flooding and the mean wind speed during the flood event was 8.69 ± 0.61m s^{-1}. Thus, the increase in turbidity observed at the start of the flood event was due in part to resuspension of sediment adjacent to the reef, in addition to the influence of the flood plume (Fig. 6.2).

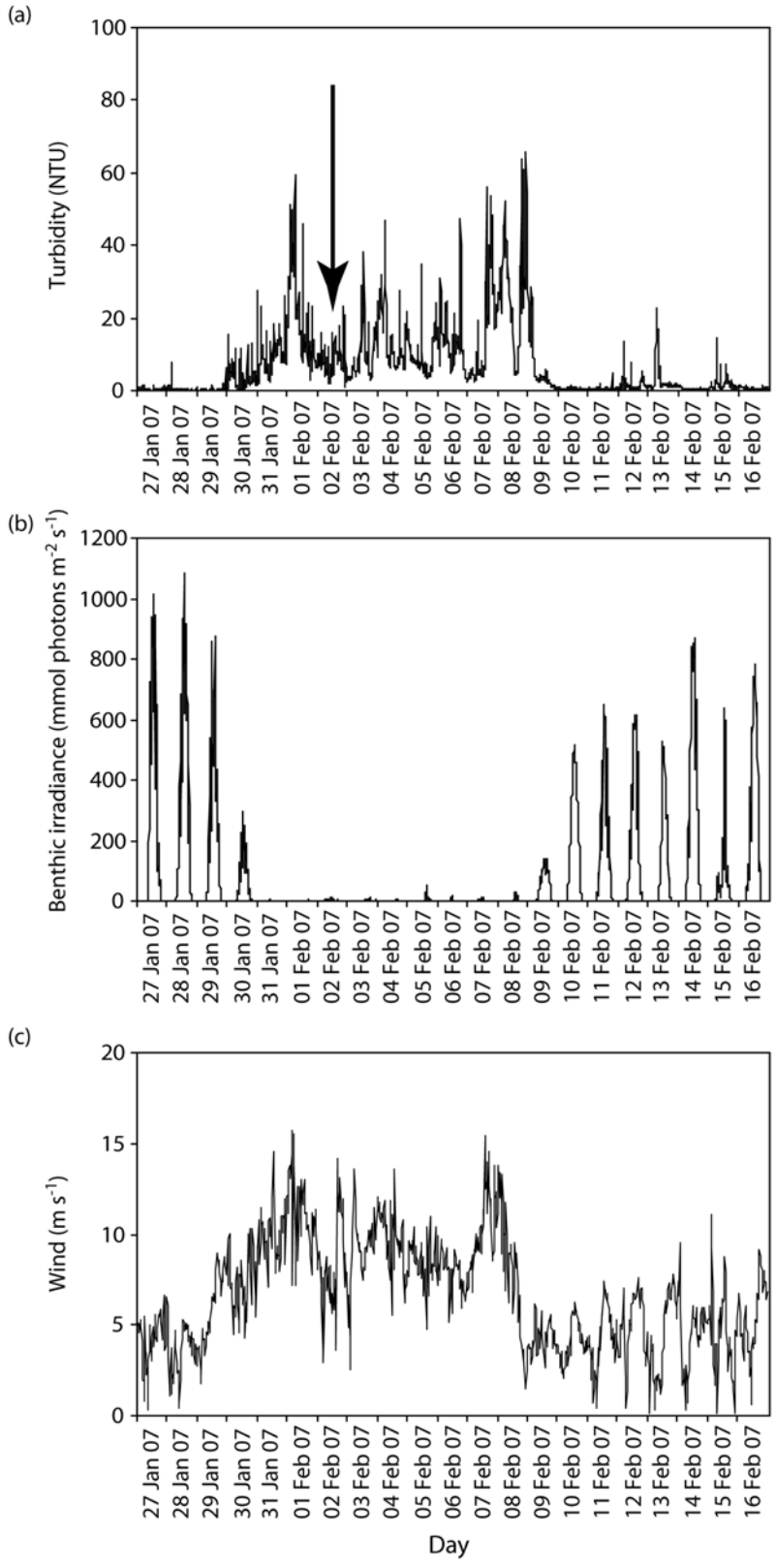

Fig. 6.5. (a) Turbidity (NTU), (b) benthic irradiance (μmol photons m^{-2} s^{-1}) and (c) wind speed (m s^{-1}) recorded during the flood event in February 2007. Arrow indicates the commencement of major flooding in the Haughton River. A peak level of 3.8 m was recorded above the Burdekin Falls Dam spillway on 4th February 2007 (Bureau of Meteorology 2007).

The simultaneous measurement of light and turbidity by a logger provided insight to the effect of changes in turbidity on benthic irradiance and the attenuation coefficient for downward irradiance (K_d) on the fringing reef (depth of ~3.5 m) at Horseshoe Bay. Exploratory analysis showed an inverse relationship between noon benthic irradiance and turbidity with the extinction of benthic irradiance at ~3.5 m when turbidity exceeded ~15 NTU at Horseshoe Bay (Fig. 6.6a). However, as data were being compared for noon irradiance from a time series spanning 2-years, it was necessary to account for differences in the water depth of the logger, i.e. tidal regime, and also for changes in solar zenith angle. Comparisons of the normalised K_d and turbidity showed a linear relationship that explained approximately 68% of the variance between these parameters (Fig. 6.6b). From this relationship, an increase in turbidity to 3 NTU, a level commonly reached during this study, resulted in a ~88% reduction in irradiance intensity to levels around 200 µmol photons m^{-2} s^{-1} on the fringing reef at Horseshoe Bay.

6.3.3 Water column nutrients

There were temporal differences in concentrations of water quality parameters such as chlorophyll *a*, particulate nitrogen and phosphorus, particulate organic carbon, dissolved inorganic nitrogen and dissolved organic phosphorus; however this variability occurred at small temporal scales with differences detected among times of sampling within each of the seasons and years (Fig. 6.7). For example, there was great variation among sampling times for concentrations of chlorophyll *a* and particulate nutrients especially in October 2006 (Fig. 6.7), which followed a turbidity event in Horseshoe Bay whereby turbidity averaged 8.29 ± 0.11 NTU for a period of 16 d (Fig. 6.4). Dissolved organic nitrogen varied inconsistently between years and seasons, and among locations. At Broadhurst Reef, concentrations of dissolved organic nitrogen were greater in the Dry compared with the Wet Season of Year 1 but there were no differences between seasons or years at the other locations ($F_{2,16} = 1.12$, $P = 0.0227$; Table 6.1, Fig. 6.7). There were no differences between years and seasons or among locations for concentrations of dissolved inorganic phosphorus (Fig. 6.7). In addition to these temporal differences, the patterns of variation for some water quality parameters were also characterised by differences among locations. For example, concentrations of chlorophyll *a* ($F_{2,16} = 7.32$, $P = 0.0055$; Table 6.1, Fig. 6.7) were approximately 2-fold greater at Horseshoe Bay (0.66 ± 0.14 µg L^{-1}) than Davies (0.25 ± 0.03 µg L^{-1}) or Broadhurst Reefs (0.29 ± 0.03 µg L^{-1}). A similar pattern occurred for particulate organic carbon ($F_{2,36} = 17.34$, $P = 0.0001$; Table 6.1, Fig. 6.7) with levels approximately 1.7-fold greater at Horseshoe Bay (21.60 ± 3.52 µmol L^{-1}) than Davies (12.96 ± 1.33 µmol L^{-1}) or Broadhurst Reefs (12.91 ± 1.17 µmol L^{-1}).

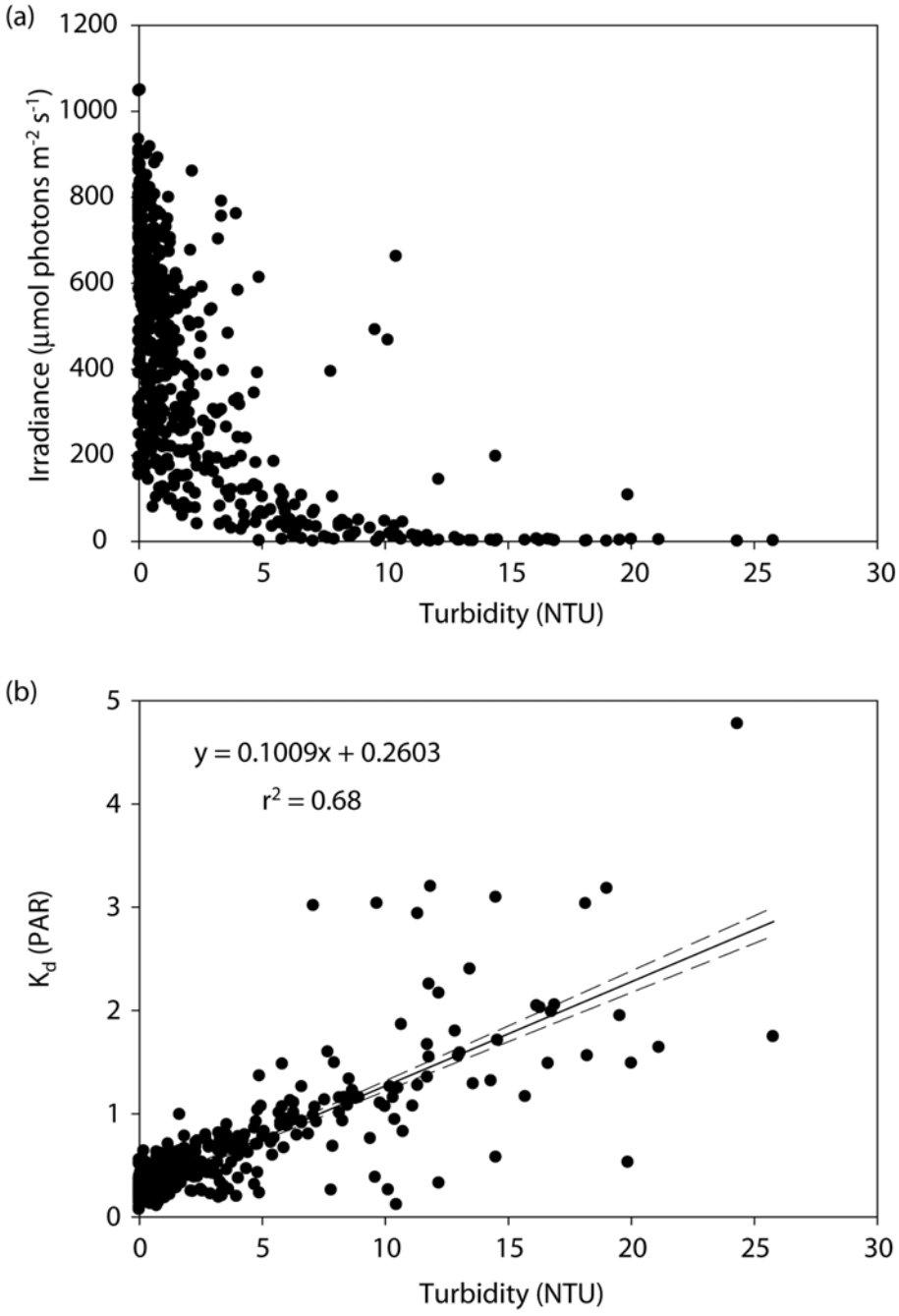

Fig. 6.6. Relationship between (a) benthic irradiance at noon and turbidity, and (b) the attenuation coefficient for noon downward irradiance (K_d), corrected for tide and solar zenith angle, and turbidity recorded by a logger deployed at 2 m depth at Horseshoe Bay between May 2005 and May 2007. Dashed lines are 95% confidence intervals.

Table 6.1. Summary of four factor ANOVAs comparing water quality variables between years and seasons, and among locations on the GBR. * denotes terms that were eliminated at $P > 0.25$. For *post hoc* tests, means (± SE) are untransformed and in ascending order. Underlined means were not significantly different from each other. Abbreviations: HB = Horseshoe Bay; DR = Davies Reef; BR = Broadhurst Reef.

Variate		Source of variation	df	MS	*F*	*P*	*F* vs.	*Post hoc* tests			
(a) Chlorophyll *a* (µg L^{-1})	1	Year	1	0.696	0.33	0.5808	4				
transform: ln(x)	2	Season	1	14.408	-	-	-				
C = 0.1725 (ns)	3	Location	2	4.979	7.32	0.0055	8	DR	BR	<	HB
	4	Time(Y x S)	8	2.100	3.09	0.0261	8	0.25	0.29		0.66
	5	Y x S	1	2.827	1.35	0.2795	4	0.05	0.05		0.20
	6	*Y x L	2	0.235	0.35	0.7126	8				
	7	S x L	2	0.163	0.24	0.7901	8				
	8	L x T(Y x S)	16	0.680	1.75	0.0812	10				
	9	*Y x S x L	2	0.314	0.46	0.6378	8				
	10	Residual	36	0.389							
(b) Total suspended solids (mg L^{-1})	1	Year	1	0.146	0.05	0.8344	4				
transform: none	2	Season	1	2.616	-	-	-				
C = 0.2102 (ns)	3	Location	2	18.825	13.83	0.0003	8				
	4	Time(Y x S)	8	3.138	2.31	0.0737	8				
	5	Y x S	1	0.031	0.01	0.9238	4				
	6	*Y x L	2	1.254	0.92	0.4180	8				
	7	S x L	2	0.408	0.30	0.7448	8				
	8	L x T(Y x S)	16	1.361	7.12	<0.0001	10				
	9	*Y x S x L	2	0.566	0.42	0.6667	8				
	10	Residual	36	0.191							

Variate		Source of variation	df	MS	*F*	*P*	*F* vs.	*Post hoc* tests			
(c) Particulate nitrogen (µmol L^{-1})	1	Year	1	1.922	1.60	0.2413	4				
transform: none	2	Season	1	0.078	-	-	-				
C = 0.3492 (*P* <0.05)	3	Location	2	1.480	5.13	0.0190	8				
	4	Time(Y x S)	8	1.200	4.16	0.0074	8				
	5	Y x S	1	0.024	0.02	0.8908	4				
	6	*Y x L	2	0.080	0.28	0.7627	8				
	7	S x L	2	0.019	0.07	0.9365	8				
	8	L x T(Y x S)	16	0.289	2.53	0.0105	10				
	9	*Y x S x L	2	0.053	0.18	0.8346	8				
	10	Residual	36	0.114							
(d) Particulate phosphorus (µmol L^{-1})	1	Year	1	10.238	-	-	-				
transform: ln(x)	2	Season	1	0.821	-	-	-				
C = 0.1997 (ns)	3	Location	2	10.995	8.00	0.1111	6				
	4	Time(Y x S)	8	1.278	2.67	0.0453	8				
	5	Y x S	1	0.000	0.00	0.9863	4				
	6	Y x L	2	1.374	2.86	0.0865	8				
	7	S x L	2	0.537	1.12	0.3508	8				
	8	L x T(Y x S)	16	0.480	8.07	<0.0001	10				
	9	*Y x S x L	2	0.335	0.70	0.5118	8				
	10	Residual	36	0.060							
(e) Particulate organic carbon (µmol L^{-1})	1	Year	1	1.223	1.00	0.3462	4				
transform: ln(x)	2	Season	1	1.560	-	-	-				
C = 0.1695 (ns)	3	Location	2	1.824	13.21	<0.0001	10	BR	DR	<	HB
	4	Time(Y x S)	8	1.221	8.84	<0.0001	10	12.91	12.96		21.60
	5	Y x S	1	1.227	1.00	0.3455	4	1.18	1.33		3.52

Variate		Source of variation	df	MS	*F*	*P*	*F* vs.	*Post hoc* tests
	6	*Y x L	2	0.126	0.91	0.4112	10	
	7	S x L	2	0.209	1.51	0.2345	10	
	8	*L x T(Y x S)	16	0.105	0.76	0.7148	10	
	9	*Y x S x L	2	0.001	0.01	0.9921	10	
	10	Residual	36	0.138				
(f) Dissolved inorganic nitrogen (µmol L^{-1})	1	Year	1	15.614	-	-	-	
transform: none	2	Season	1	1.445	-	-	-	
C = 0.7351 (*P* <0.01)	3	Location	2	1.650	1.92	0.3420	6	
	4	Time(Y x S)	8	1.733	3.98	0.0091	8	
	5	Y x S	1	2.641	-	-	-	
	6	Y x L	2	0.857	1.97	0.1723	8	
	7	S x L	2	0.181	0.23	0.8160	9	
	8	L x T(Y x S)	16	0.436	0.43	0.9649	10	
	9	Y x S x L	2	0.802	1.84	0.1910	8	
	10	Residual	36	1.023				
(g) Dissolved inorganic phosphorus (µmol L^{-1})	1	Year	1	0.002	0.47	0.5129	4	
transform: none	2	Season	1	0.020	-	-	-	
C = 0.4245 (*P* <0.01)	3	Location	2	0.002	1.23	0.3183	8	
	4	Time(Y x S)	8	0.003	2.45	0.0602	8	
	5	Y x S	1	0.009	2.88	0.1284	4	
	6	*Y x L	2	0.002	1.15	0.3423	8	
	7	S x L	2	0.002	1.31	0.2978	8	
	8	L x T(Y x S)	16	0.001	1.43	0.1806	10	
	9	*Y x S x L	2	0.000	0.27	0.7681	8	
	10	Residual	36	0.001				

Variate		Source of variation	df	MS	*F*	*P*	*F* vs.	*Post hoc* tests
(h) Dissolved organic nitrogen (µmol L^{-1})	1	Year	1	0.118	-	-	-	
transform: none	2	Season	1	1.825	-	-	-	
C = 0.2267 (ns)	3	Location	2	12.021	0.30	0.7669	6	
	4	Time(Y x S)	8	31.688	2.15	0.0918	8	
	5	Y x S	1	196.027	-	-	-	
	6	Y x L	2	39.549	2.68	0.0990	8	
	7	S x L	2	16.466	0.23	0.8125	9	
	8	L x T(Y x S)	16	14.748	1.12	0.3773	10	
	9	Y x S x L	2	71.340	4.84	0.0227	8	
	10	Residual	36	13.214				
(i) Dissolved organic phosphorus (µmol L^{-1})	1	Year	1	1.897	8.54	0.0192	4	
transform: none	2	Season	1	0.262	-	-	-	
C = 0.1897 (ns)	3	Location	2	0.067	0.20	0.8214	8	
	4	Time(Y x S)	8	0.222	0.66	0.7213	8	
	5	Y x S	1	4.113	18.52	0.0026	4	
	6	*Y x L	2	0.021	0.06	0.9402	8	
	7	S x L	2	0.124	0.37	0.6982	8	
	8	L x T(Y x S)	16	0.338	6.93	<0.0001	10	
	9	*Y x S x L	2	0.026	0.08	0.9267	8	
	10	Residual	36	0.049				

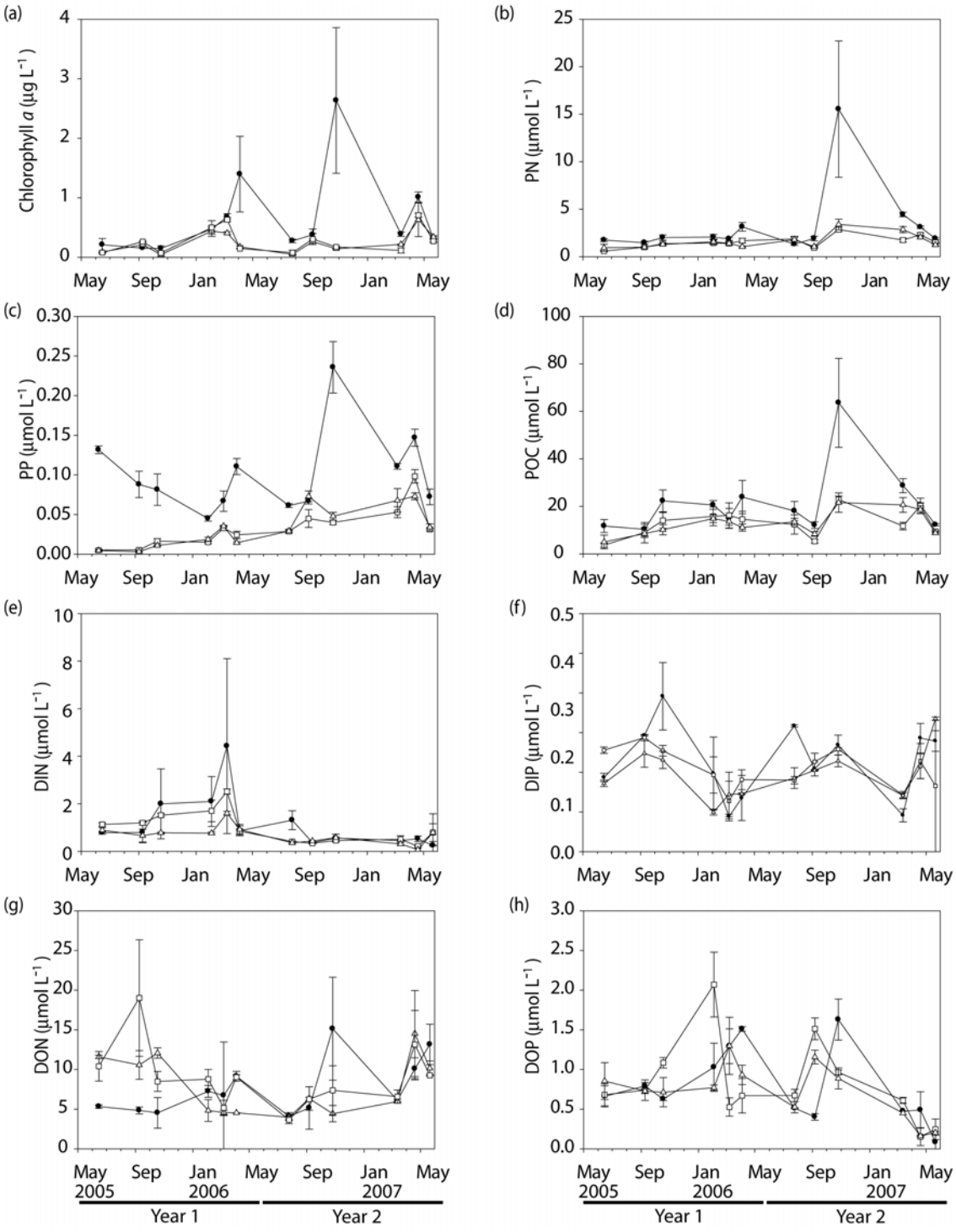

Fig. 6.7. Mean concentrations of water column (a) chlorophyll *a* (µg L^{-1}), (b) particulate nitrogen (µmol L^{-1}), (c) particulate phosphorus (µmol L^{-1}), (d) particulate organic carbon (µmol L^{-1}), (e) dissolved inorganic nitrogen (µmol L^{-1}), (f) dissolved inorganic phosphorus (µmol L^{-1}), (g) dissolved organic nitrogen (µmol L^{-1}), (h) dissolved organic phosphorus (µmol L^{-1}) sampled at Horseshoe Bay (●), and Davies (□) and Broadhurst Reefs (△).

6.3.4 Coral indicators

The PCA illustrated relationships of physiological variables of *P. damicornis* among each other and their distribution across the locations and times of sampling. Physiological measures of corals from Horseshoe Bay such as concentration of chlorophyll *a*, symbiont density and colony brightness of *P. damicornis* associated positively with the WQI and negatively with mean 14 d benthic irradiance (Fig. 6.8a). In general, physiological measures of corals from Horseshoe Bay tended to be spatially distinct from those at the mid-shelf reefs although there was some overlap of the measures during the study (Fig. 6.8a). The temporal PCA showed the physiological measures of *P. damicornis* grouped together in the Dry Season of Year 1 but there was no separation among seasons in Year 2 (Fig. 6.8b).

The patterns of variability of the coral indicators were dominated by inconsistent variation between years and seasons and among locations (Year x Season x Location interactions; Table 6.2). At Horseshoe Bay, the density of symbionts of *P. damicornis* was greater in the Dry than the Wet Season of Year 1 but there were no differences between seasons at this location in Year 2 nor between seasons for either year at Davies and Broadhurst Reef ($F_{2,16} = 7.08$, $P = 0.0063$; Table 6.2 and 6.3, Fig. 6.9). Similarly, the colonies of *P. damicornis* at Horseshoe Bay were darker in the Dry than the Wet Season of Year 1 but there were no differences between seasons at this location in Year 2 nor were there any differences for colony brightness between seasons for either year at Davies and Broadhurst Reef ($F_{2,16} = 7.03$, $P = 0.0064$; Table 6.2 and 6.3, Fig. 6.9). These patterns were similar for concentrations of chlorophyll *a* (μg cm^{-2}) of *P. damicornis,* which were greater in Dry compared with the Wet Season of Year 1 in Horseshoe Bay. However, this pattern was reversed in Year 2 where greater amounts of chlorophyll *a* occurred in the Wet than Dry Season ($F_{2,16} = 10.82$, $P = 0.0011$; Table 6.2 and 6.3, Fig. 6.9). The content of chlorophyll *a* per symbiont (pg $cell^{-1}$) varied inconsistently between years and seasons (Fig. 6.9). In Year 1, there was more chlorophyll *a* per symbiont in the Wet than Dry Season but there were no differences between seasons in Year 2 ($F_{1,16} = 8.42$, $P = 0.0032$; Table 6.2 and 6.3, Fig. 6.9). The density of macro-bioeroders of *Porites* differed among locations with more macro-bioeroders recorded at Horseshoe Bay than at either Davies or Broadhurst Reefs ($F_{2,2} = 104.35$, $P = 0.0095$; Fig. 6.9).

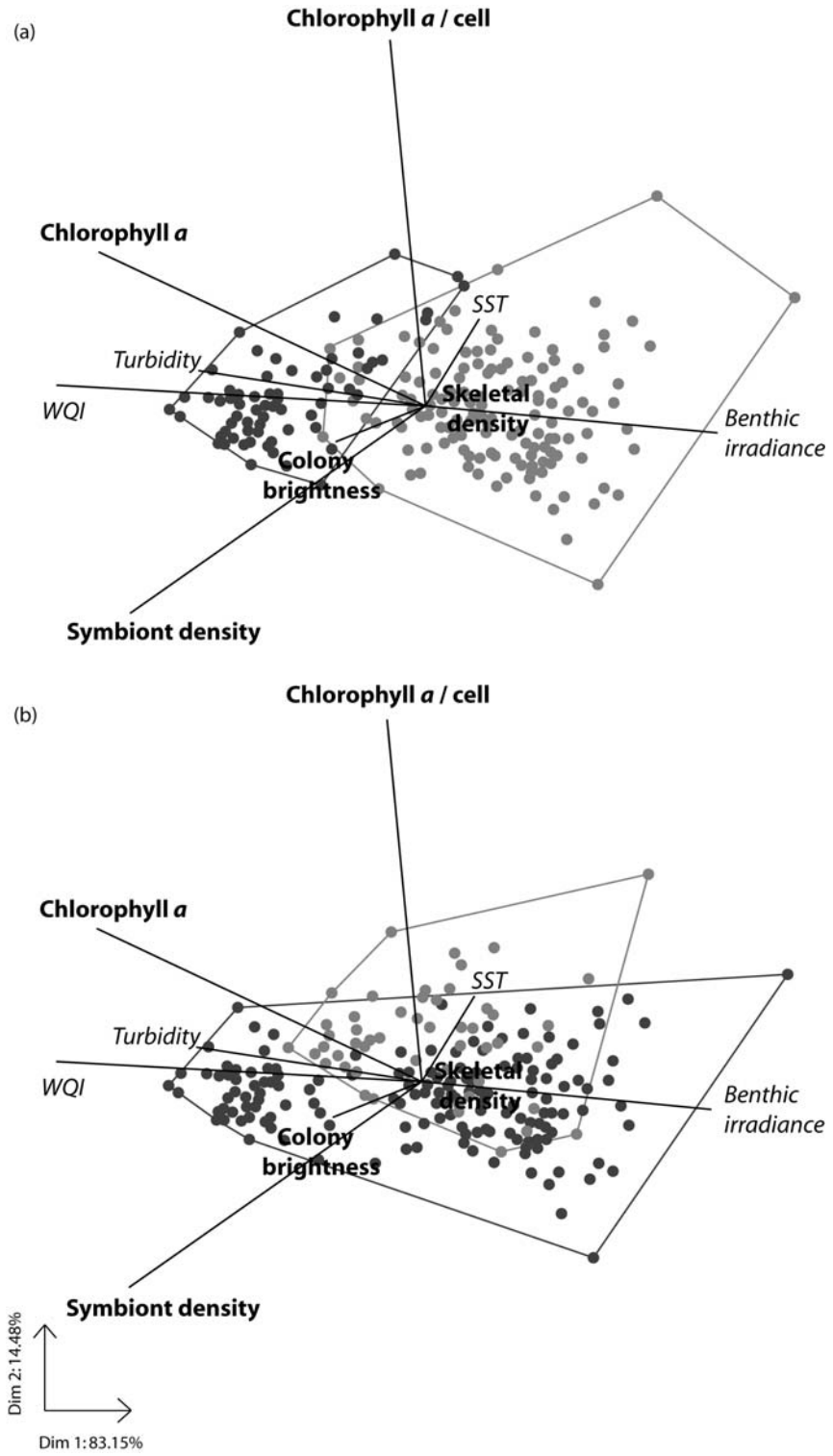

Fig. 6.8. Principal components biplot of physiological variables of *P. damicornis* grouped by (a) locations: Horseshoe Bay (dark grey) and mid-shelf reefs (light grey); and (b) seasons: Dry Season of Year 1 (light grey), and Wet Season of Year 1 and both Dry and Wet Season of Year 2 (dark grey). Environmental variables are over-laid on the plot. Abbreviations: *WQI* = water quality index, *SST* = sea surface temperature. Data for benthic irradiance, turbidity and SST are 14 d averages for time preceding each sampling event.

Table 6.2. Summary of four factor ANOVAs comparing physiological variables of (a – e) *Pocillopora damicornis* and (f – g) massive *Porites* between years and seasons, and among locations on the GBR. * denotes terms that were eliminated at $P > 0.25$.

Variate		Source of variation	df	MS	*F*	*P*	*F* vs.
(a) Symbiont density	1	Year	1	0.207	-	-	-
(cells cm^{-2})	2	Season	1	4.819	-	-	-
transform: ln(x)	3	Location	2	37.090	13.41	0.0694	6
C = 0.1223 (ns)	4	Time(Y x S)	8	0.485	1.41	0.2664	8
	5	Y x S	1	0.594	-	-	-
	6	Y x L	2	2.766	8.02	0.0039	8
	7	S x L	2	0.684	0.28	0.7811	9
	8	L x T(Y x S)	16	0.345	2.04	0.0127	10
	9	Y x S x L	2	2.440	7.08	0.0063	8
	10	Residual	180	0.169			
(b) Chlorophyll *a*	1	Year	1	0.016	-	-	-
(µg cm^{-2})	2	Season	1	0.136	-	-	-
transform: ln(x+1)	3	Location	2	34.607	20.48	0.0465	6
C = 0.0887 (ns)	4	Time(Y x S)	8	0.203	1.32	0.3016	8
	5	Y x S	1	0.182	-	-	-
	6	Y x L	2	1.690	10.98	0.0010	8
	7	S x L	2	0.218	0.13	0.8843	9
	8	L x T(Y x S)	16	0.154	1.76	0.0398	10
	9	Y x S x L	2	1.664	10.82	0.0011	8
	10	Residual	180	0.087			
c) Chlorophyll *a*/cell	1	Year	1	15.995	2.88	0.1281	4
(pg $cell^{-1}$)	2	Season	1	144.077	-	-	-
transform: none	3	Location	2	22.050	8.42	0.0032	8
C = 0.3073 ($P < 0.01$)	4	Time(Y x S)	8	5.552	2.12	0.0956	8
	5	Y x S	1	61.398	11.06	0.0011	4
	6	*Y x L	2	2.469	0.94	0.4102	8
	7	S x L	2	8.846	3.38	0.0598	8
	8	L x T(Y x S)	16	2.619	1.09	0.3716	10
	9	*Y x S x L	2	1.938	0.74	0.4927	8
	10	Residual	180	2.413			
(d) Skeletal density	1	Year	1	0.812	13.35	0.0065	4
(g cm^{-3})	2	Season	1	0.090	-	-	-
transform: none	3	Location	2	0.089	1.48	0.2579	8
C = 0.1365 ($P < 0.05$)	4	Time(Y x S)	8	0.061	1.01	0.4649	8
	5	Y x S	1	0.242	3.98	0.0811	4
	6	*Y x L	2	0.003	0.05	0.9519	8
	7	S x L	2	0.021	0.34	0.7156	8
	8	L x T(Y x S)	16	0.060	3.62	<0.0001	10
	9	*Y x S x L	2	0.032	0.53	0.6008	8
	10	Residual	180	0.017			

Variate		Source of variation	df	MS	*F*	*P*	*F* vs.
(e) Colony brightness	1	Year	1	1.852	-	-	-
P. damicornis	2	Season	1	8.167	-	-	-
transform: none	3	Location	2	96.501	19.40	0.0490	6
C = 0.2148 (*P* <0.01)	4	Time(Y x S)	8	0.563	1.12	0.4003	8
	5	Y x S	1	20.782	-	-	-
	6	Y x L	2	4.973	9.91	0.0016	8
	7	S x L	2	7.983	2.26	0.3066	9
	8	L x T(Y x S)	16	0.502	2.59	0.0012	10
	9	Y x S x L	2	3.529	7.03	0.0064	8
	10	Residual	180	0.194			
(f) Macro-bioeroders	1	Year	1	2.142	-	-	-
(m^{-2})	2	Season	1	0.196	-	-	-
transform: none	3	Location	2	987.201	104.35	0.0095	6
C = 0.0774 (*P* <0.01)	4	Time(Y x S)	8	4.127	1.97	0.0482	10
	5	Y x S	1	11.176	2.71	0.1385	4
	6	Y x L	2	9.460	4.51	0.0114	10
	7	S x L	2	3.013	1.44	0.2388	10
	8	*L x T(Y x S)	16	2.512	1.20	0.2649	10
	9	*Y x S x L	2	0.007	0.00	0.9966	10
	10	Residual	684	2.100			
(g) Colony	1	Year	1	0.009	-	-	-
brightness *Porites*	2	Season	1	0.584	-	-	-
transform: none	3	Location	2	133.690	711.70	0.0014	6
C = 0.0656 (ns)	4	Time(Y x S)	8	2.333	2.41	0.0636	8
	5	Y x S	1	0.059	-	-	-
	6	Y x L	2	0.188	0.19	0.8253	8
	7	S x L	2	15.867	5.47	0.1546	9
	8	L x T(Y x S)	16	0.967	2.51	0.0009	10
	9	Y x S x L	2	2.902	3.00	0.0781	8
	10	Residual	684	0.385			

Table 6.3. Summary of *post hoc* tests of physiological variables of *Pocillopora damicornis* and massive *Porites* between years and seasons and among locations on the GBR. Means (± SE) are untransformed and in ascending order. Underlined terms were not significantly different from each other. Abbreviations: HB = Horseshoe Bay, DR = Davies Reef, BR = Broadhurst Reef.

Variate	*Post hoc* tests								
(a) Symbiont density	Year x Season x Location:								
	Year 1 HB:	Wet	<	Dry	Year 1 DR:	Wet	Dry	Year 1 BR:	Wet	Dry
(cells cm^{-2})	Mean	$1.16x10^6$		$2.95x10^6$	Mean	$0.64x10^6$	$0.67x10^6$	Mean	$0.89x10^6$	$0.90x10^6$
	SE	$(0.10x10^6)$		$(0.12x10^6)$	SE	$(0.72x10^6)$	$(0.33x10^6)$	SE	$(0.09x10^6)$	$(0.06x10^6)$
	Year 2 HB:	Dry		Wet	Year 2 DR:	Wet	Dry	Year 2 BR:	Wet	Dry
	Mean	$2.88x10^6$		$3.06x10^6$	Mean	$0.59x10^6$	$0.80x10^6$	Mean	$0.72x10^6$	$0.75x10^6$
	SE	$(0.15x10^6)$		$(0.21x10^6)$	SE	$(0.11x10^6)$	$(0.07x10^6)$	SE	$(0.11x10^6)$	$(0.08x10^6)$
(b) Chlorophyll *a* (μg cm^{-2})	Year x Season x Location:								
	Year 1 HB:	Wet	<	Dry	Year 1 DR:	Dry	< Wet	Year 1 BR:	Dry	Wet
	Mean	7.46		10.96	Mean	1.89	3.57	Mean	3.20	4.35
	SE	(0.42)		(0.46)	SE	(0.20)	(0.44)	SE	(0.40)	(0.48)
	Year 2 HB:	Dry	<	Wet	Year 2 DR:	Wet	Dry	Year 2 BR:	Wet	Dry
	Mean	12.28		15.07	Mean	2.12	2.53	Mean	2.73	2.77
	SE	(0.77)		(0.80)	SE	(0.38)	(0.20)	SE	(0.33)	(0.25)
(c) Chlorophyll *a* / cell (pg $cell^{-1}$)	Year x Season:									
	Year 1	Dry	<	Wet	Year 2	Dry	Wet			
	Mean	3.34		6.04	Mean	3.86	4.43			
	SE	(0.14)		(0.36)	SE	(0.16)	(0.18)			

Variate		*Post hoc* tests								
(d) Skeletal density (g cm^{-3})	Year	Year 1	<	Year 2						
	Mean	2.51		2.64						
	SE	(0.01)		(0.02)						
(e) Colony brightness:	Year x Season x Location:									
	Year 1 HB:	Wet	<	Dry	Year 1 DR:	Wet	Dry	Year 1 BR:	Wet	Dry
P. damicornis	Mean	3.75		6.00	Mean	3.08	3.39	Mean	3.19	3.67
	SE	(0.14)		(0.00)	SE	(0.09)	(0.10)	SE	(0.09)	(0.11)
	Year 2 HB:	Wet		Dry	Year 2 DR:	Dry	Wet	Year 2 BR:	Dry	Wet
	Mean	5.64		5.69	Mean	3.03	3.17	Mean	3.03	3.64
	SE	(0.18)		(0.13)	SE	(0.11)	(0.09)	SE	(0.12)	(0.11)
(f) Macro-bioeroders (m^{-2})	Location:	DR		BR	< HB					
	Mean	3.77		7.17	169.83					
	SE	(0.80)		(3.80)	(16.11)					

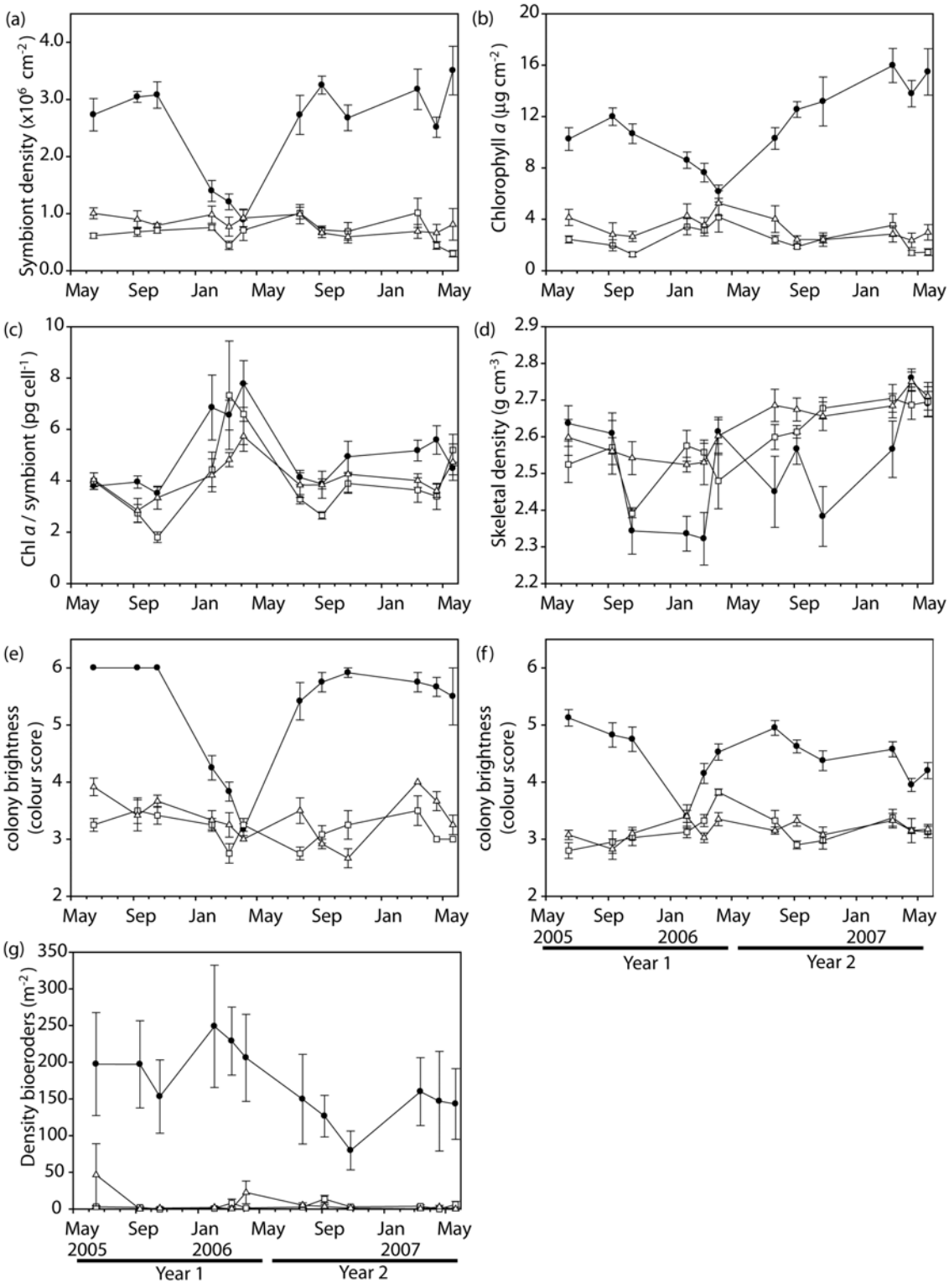

Fig. 6.9. Summary of mean (± SE) (a) symbiont density (cells cm^{-2}), (b) chlorophyll *a* (µg cm^{-2}), (c) chlorophyll *a* symbiont $cell^{-1}$ (pg $cell^{-1}$), (d) skeletal density (g cm^{-3}), (e) colony brightness of *P. damicornis*, and (f) colony brightness, (g) density of macro-bioeroders of *Porites* sampled at each of Horseshoe Bay (●), and Davies (□) and Broadhurst Reefs (△).

The model selection showed that there was no clear predictor that contributed consistently to the fit of the models for the response variables of *P. damicornis* and *Porites* (Table 6.4). Location was an important predictor for symbiont density and concentrations of chlorophyll *a* of *P. damicornis* (Fig. 6.10), colony brightness for both taxa (Fig. 6.10 and Fig. 6.11) and the density of macro-bioeroders of *Porites* (Fig. 6.11). However, changes in turbidity, benthic irradiance, SST and the WQI also needed to be considered in the models particularly for skeletal density and the concentration of chlorophyll *a* per symbiont of *P. damicornis*.

Symbiont density of *P. damicornis* varied inconsistently among locations with changes in benthic irradiance and the WQI (statistical interactions; Table 6.5). However, the best predictor of symbiont density was mean 14 d SST ($F_{1,210} = 327.48$, $P < 0.0001$; Fig. 6.10). This was evidenced by the decrease in symbiont density during the Wet Season of Year 1 when summer water temperatures were elevated on the GBR (Fig. 6.9a). The WQI and Location were important predictors for chlorophyll *a* of *P. damicornis*. Concentrations of chlorophyll *a* of *P. damicornis* increased with increases in the WQI ($F_{1,210} = 327.48$, $P < 0.0001$; Fig. 6.10) and were greater at Horseshoe Bay than Davies or Broadhurst Reefs ($F_{2,210} = 87.22$, $P < 0.0001$; Fig. 6.10). Colony brightness of *P. damicornis* varied inconsistently among locations with changes in SST and benthic irradiance (statistical interactions; Table 6.5).

Changes in SST and benthic irradiance were important predictors for responses of chlorophyll *a* per symbiont cell of *P. damicornis* (Table 6.5). Interestingly, the amount of chlorophyll *a* per symbiont cell increased with increases in SST ($F_{2,213} = 32.94$, $P < 0.0001$; Fig. 6.10) but decreased with increases in benthic irradiance ($F_{2,213} = 36.96$, $P < 0.0001$; Fig. 6.10). In contrast, changes in the WQI and SST were important predictors for responses of skeletal density of *P. damicornis*. Skeletal density decreased with increases in the WQI ($F_{2,212} = 8.66$, $P = 0.0036$; Fig. 6.10) and SST ($F_{2,212} = 8.80$, $P = 0.0034$; Fig. 6.10).

For the *Porites* indicators, changes in turbidity, the WQI and Location were useful predictors of colony brightness (Table 6.5). Colony brightness increased with increases in turbidity ($F_{1,711} = 89.20$, $P < 0.0001$; Fig. 6.11) and WQI ($F_{1,711} = 337.99$, $P < 0.0001$; Fig. 6.11) with the colonies darker at Horseshoe Bay than at Davies and Broadhurst Reefs ($F_{2,711} = 72.74$, $P < 0.0001$; Fig. 6.11). Location was a strong predictor of the density of macro-bioeroders in *Porites* with greater densities recorded on colonies from Horseshoe Bay compared with either Davies or Broadhurst Reefs ($F_{2,717} = 403.96$, $P < 0.0001$; Fig. 6.11).

Table 6.4. Summary of analyses for model selection to examine the relationship between physiological measures of *P. damicornis* (a – e) and massive *Porites* (f – g) with physical variables (predictors). Predictors selected by dropping terms from the full model based on calculation of Akaike Information Criterion (AIC). Data for sea surface temperature (SST), benthic irradiance and turbidity averaged over the 14 d period preceding the site visit.

Variate	df	AIC	*F*	*P*
(a) Symbiont density (cells cm^{-2})		-154.91		
Benthic irradiance	1	-146.69	10.18	0.0016
WQI	1	-145.86	11.03	0.0011
SST	1	-133.58	23.95	<0.0001
Location	2	-52.80	66.61	<0.0001
(b) Chlorophyll *a* (µg cm^{-2})		-166.95		
WQI	1	-153.04	16.21	0.0001
Location	2	-41.62	86.91	<0.0001
(c) Chlorophyll *a* / cell (pg $cell^{-1}$)		-290.38		
Benthic irradiance	1	-258.05	36.69	<0.0001
SST	1	-243.92	53.58	<0.0001
(d) Skeletal density (g cm^{-3})		-1025.30		
Turbidity	1	-1022.35	4.92	0.0277
SST	1	-1018.34	8.98	0.0031
WQI	1	-1013.07	14.44	0.0002
(e) Colony brightness: *P. damicornis*		-588.28		
Benthic irradiance	1	-586.43	3.79	0.0530
SST	1	-576.02	14.39	0.0002
Location	2	-452.60	95.91	<0.0001
(f) Macro-bioeroders (m^{-2})		2100.10		
Turbidity	1	2100.80	2.70	0.1037
Location	2	2550.60	315.00	<0.0001
(g) Colony brightness: massive *Porites*		-1926.31		
WQI	1	-1919.28	9.03	0.0028
Turbidity	1	-1918.32	9.99	0.0016
Location	2	-1797.51	72.41	<0.0001

Table 6.5. Summary of ANOVAs comparing physiological measures of *P. damicornis* (a – e) and massive *Porites* (f – g) among locations and with environmental variables.

Variate	Source of variation	df	MS	*F*	*P*
(a) Symbiont density (cells cm^{-2})	SST	1	11.34	25.67	<0.0001
	WQI	1	99.03	224.09	<0.0001
	Benthic irradiance	1	0.005	0.01	0.9138
	Location	2	31.64	71.59	<0.0001
	SST x Loc	2	0.721	1.63	0.1982
	WQI x Loc	2	1.441	3.26	0.0403
	Benthic irradiance x Loc	2	2.632	5.96	0.0031
	Residual	204	0.442		
(b) Chlorophyll *a* (µg cm^{-2})	WQI	1	147.91	327.48	<0.0001
	Location	2	39.39	87.22	<0.0001
	WQI x Loc	2	0.621	1.38	0.2549
	Residual	210	0.452		
(c) Chlorophyll *a* / cell (µg cm^{-2})	SST	1	8.469	32.94	<0.0001
	Benthic irradiance	1	9.435	36.69	<0.0001
	Residual	213	0.257		
(d) Skeletal density (g cm^{-3})	WQI	1	0.074	8.66	0.0036
	SST	1	0.075	8.80	0.0034
	Turbidity	1	0.042	4.92	0.0277
	Residual	212	0.009		
(e) Colony brightness: *P. damicornis*	SST	1	1.193	21.27	<0.0001
	Benthic irradiance	1	9.243	164.72	<0.0001
	Location	2	6.154	109.67	<0.0001
	SST x Loc	2	0.590	10.52	<0.0001
	Benthic irradiance x Loc	2	0.371	6.61	0.0016
	Residual	207	0.056		
(f) Macro-bioeroders (m^{-2})	Location	2	7442.2	403.96	<0.0001
	Residual	717	18.40		
(g) Colony brightness: massive *Porites*	Turbidity	1	6.074	89.20	<0.0001
	WQI	1	23.01	337.99	<0.0001
	Location	2	4.953	72.74	<0.0001
	Turbidity x Loc	2	0.145	2.13	0.1191
	WQI x Loc	2	0.102	1.49	0.2255
	Residual	711	0.068		

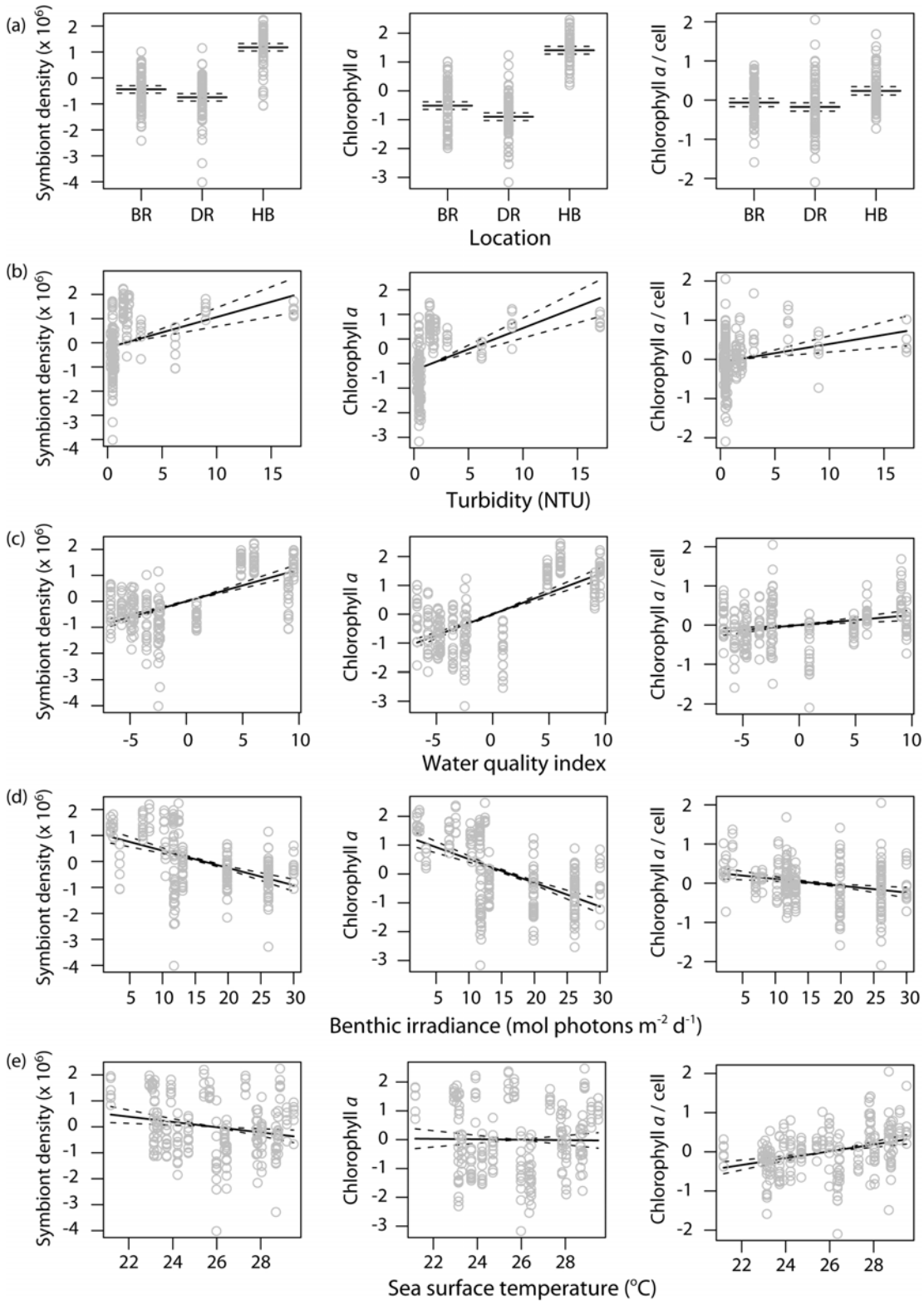

Fig. 6.10. Partial residual plots showing the estimated dependencies (± 1 standard error) of symbiont density, concentration of chlorophyll *a*, chlorophyll per symbiont, skeletal density and colony brightness of *P. damicornis* on (a) location, (b) sea surface temperature, (c) turbidity, (d) benthic irradiance and (e) water quality index. Each partial effects plot is adjusted for the effects of the other five explanatory variables.

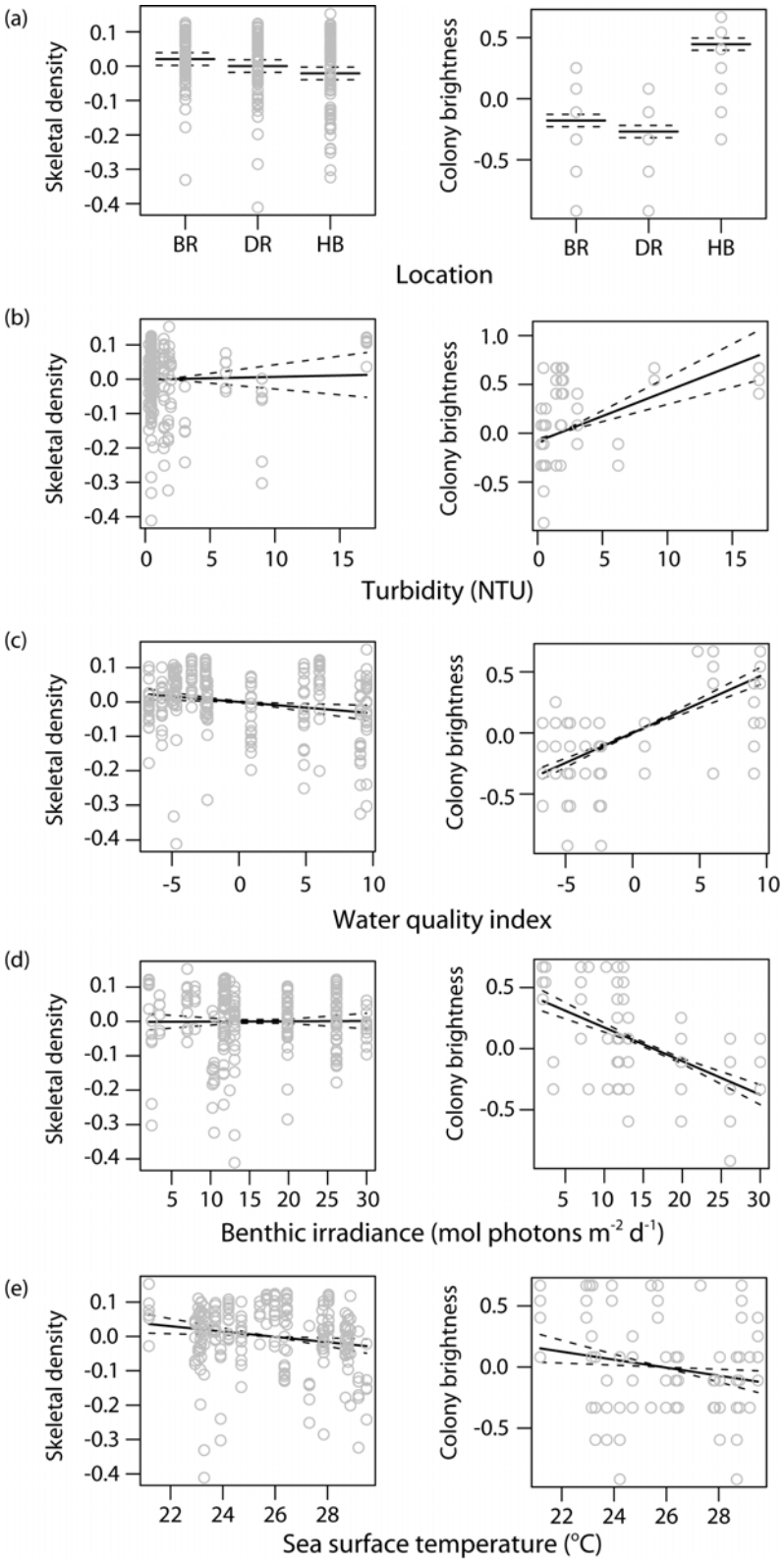
(a)
Skeletal density
Colony brightness
BR
DR
HB
Location
(b)
Turbidity (NTU)
(c)
Water quality index
(d)
Benthic irradiance (mol photons m-2 d-1)
(e)
Sea surface temperature (°C)

Fig. 6.10. cont

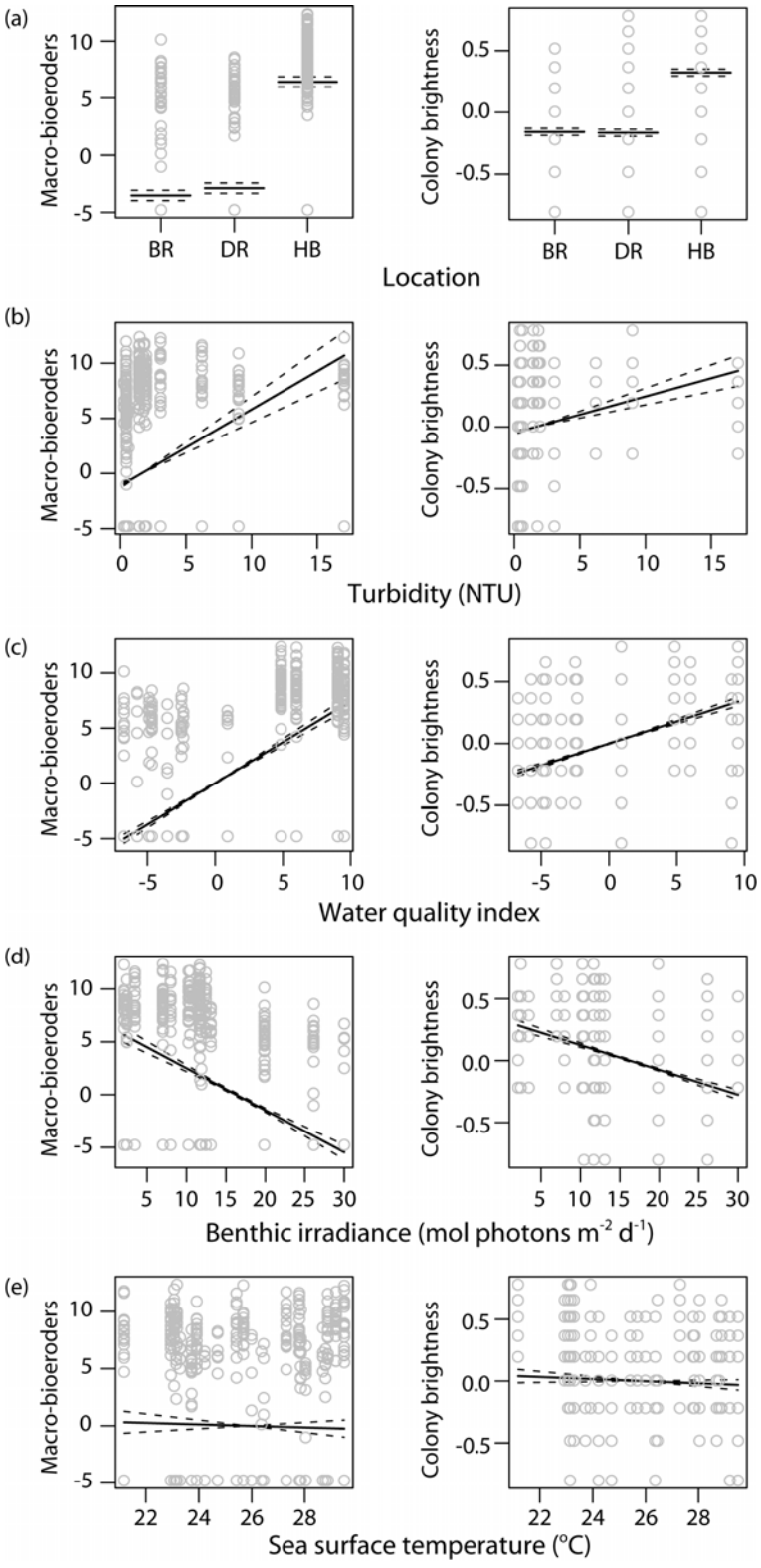

Fig. 6.11. Partial residual plots showing the estimated dependencies (± 1 standard error) of the density of macro-bioeroders and colony brightness of massive *Porites* on (a) location, (b) sea surface temperature, (c) turbidity, (d) benthic irradiance and (e) water quality index. Each partial effects plot is adjusted for the effects of the other five explanatory variables.

6.4 Discussion

This study is the first to document the temporal dynamics of coral bioindicators and environmental conditions on a coastal coral reef on the Great Barrier Reef over a 2-year study period. The symbionts of *P. damicornis* and colony brightness of *Porites* appeared to be seasonally modulated in Year 1, which is consistent with studies in other coral systems (Stimson 1997; Brown et al. 1999b; Fagoonee et al. 1999; Fitt et al. 2000). This was not the case in Year 2, however, where there was no clear difference between seasons for many of the bioindicators examined. The interruption of this seasonality coincided with a major flood event (Fig. 6.2) but also with slightly cooler SST than the previous year. Indeed, the predictive models found support for a range of environmental parameters for the bioindicators examined including spatial differences between coastal and mid-shelf locations, changes in water quality, SST, turbidity and benthic irradiance. Thus, our findings are discussed within the context of seasonal changes in water quality as well as temporal differences in SST.

Responses of symbiont density, concentrations of chlorophyll *a,* skeletal density of *P. damicornis*, and colony brightness of *Porites* were related to seasonal changes in water quality. Laboratory studies have previously demonstrated physiological responses of corals to changes in water quality (Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989; Marubini and Davies 1996). Similarly, long-term studies in the field have found positive relationships between symbiont density and nutrient availability (Stimson 1997; Fagoonee et al. 1999) although Brown et al. (1999b) did not find any relationships between these parameters in Indonesia, most likely due to the lack of seasonality of nutrient availability at their study site. Here, levels of water column chlorophyll *a* were 1.6-fold greater during the Wet than Dry Season, a finding that is in agreement with Brodie et al. (2007). The predictive models showed that seasonal changes in the WQI had some influence on responses such as symbiont density, concentrations of chlorophyll *a,* skeletal density of *P. damicornis* and colony brightness of *Porites*. However, other environmental parameters such as SST, turbidity, benthic irradiance and spatial differences among locations were also important predictors for these bioindicators. Interestingly, the density of macro-bioeroders in *Porites* did not show any response to seasonal changes in SST, WQI or to the acute effects of a major flood event (*sensu* Hutchings et al. 2005). Nevertheless, the density of macro-bioeroders was consistently greater at the coastal location than the mid-shelf reference locations indicating a high specificity to spatial differences in water quality. Thus, the density of macro-bioeroders may be an appropriate indicator of the effects of chronic exposures to changes in water quality on coastal coral reefs. These results demonstrated that coral bioindicators have differences in specificity to changes in water quality on coastal corals reefs, which has important implications for the selection of bioindicators for monitoring programmes.

The inverse relationship observed between symbiont density and chlorophyll *a* concentration of *P. damicornis*, and colony brightness of both study taxa, with irradiance and SST during Year 1 at the coastal location (Fig. 6.9) was consistent with seasonal regulation of symbiont density reported from other coral reef systems (e.g. Stimson 1997; Brown et al. 1999b; Fagoonee et al. 1999). Interestingly, a four year study of seasonal patterns in five species of corals from the Bahamas by Fitt et al. (2000) showed that symbiont densities were consistently greater during the cooler winter months than summer leading to the conclusion that corals undergo some degree of bleaching every year regardless of whether or not it was a so-called 'bleaching year'. In Year 1 of this study, mean summer SSTs reached levels known to cause thermal stress to corals and low-level bleaching events, i.e. <10% bleached coral cover, occurred in many regions of the GBR including the Townsville region over the summer of 2005/06 (Great Barrier Reef Marine Park Authority 2006). Thus, the observed pattern in symbiont density at the coastal location in Year 1 was most likely a physiological response to thermal stress. In contrast, the mean summer SSTs in Year 2 were slightly cooler, which may have hindered decreases in symbiont density. Alternatively, symbiont density may have remained high throughout Year 2 in response to the increased nutrient availability during the summer flood event. The relative importance of these two factors in contributing to the observed patterns for symbiont density, concentration of chlorophyll *a* and colony brightness is uncertain and warrants further study, incorporating more years without bleaching conditions.

The positive relationship between chlorophyll *a* content of symbiont cells of *P. damicornis* with SST at the coastal and mid-shelf locations as observed in Year 1 contrasts with previous studies of seasonal dynamics of chlorophyll *a* content and symbiont density in corals (e.g. Fitt et al. 2000). A possible explanation for this may be shuffling of different *Symbiodinium* genotypes. Symbiont shuffling is a mechanism that involves changes in the relative abundance of co-occurring *Symbiodinium* types that may differ physiologically (Little et al. 2004; Berkelmans and van Oppen 2006). Shuffling of *Symbiodinium* types may thus provide selective physiological advantages to the coral host exposed to changing environmental conditions, e.g. changes in SST and irradiance (Rowan et al. 1997; Berkelmans and van Oppen 2006). Recently, Apprill et al. (2007) showed that subpopulations of the same *Symbiodinium* genotype (clade C) differed in their fluorescence properties due to variable chlorophyll *a* content possibly as an adaptation to specific light regimes. Characterisation of *Symbiodinium* genotypes of *P. damicornis* was not done as part of this study although Ulstrup et al. (2006a) showed *P. damicornis* at Magnetic Island contained only one genotype (clade C1). However, the possibility that symbiont shuffling may have contributed to the patterns observed in *P. damicornis*, particularly if the retained *Symbiodinium* type (or subpopulation) had greater chlorophyll *a* content than those that were expelled, cannot be discounted until further studies are completed.

Weather-dependent turbidity events are important influences on environmental conditions on coastal coral reefs (Larcombe et al. 1995; Anthony et al. 2004; Orpin et al. 2004; Alongi and McKinnon 2005). During this study, there were 10 turbidity events lasting ≥5 d whereby turbidity was elevated to ≥5 NTU, i.e. causing a ~94% reduction in benthic irradiance intensity. Anthony et al. (2004) compared patterns of benthic irradiance with predictions of the minimum saturating irradiance (E_k) for *Turbinaria mesenteria* and found that variation in environmental conditions resulted in alternating periods of light limitation and light stress on cycles of between 2 to 8 weeks related predominately to changes in turbidity. The E_k of *Symbiodinium* associated with *P. damicornis* was approximately 206 ± 8 µmol photons m^{-2} s^{-1} (mean ± SE, n=24) for corals sampled from four coastal coral reefs of the GBR at a comparable depth to that used here (Chapter 3). In this study, the simultaneous *in situ* measurement of turbidity and benthic irradiance by a logger deployed at an average depth of ~3.5 m allowed the quantification of turbidity beyond which light limitation for corals may occur. The linear relationship between K_d and turbidity showed that benthic irradiance (E_z) was ~200 µmol photons m^{-2} s^{-1} when turbidity reached 3 NTU. Thus, long-term average turbidity >3 NTU may lead to light limitation (i.e. $E_z < E_k$), and hence sublethal photo-physiological stress for *Symbiodinium* hosted by *P. damicornis*. At 4.5 NTU, benthic irradiance was approximately 6 – 8% of surface irradiance, which was the minimum amount of downward irradiance required for coral reef development in the Whitsunday Islands (Chapter 2). Hence, long-term average turbidity >5 NTU is likely to represent a threshold for severe stress. Physiological responses of *Symbiodinium* to light limitation may in part explain the consistency observed in spatial differences of parameters such as symbiont density and concentrations of chlorophyll *a* (Falkowski and Dubinsky 1981; Dubinsky et al. 1984). However, given that re-mobilisation of particulate nutrients bound to sediments are likely to be a feature of these weather-dependent turbidity events (Alongi and McKinnon 2005), increased nutrient availability may have also influenced the population dynamics of *Symbiodinium* (Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989).

In conclusion, this study has highlighted the importance of understanding temporal patterns of variation as part of the process of selecting bioindicators for monitoring the effects of changes in water quality on coastal coral reefs. Importantly, the study revealed that the specificity to changes in water quality varied among bioindicators. For example, the best predictor of symbiont density of *P. damicornis*, which in turn influenced colony brightness, was mean 14 d SST followed by seasonal changes in water quality and mean 14 d benthic irradiance. Thus, temporal variability of a range of environmental parameters need to be considered if physiological measures such as colony brightness are used in water quality monitoring programmes on coastal coral reefs. Our findings have also further enhanced the knowledge of environmental conditions on coastal coral reefs by quantifying potential stress thresholds of turbidity for corals occurring at shallow depths.

The extinction of benthic irradiance when turbidity exceeded ~15 NTU is notable, however, as 94% extinction occurs at a much lower value of only 5 NTU, large increases in turbidity to 15 NTU or more make little difference to the light levels and thus the energy balance of corals. However, the biological responses of corals will vary depending on depth and species as well as the duration of exposure to turbidity. A detailed understanding of the physiological responses of a range of coastal corals using dose-response experiments is required before long-term turbidity >3 NTU for sublethal stress and >5 NTU for severe stress can be considered as 'thresholds of concern'.

Chapter 7.0 Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef

7.1 Introduction

Massive corals record an environmental history in their calcium carbonate skeletons (Dodge and Vaisnys 1975). They grow by precipitating calcium carbonate on previously deposited skeleton thereby creating a series of growth bands. The annual nature of the growth bands is well understood (Knutson et al. 1972) as are other characteristics, including environmental effects on isotopic composition (Gagan et al. 2000; McCulloch et al. 2003), luminescence (Isdale 1984), and the growth parameters skeletal density, annual extension and calcification rate (Barnes and Lough 1989). Massive corals of the genus *Porites* are long-lived, and distributed widely throughout the Indo-Pacific Ocean, across a range of habitats from turbid inshore to clear offshore waters. Their skeletal records are, therefore, eminently useful as a tool for detecting long-term changes in environmental conditions in tropical ocean surface waters.

Environmental controls on the growth of scleractinian corals include seawater temperature (Jokiel and Coles 1978; Lough and Barnes 2000; Marshall and Clode 2004), light (Goreau and Goreau 1959; Bak 1974; Yentsch et al. 2002), carbonate saturation state (Marubini et al. 2001), water motion (Scoffin et al. 1992; Lesser et al. 1994) and water quality (Marubini and Davies 1996; Fabricius 2005). Recent attention has focused on the effects of rising concentrations of atmospheric greenhouse gases due to human activities on corals and coral reefs (Hughes et al. 2003; Lesser 2004). Rising concentrations of atmospheric greenhouse gases (IPCC 2001; IPCC 2007) has been associated with warming of the tropical oceans, resulting in an increased frequency of mass coral bleaching events since the 1970s (Hoegh-Guldberg 2005). Concentrations of the principle greenhouse gas CO_2 have risen ~35% in the atmosphere since the late 18th century, presently increasing at about 1% annually. The current concentration of ~379 ppm in 2005 (WMO Greenhouse Gas Bulletin 2006) is considered to be unprecedented in at least the past 650,000 years (Petit et al. 1999; Siegenthaler et al. 2005). High atmospheric CO_2 leads to increased concentrations of dissolved CO_2 in seawater shifting the seawater carbonate equilibrium towards higher levels of bicarbonate (HCO_3^-) by: $CO_{2(aq)} + H_2O + CO_3^{2-} \leftrightarrow 2HCO_3^-$. The dissolution of CO_2 reduces pH in ocean surface waters, lowers the availability of carbonate (CO_3^{2-}) ions and decreases the calcium carbonate saturation state (Ω), a process called ocean acidification (e.g. Caldeira and Wickett 2003). Aragonite saturation is predicted to decrease by around 30% by 2050, which is expected to have negative consequences on the growth rates of a range of calcifying biota (Kleypas et al. 1999; Feely et al. 2004; Orr et al. 2005). Although evidence from laboratory experiments has confirmed decreases in calcification rates with reduced aragonite saturation (Gattuso et al. 1998; Langdon et al. 2000; Leclercq et al. 2000; Schneider and Erez 2006), data from field studies showing long-term declines in coral calcification rates are lacking (Kleypas et al. 1999). The aim of this study was to examine temporal and spatial variation

in the growth parameters skeletal density, linear extension and calcification rate in massive *Porites* from two nearshore regions of the Great Barrier Reef (GBR) and to interpret these data in the context of changing environmental conditions.

7.2 Materials and methods

7.2.1 Study area and sampling design

To examine spatial and temporal variation in the coral growth parameters skeletal density, annual extension and calcification rate, ten colonies of massive *Porites* were collected at each of two coral reefs within each of two regions (Far Northern and Northern, ~450 km apart; Fig. 7.1) on the GBR, Australia, in January 2004. In the Far Northern Region, colonies were collected from fringing reefs at Hannah (13º 52'S, 143º 43'E) and Hay Islands (13º 40'S, 143º 41'E), and in the Northern Region from High (17º 10'S, 146º 00'E) and Kent Islands (17º 40'S, 146º 11'E). The four reefs are located in the coastal zone (i.e. within the 20 m isobath) of the GBR lagoon (Alongi and McKinnon 2005). Mean annual sea surface temperature (SST) is ~0.5°C higher in the Far Northern than in the Northern Region (Rayner et al. 2003). All colonies were ≥30 cm in diameter and were collected from the leeward side of the islands at shallow depths (1 – 3 m below lowest astronomical tide). In total, 40 colonies were collected during the study but two colonies were excluded due to severe internal bioerosion, leaving a total of 38 colonies for the analysis of growth parameters.

7.2.2 Sclerochronology

The growth parameters skeletal density, annual extension and calcification rate were determined for each colony following procedures described previously (Barnes and Lough 1989; Chalker and Barnes 1990; Lough and Barnes 1990a; Lough and Barnes 1990b). A slice (~7 mm thick) was cut from the centre of each colony using a large saw with freshwater applied as lubricant and dried for 12 h at 60°C. Each slice was then X-rayed using Kodak lanex regular, double sided emulsion (100 mA, 0.032 sec, 45 Kv, 150 FFD; Rochester, NY, USA; Fig. 7.4a). The positive X-ray prints were then used to identify two tracks on each colony with clear annual density bands avoiding convolutions in coral growth and bore holes from bioeroders (Lough et al. 1999). Along these tracks, skeletal density was determined with a gamma densitometer at 0.25 mm intervals. The X-ray prints were also used to date the annual growth bands based on the assumption that skeleton of greatest density is deposited in summer (Lough and Barnes 1990a). Once each growth band was dated, it was possible to calculate (i) mean annual skeletal density as the average density between adjacent annual density minima (g cm-3); (ii) mean annual extension rate as the linear distance between adjacent annual density minima (cm yr-1); and (iii) mean annual rate of calcification (g cm-2 yr-1) as the product of skeletal density and annual extension. The three

variables were then averaged across the corresponding growth year from the two densitometer tracks (Lough and Barnes 2000).

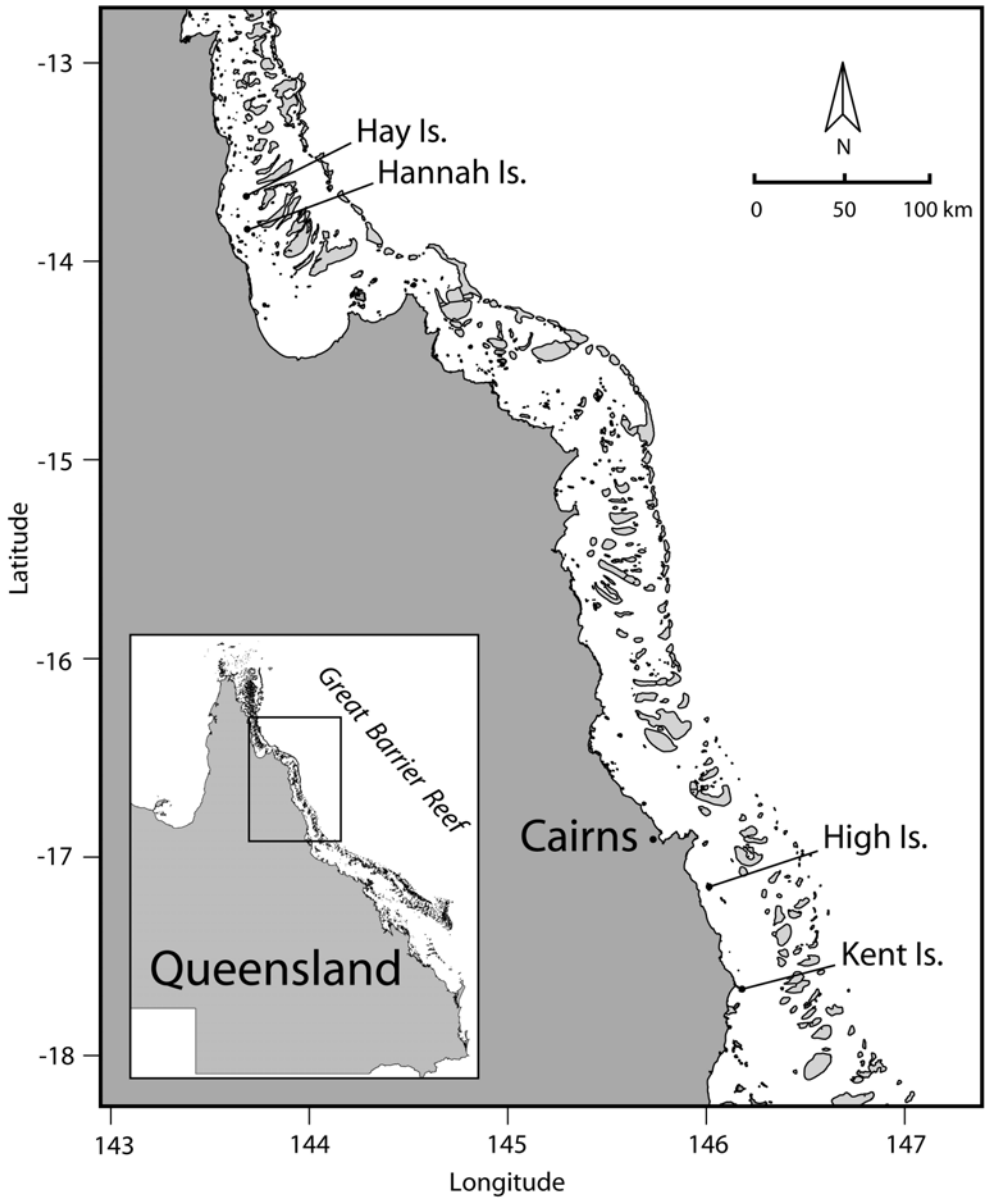

Fig. 7.1. Study sites for sampling of colonies of massive *Porites* on the Great Barrier Reef. Hay and Hannah Islands in the Far Northern Region, High and Kent Islands in the Northern Region of the GBR.

7.2.3 Sea surface temperature

Sea surface temperatures (SST) were obtained for the 1º latitude by longitude box closest to the study locations (centred on 13.5ºS, 143.5ºE for the Far Northern and 17.5ºS, 146.5ºE for the Northern Region; Fig. 7.4b) for 1971 – 2003 from the global HadISST 1.1 database

(http://www.badc.nerc.ac.uk/data/HadISST/; Rayner et al. 2003). Average annual SST corresponding (approximately) to the coral growth years was calculated as arithmetic means of the average monthly values for each box.

7.2.4 Statistical analyses

The statistical analyses investigated how the growth variables (skeletal density, annual extension and calcification rate) varied with year, SST and reef. The age of the annual growth bands in the colonies ranged from 1971 to 2003 (Fig. 7.4c), but there were few bands recorded prior to 1988, and hence the data selected for analysis focused on the 16 year period from 1988 – 2003. Thus, the data obtained from the 38 colonies were unevenly distributed across years and reefs (Table 7.1).

The data comprised repeated measures across years on colonies. Such measures are likely to be correlated for individual colonies (Lough and Barnes 1997) and exploratory data analysis suggested this to be the case (Fig. 7.2). This correlation was modelled by fitting profiles over time for each of the colonies as part of linear mixed models analyses (Laird and Ware 1982; Pinheiro and Bates 2000). These models comprise fixed and random effects, and a hierarchy of models was explored as follows. For each response, a saturated fixed model was selected initially and was adequately complex to include all effects of interest. It contained smooth trends over years (natural splines, df = 4), smooth effects in SST (natural splines, df = 4), reef effects and all first-order interactions between these terms. The random components of the model were then selected based on the Akaike Information Criterion (AIC) with the model fitted by restricted maximum likelihood estimation (Pinheiro and Bates 2000). This involves calculation of AIC for all models of interest and then choosing the one with the minimum AIC. The random effects considered included combinations of (1) smooth profiles across years (natural splines, df = 3), (2) linear profiles over years and (3) random intercepts for each coral. The random effects selected were: (1) for skeletal density, linear trends in years with additive effects of colonies, and (2) for annual extension and calcification rate, only effects of colonies. Once the random structure was selected, the fixed components of the model were assessed for each response. A preliminary analysis showed interactions to be negligible and only main effects were considered thereafter. For each response, the degree of smoothness for terms involving years and SST were estimated by cross-validation (Wood 2006). The estimates are documented in Table 7.2. All analyses were done using the statistical program R (R Development Core Team 2006).

Table 7.1. The numbers of colonies observed by (a) year and (b) reef shows the imbalance in the data due to fewer colonies having bands in earlier years.

(a)	Year	1988	1989	1990	1991	1992	1993	1994	1995
	n	14	17	19	21	24	28	33	35
	Year	1996	1997	1998	1999	2000	2001	2002	2003
	n	36	37	38	38	38	38	38	38

(b)	Reef	Hannah	Hay	High	Kent
	n	9	9	10	10

Table 7.2. Cross-validated estimates of smoothness (degrees of freedom) of trends in years and sea surface temperature for skeletal density, annual extension and calcification. Estimates were based on linear mixed effects models.

Model terms	Skeletal Density	Annual Extension	Calcification
Years	3.00	1.20	1.39
Sea-surface temperature	1.00	3.58	3.11

7.3 Results

There was significant variation in all three growth parameters among the 38 Porites colonies over the period 1988 – 2003 (Fig. 7.2). When averaged across colonies, skeletal density declined over time from 1.32 g cm^{-3} (SE = 0.017) in 1988 to 1.25 g cm^{-3} (0.013) in 2003, an average annual decline of 0.00475 g cm^{-3} (0.0017) or 0.36% yr^{-1} (0.13) (Fig. 7.3a). Annual extension declined from 1.52 cm yr^{-1} (0.035) to 1.28 cm yr^{-1} (0.026), i.e. 0.0133 cm yr^{-1} (0.0039) or 1.02% yr^{-1} (0.39). Consequently, calcification rate declined from 1.96 g cm^{-2} yr^{-1} (0.049) to 1.59 g cm^{-2} yr^{-1} (0.041), equivalent to an annual decline of 0.0243 g cm^{-2} yr^{-1} (0.0051) or 1.29% yr^{-1} (0.30). SST had no effect on skeletal density, but a modal effect on annual extension and calcification with maxima at ~26.7°C (Fig. 7.3b). At higher and lower temperatures both parameters declined by ~15% per °C. Differences in coral growth parameters across the four reefs were small when adjusted for temporal trends and regional differences in SST, with marginally lower extension and calcification rates on the two northern reefs compared to the far northern reefs (Fig. 7.3c).

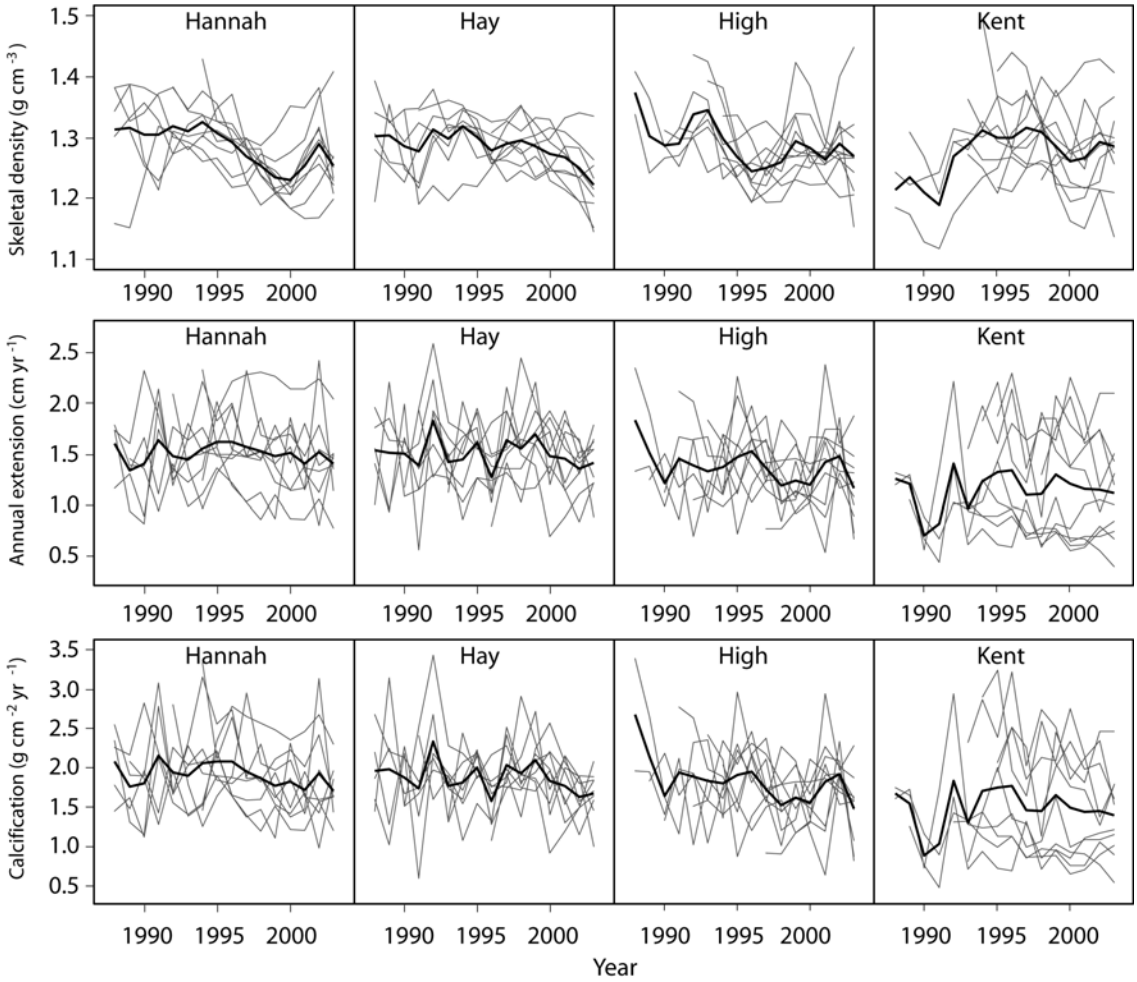

Fig. 7.2. Temporal profiles for skeletal density, annual extension and calcification rate over years. The red lines indicate individual corals and the black lines indicate the mean profiles. The variation of annual extension and calcification are large (coefficient of variation, CV = 30.5% and 30.3% respectively) compared with skeletal density (CV = 9.1%).

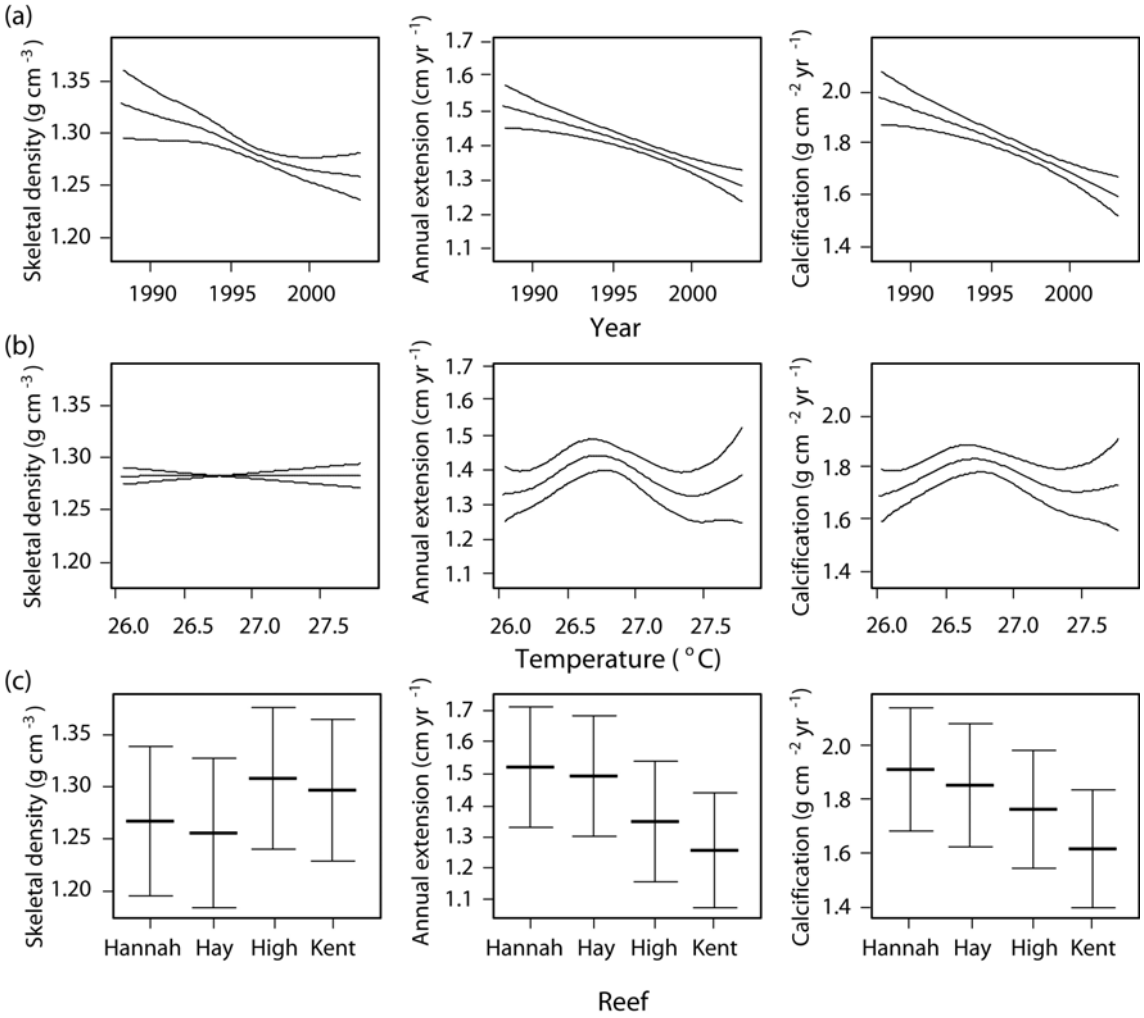

Fig. 7.3. Partial effects plots showing the estimated dependencies (with 95% confidence intervals) of skeletal density, annual extension and calcification on (a) year, (b) sea surface temperature and (c) reef. Hannah and Hay Island are in the Far Northern Region, High and Kent Island in the Northern Region of the Great Barrier Reef. Each partial effects plot is adjusted for the effects of the other two explanatory variables.

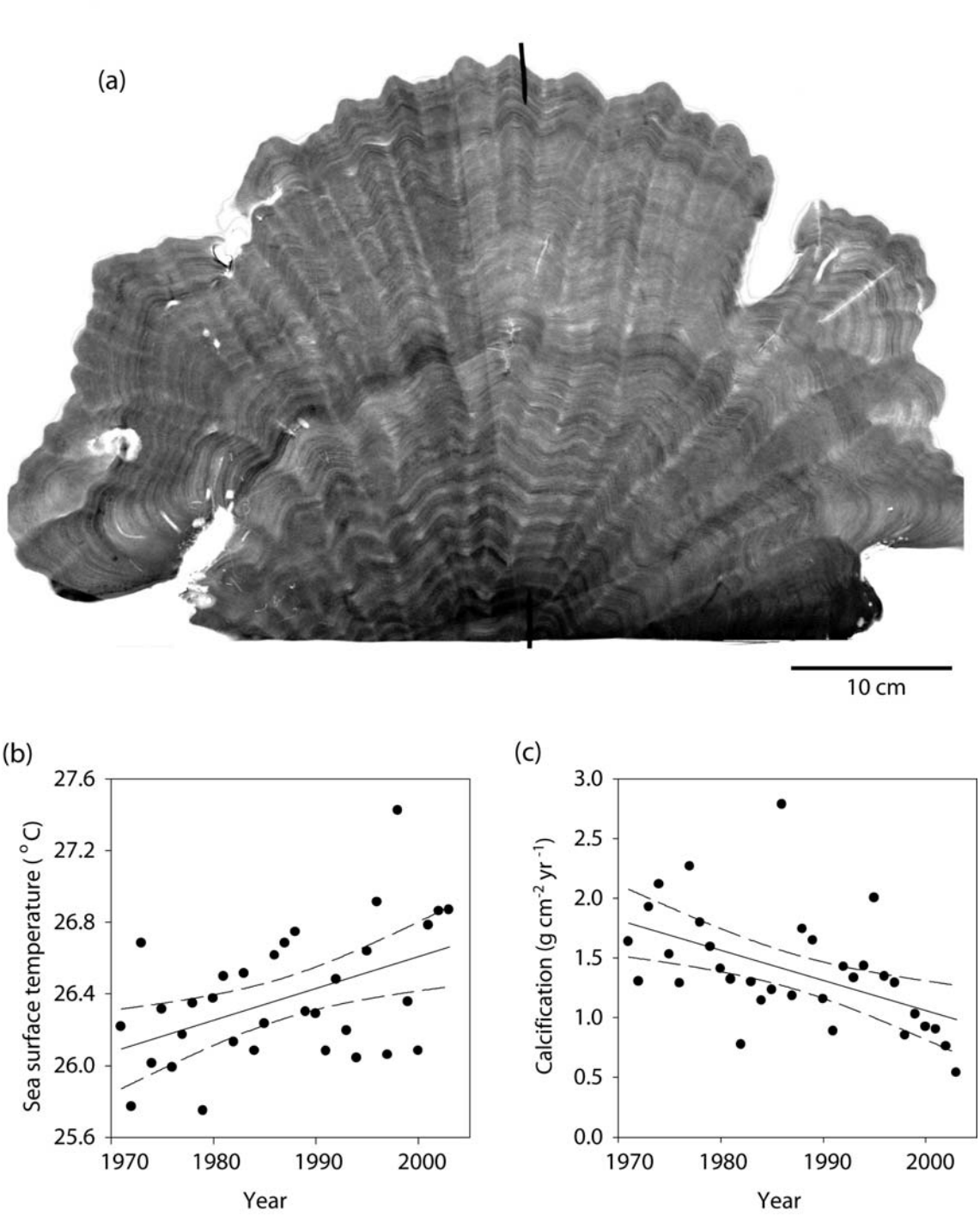

Fig. 7.4. (a) X-ray of a coral slice showing a 33-year growth record for a massive *Porites* from Kent Island in the Northern Region of the Great Barrier Reef, (b) mean annual sea surface temperature for the Northern Region over the same period and (c) calcification rate of the colony. Dashed lines are 95% confidence intervals.

7.4 Discussion

This study has shown that calcification rates in massive *Porites* in two nearshore regions ~450 km apart on the GBR have declined by 21% over a 16-year study period between 1988 – 2003. A range of environmental factors known to influence coral growth may have contributed to this decline. Seawater temperature is an important environmental factor controlling coral growth (Highsmith 1979; Crossland 1984). Several laboratory studies have found non-linear responses in calcification to temperature, with a peak around 25 – 26°C and decreasing beyond this range (Jokiel and Coles 1978; Marshall and Clode 2004). The finding of a modal response in coral calcification to SST, with maxima at 26.7°C, suggests a thermal optimum in calcification may occur around this SST also in the field. A previous study has shown that along a latitudinal gradient, long-term average growth rates in *Porites* were related linearly to long-term mean annual SST, with each 1°C increase in SST corresponding to an increase of 0.39 g cm^{-2} yr^{-1} in calcification and 3.1 mm yr^{-1} in annual extension (Lough and Barnes 2000). The results of that study are not strictly comparable with the results presented here since effects of SST were estimated after adjusting for reef (hence latitudinal) effects and temporal trends. However, the finding of a non-linear relationship of coral growth and temperature adds further evidence to recent arguments (Kleypas et al. 2005) rebutting a prediction of ~35% increase in coral calcification beyond pre-industrial levels due to warming oceans (McNeil et al. 2004).

Thermal stress is also an important environmental control on coral growth, occurring with increasing frequency and intensity within recent decades. Increases in SST above the upper thermal limit of corals can have negative physiological consequences on coral energetic reserves (Anthony et al. 2007) and tissue biomass (Fitt et al. 2000). Further, Suzuki et al. (2003) found that calcification of massive *Porites* from the GBR declined following the 1998 bleaching event. Mean monthly SST maxima for the Northern and Far Northern Region are 28.87 and 29.13°C, respectively for the period 1900 – 2003 (HadISST dataset). The cumulative number of degree heating months (DHM), an index of thermal stress and an extension of the degree heating week indicator (Liu et al. 2003), was 1.33 in the Northern Region in both 1998 and 2002, and 1.06 and 0.88 in the Far Northern Region. Indeed, nearshore reefs in the northern study area experienced severe (>60%) bleaching in 1998 and moderate (1 – 30%) bleaching in 2002 (Berkelmans et al. 2004). The Far Northern Region was not surveyed in 1998 but experienced major bleaching (i.e. 30 – 60% bleached coral cover) in 2002. Thus, an increasing frequency in thermal stress may in part explain the observed decline in calcification of *Porites* colonies in the northern GBR.

A range of other environmental factors are also known to affect coral growth, in particular light and turbidity (Barnes and Chalker 1990). While the growth parameters in shallow-water massive *Porites* (n=245) along a 9º latitudinal gradient on the GBR were unrelated to surface irradiance

(Lough and Barnes 2000), linear extension in four species of massive corals decreased along a light gradient from 1 to 30 m water depth (Huston 1985). Similarly, skeletal density and calcification rate in the coral *Montastraea annularis* increased with decreasing turbidity and sedimentation, while linear extension decreased (Carricart-Ganivet and Merino 2001) although this may have been a growth response to increasing SST (Carricart-Ganivet 2004). Wave energy is also an important environmental factor influencing coral growth. Colonies growing in wave exposed conditions have greater skeletal density and lower linear extension compared with those protected from wave action (Scoffin et al. 1992). In this study, all colonies were sampled on the leeward side of continental islands. As light, turbidity and waves vary spatially in relation to sediment resuspension by wind on the GBR (Larcombe et al. 1995; Orpin et al. 2004), these factors may have contributed to the marginal differences in coral growth between the four reefs. Dissolved inorganic nutrients and sedimentation can also have negative effects on coral growth (e.g. Ferrier-Pages et al. 2000) and review by Fabricius (2005). In the Northern Region, land use in catchments has intensified over the last 150 years (predominantly for cattle grazing, and sugarcane and banana cropping; Furnas 2003). In contrast, the Far Northern Region is sparsely populated, has no cropping and only localised low-density cattle grazing, and hence the amount of pollutants in terrestrial runoff is low compared with the Northern Region (Brodie et al. 2007). Levels of nutrients and turbidity in reef waters are indeed substantially lower in the Far Northern than in the Northern Region (Fabricius and De'ath 2004). However, the coral growth parameters of this study showed only minor differences between regions after controlling for temperature effects. The observed temporal decline in coral growth in both regions is, therefore, not consistent with changing water quality.

Large-scale interdecadal changes in ocean chemistry may also potentially explain the decline in coral calcification. Currently, the surface waters on coral reefs are supersaturated with the calcium carbonate minerals aragonite and calcite. Given that calcification rates of marine biota are proportional to the saturation state of calcium carbonate, the predicted decline in the saturation of aragonite under various climate change scenarios is cause for considerable concern (Smith and Buddemeier 1992; Feely et al. 2004). For example, Kleypas et al. (1999) estimated that aragonite saturation state (Ω_{arag}) had decreased from pre-industrial levels of 4.6 ± 0.2 to current levels of 4.0 ± 0.2. A further study by Kleypas and Langdon (2002) estimated that the doubling of atmospheric pCO_2 by 2065 would result in a decrease in the concentrations of seawater CO_3^{2-} of ~35%. Similarly, Orr et al. (2005) predicted that the upper ocean layers at high latitudes would become undersaturated with aragonite by 2050 and further suggested that current carbonate concentrations in tropical surface waters had already declined by 29 μmol kg^{-1} (~10%) compared with pre-industrial levels.

Recognising that carbonate chemistry is a key determinant of calcification rates in corals, a number of experiments have reported the effects of manipulating aragonite saturation, pH and pCO_2 on coral growth (Gattuso et al. 1998; Marubini and Atkinson 1999; Langdon et al. 2000; Leclercq et al. 2000; Marubini et al. 2001). For example, Langdon et al. (2000) found a 12-fold increase in coral calcification corresponding to a 55% increase in CO_3^{2-} concentration, while (Leclercq et al. 2000) also reported linear declines with ~30% decrease in calcification when aragonite saturation decreased from Ω_{arag} 5.4 to 1.3 as a function of increasing pCO_2. Similarly, Schneider and Erez (2006) found that a ~30% decrease in CO_3^{2-} concentration resulted in a ~50% decline in calcification in *Acropora eurystoma.* These and other studies show that lowering aragonite saturation, as a function of increasing concentrations of atmospheric CO_2, can lead to declines in coral growth.

A 300 year coral core showed that pH varied naturally by 0.3 pH units over ~50 year cycles in the semi-enclosed lagoon of Flinders Reef (located in oceanic waters 150 km off the GBR in the Coral Sea), which was interpreted in the context of interdecadal climate variability influencing lagoonal flushing by trade winds (Pelejero et al. 2005). Contrary to results from laboratory experiments, calcification in this coral remained unrelated to variation in aragonite saturation and pH within the lagoon of Flinders Reef had no apparent effect on calcification (Pelejero et al. 2005). However, the reconstruction is based on a single coral core in a semi-enclosed environment, thus limiting generalisations about effects of variations in seawater pH on calcification and on processes in more open regions like the GBR. Indeed, the variation among the temporal profiles of individual colonies suggests that the observed changes in calcification may not have been detected without the substantial number of colony replicates used in this study.

Since data on aragonite saturation for the GBR are lacking, it is not possible to determine whether the observed decline in calcification was due to changes in seawater chemistry. However, the atmospheric concentration of CO_2 at Mauna Loa, Hawaii, was 351.44 ppm in 1988 increasing to 375.61 ppm in 2003 (Keeling and Whorf 2005) representing an increase of 6.4% (0.40% yr^{-1}) over the study period. Assuming a Ω_{arag} of 4.0 in 2003 (Kleypas et al. 1999), the increase in atmospheric CO_2 corresponds to an approximate Ω_{arag} of 4.26 in 1988, equivalent to a 6.1% decline in saturation. Experimental evidence suggests the relationship between coral calcification and aragonite saturation is linear (Marubini and Thake 1999; Langdon et al. 2000; Leclercq et al. 2000; Schneider and Erez 2006) although some have reported nonlinear responses (Gattuso et al. 1998; Ohde and van Woesik 1999). Nevertheless, the 21% decline in coral calcification presented here is 3.5-fold greater than is predicted from laboratory studies. The discrepancy between these results and the laboratory and mesocosm studies suggests the existence of some other factors or synergistic mechanisms contributing to the observed decline in coral growth.

Growth records from long cores of massive *Porites* showed that mean calcification was ~4% higher in the 50 year period from 1930 – 1979 compared with the previous 50 years (i.e. 1880 – 1929) (Lough and Barnes 1997). It was suggested that calcification in some corals might, at least initially, increase with rising SST (Lough and Barnes 2000; Carricart-Ganivet 2004) and air temperature (Bessat and Buigues 2001). Up to 1982, there was no evidence of a size or age dependent decline in calcification rates in long cores spanning several centuries of growth (Lough and Barnes 1997). We found a decrease in calcification for the subsequent period between 1988 until 2003, despite a concurrent average SST increase of 0.024 ± 0.017°C yr^{-1} on the GBR. This suggests that calcification rates in massive corals have decreased in response to changing environmental conditions since the studies by Lough and Barnes (1997, 2000) were completed.

The synergistic effects of elevated seawater temperatures and changing seawater chemistry on coral physiology have only recently gained attention. Calcification in *Stylophora pistillata* declined by 50% in experimental treatments of elevated seawater temperatures and pCO_2 (Reynaud et al. 2003). The long-term effects of the increasing frequency of mass bleaching events, coupled with changing seawater chemistry, on the growth rates of corals on the GBR are poorly understood, but the results of Reynaud et al. (2003) provide some insight to the patterns of decline reported here. A recent study suggested that coral calcification should have started declining due to a lowering of aragonite saturation (Kleypas et al. 1999). Here, it has not been possible to assess the observed decline in calcification rates in massive *Porites* in the context of changes in aragonite saturation state as these data are not available for the GBR. However, the existence of a 21% decline in coral calcification in the two study regions is of concern. Given the economic and ecological value of the GBR and other coral reefs around the world, the monitoring of pH and aragonite saturation, coupled with controlled experiments on synergistic effects of increasing SST and a range of water quality variables including aragonite saturation, are required to better understand the links between environmental change and their effects on coral growth.

Chapter 8.0 General discussion, conclusions and future research

8.1 Selecting candidate coral indicators

Coral reefs around the world are declining due to a range of natural and anthropogenic disturbances (Pandolfi et al. 2003; Wilkinson 2004). Changes in water quality due to terrestrial runoff are a significant threat to coral reefs in the coastal zone (Bell and Elmetri 1995; Haynes and Michalek-Wagner 2000; Alongi and McKinnon 2005; Fabricius 2005). The aim of this thesis has been to assess a range of coral indicators at different spatial and temporal scales and identify those most suitable for inclusion into a 'toolbox' for assessing the condition of coastal reefs particularly with regards to changing water quality on the GBR.

To aid selection of coral indicators, candidate indicators were assessed against the selection criteria in Chapter 1.2.2 and ranked at a scale of 1 to 5 determined from the sum of positive scores for each criteria (following Fabricius and De'ath 2004; Table 8.1). Response time was excluded from the scores as it was considered that both rapid and slower responding indicators could provide useful information in monitoring programmes, although this would depend on the question to be addressed. For example, an indicator with a long response time would be inappropriate for monitoring short-term disturbances, e.g. dredging operations. Indicators with a score ≥4 (of a maximum of 5) were 'highly recommended' for use in programmes to assess the effects of changing water quality on corals. An example of a high priority indicator was symbiont photo-physiology as responses of *Symbiodinium* are known to be rapid (e.g. minutes to days) and monotonic with increasing exposure to sedimentation and pollutants, and reduced irradiances under experimental (Philipp and Fabricius 2003; Negri et al. 2005; Ulstrup et al. 2006b; Weber et al. 2006) and field conditions (Chapter 3). Indicators that ranked 3 had a 'medium' level recommendation due to satisfying only some of the selection criteria. For example, lipid content provides valuable information on the energetic reserves of a coral that are fundamental for processes such as growth and reproduction (Anthony et al. 2002). However, lipid content varies naturally with reproductive cycles (Leuzinger et al. 2003), which has the potential to obscure responses to changing water quality. Indicators that ranked <2 may provide useful, often complimentary, information about the responses of corals to key stressors, but have a 'low' level of recommendation. Indicators that were highly recommended included symbiont photo-physiology, colony brightness, skeletal and tissue growth, and bioeroder density in massive *Porites*, coral recruitment, community structure of corals, indicator organisms other than corals and maximum depth of coral reef development. It has been beyond the scope of this study to examine responses in all these potential measures, thus coral recruitment, community structure of corals and indicator organisms other than corals are not discussed further.

Table 8.1. Assessment framework for identifying indicators of the effects of changes in water quality on coastal corals of the GBR. Indicators are assessed against the criteria defined in Chapter 1.2.2. Rank denotes the sum of positive scores when assessed against each criterion and determines the level of recommendation. Abbreviations: Med. = Medium; Rec. = Recommendation.

Response	Method	Response time	(1) Specificity	(2) Monotonic	(3) Variability	(4) Practicality	(5) Relevance	Advantages	Disadvantages	Rank	Rec.
Colony											
Symbiont photo-physiology	PAM fluorometry (Ralph et al. 2005; Chapter 3).	Immediate to days	Med. (+)	Yes (+)	High (-)	Yes (+)	High (+)	Provides a measure of sublethal stress.	Specialised tool, initial cost of equipment high but cost of measurements is low.	4	High
Colony brightness	Colour charts, spectrometry (Siebeck et al. 2006).	Weeks	Med. (+)	Yes (+)	High (-)	Yes (+)	High (+)	Simple method to quantify changes in pigment content and density of symbionts.	Background spatial and temporal variation in colour brightness need to be determined.	4	High
Colony brightness	Chlorophyll *a* extraction (Hoegh-Guldberg and Smith 1989).	Weeks	Med. (+)	Yes (+)	High (-)	No (-)	High (+)	Direct quantification of the concentration of photosynthetic pigment.	Natural variation, requires specialised equipment.	3	Med.
Colony brightness	Counts of symbiont density (Hoegh-Guldberg and Smith 1989).	Weeks	Med. (+)	Yes (+)	High (-)	No (-)	High (+)	Direct quantification of the number of symbionts within the coral.	Natural variation, method time consuming.	3	Med.
Lipid content	Gravimetric determination (Harland et al. 1992).	Weeks to Months	Med. (+)	No (-)	High (-)	Yes (+)	High (+)	Energy reserves are relevant for reproduction and growth.	Seasonal and intra-colonial variation, method time consuming.	3	Med.

Response	Method	Response time	(1) Specificity	(2) Monotonic	(3) Variability	(4) Practicality	(5) Relevance	Advantages	Disadvantages	Rank	Rec.
Skeletal and tissue growth	Calipers (Barnes and Lough 1992).	Weeks to months	Med. (+)	No (-)	Low (+)	Yes (+)	High (+)	Sublethal indicator of stress.	Natural variation, method is invasive.	4	High
Skeletal chemistry	Mass spectrometry (Hoegh-Guldberg et al. 2004)	Days to months	High (+)	Yes (+)	High (-)	No (-)	High (+)	High specificity, able to identify anthropogenic sources of nitrogen.	Specialised equipment and expertise required for analysis. Inter-specific variability requires further study.	3	Med.
Partial mortality	Visual estimate (Ginsburg et al. 2001, Nugues and Roberts 2003).	Days to months	Low (-)	Yes (+)	High (-)	Yes (+)	High (+)	Indicates stressors such as sediment accumulation.	Low specificity due to other factors, e.g. predation, grazing by fishes.	3	Med.
Population											
Macro-bioeroder density in living massive *Porites*	Quantify and identify macro-bioeroders in living *Porites* colonies (Hutchings and Peyrot-Clausade 2002).	Weeks to years	High (+)	Yes (+)	High (-)	Yes (+)	High (+)	Density of filter-feeding macro-bioeroders may reflect long-term changes in the load of suspended particles.	Experimental research is needed to test links between densities of specific macro-bioeroders groups and environmental conditions.	4	High
Population structure	Quantify colony size (Meesters et al. 2001).	Months to years	Med. (+)	Yes (+)	High (-)	Yes (+)	Low (-)	Provides information on processes such as reproduction.	Method may be time consuming.	3	Med.

Response	Method	Response time	(1) Specificity	(2) Monotonic	(3) Variability	(4) Practicality	(5) Relevance	Advantages	Disadvantages	Rank	Rec.
Coral diseases	Visual estimate (Bruno et al. 2003).	Weeks	Low (-)	Yes (+)	High (-)	Yes (+)	High (+)	Increased incidence of disease reflects levels of stress to corals.	Varies according to presence of pathogens, low specificity, expertise required.	3	Med
Community											
Larval supply	Quantify rates of larval settlement using settlement tiles (Babcock and Davies 1991).	Days to weeks	Med (+)	No (-)	High (-)	Yes (+)	High (+)	Changes in larval supply provide insight to the resilience and recovery potential of coral reefs.	Local patterns of reproduction in corals must be known. Larval supply variable, may not reflect condition at settlement site.	3	Med
Coral recruitment	Quantify juvenile densities (Smith et al. 2005).	Months to years	Med (+)	Yes (+)	High (-)	Yes (+)	High (+)	High applicability.	Time consuming.	4	High
Benthic cover	Line/point intercept transects (English et al. 1997).	Months to years	Low (-)	Yes (+)	High (-)	Yes (+)	High (+)	Traditional component of reef monitoring programmes. Simple, requires low skills base.	Low specificity.	3	Med.
Community structure	Taxonomic inventories (van Woesik et al. 1999, Fabricius et al. 2005, DeVantier et al. 2006).	Months to years	High (+)	Yes (+)	Low (+)	Yes (+)	High (+)	Provides indication of mortality of susceptible, which may pre-empt mortality of other corals.	Taxonomic expertise required.	5	High

Response	Method	Response time	(1) Specificity	(2) Monotonic	(3) Variability	(4) Practicality	(5) Relevance	Advantages	Disadvantages	Rank	Rec.
Indicator organisms other than corals	Changes in relative abundances or cover of organisms associated with coral reefs (Uthicke and Nobes 2008).	Months to years	High (+)	Yes (+)	Low (+)	No (-)	High (+)	Changes may pre-empt mortality of corals but only if indicator species are more sensitive to disturbance than sensitive corals.	Taxonomic expertise required.	4	High
Maximum depth coral reef development	Quantify transition zone of zooxanthellate to azooxanthellate community (Cooper et al. 2007).	Years (?)	High (+)	Yes (+)	Low (+)	Yes (+)	High (+)	Provides indirect measure water quality components that influence water clarity and hence lead to light limitation in zooxanthellate corals.	Limited by available settlement substrata, which also needs to be assessed.	5	High

8.1.1 Symbiont photo-physiology

Photo-physiological measures of *Symbiodinium* of *Pocillopora damicornis* differed significantly along an environmental gradient in the Whitsunday Islands (Chapter 3). Most photo-physiological parameters correlated with a water quality index, however, the direction of change varied depending on the depth of sampling suggesting contrasting photo-acclimatory mechanisms of shallow and deep corals. In shallow water, elevated heat dissipation as well as a decrease in PS_{max} suggested photo-inhibition possibly in response to increasing benthic irradiance along the gradient from nearshore to outer islands. In contrast, at the deep depth, photo-physiological patterns were consistent with patterns of light/shade acclimatisation (Falkowski and Dubinsky 1981; Kühl et al. 1995; Ralph et al. 2002; Anthony and Hoegh-Guldberg 2003b; Ulstrup et al. 2006b) where PS_{max} and E_k increased along the environmental gradient from nearshore to outer islands suggesting that deep corals on nearshore reefs in the Whitsunday Islands are light-limited.

Measuring changes in symbiont photo-physiology is considered a high priority indictor for use in water quality monitoring programmes (Table 8.1). Photo-physiological responses are known to be monotonic with increasing exposure to sedimentation and pollutants, and reduced irradiances under experimental (Marubini and Davies 1996; Philipp and Fabricius 2003; Negri et al. 2005; Weber et al. 2006) and field conditions (Chapter 3). Photo-physiological responses can be measured economically once the initial set-up costs have been covered. However, symbiont photo-physiology has only medium specificity to changes in water quality as some parameters (e.g. F_v/F_m) have been shown to decrease in response to sedimentation (Philipp and Fabricius 2003; Weber et al. 2006) but also following exposure to elevated sea temperatures (e.g. Ulstrup et al. 2006a). Notwithstanding this, photo-physiological responses are rapid (i.e. time-scales of minutes to days) making this measure particularly appropriate as a sublethal indicator to changes in water quality (Marubini and Davies 1996). Detailed observer training is required for the use of chlorophyll *a* fluorescence techniques and should include expert instruction in the use of PAM fluorometers as well as a theoretical understanding of the utility of rapid light curves. The application of PAM fluorometers as monitoring tools should, therefore, be restricted to specialists.

8.1.2 Colony brightness of massive *Porites*

The 1.4-fold decrease in colony brightness of massive *Porites* from nearshore to outer islands along the environmental gradient in the Whitsunday Islands was consistent with other studies of photo-acclimatisation to enhanced nutrients (Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989) and light limitation (Falkowski and Dubinsky 1981; Dubinsky et al. 1984). The response of colony brightness to changes in water quality was validated with manipulative experiments that showed nubbins of *Porites* were darker, i.e. colony brightness increased, when exposed to

elevated nutrients and reduced irradiances. On the basis of the field and manipulative studies (Chapter 5), and existing data (Falkowski and Dubinsky 1981; Dubinsky et al. 1984; Hoegh-Guldberg and Smith 1989; Muscatine et al. 1989), colony brightness of massive *Porites* demonstrates potential as a useful indicator for incorporation into a monitoring toolbox.

Measuring changes in colony brightness is considered a high priority indictor for use in water quality monitoring programmes (Table 8.1). Changes in colony brightness can be measured with simple tools (Siebeck et al. 2006 ; Chapters 5 and 6), with an alternative being reflectance spectrometry (Chapter 4), and responses can occur within several weeks of exposure to elevated nutrients and sediments (Hoegh-Guldberg and Smith 1989), making it a useful sublethal indicator. However, responses of coral colour are considered to have a medium specificity to changes in water quality given that coral brightness also varies with changes in light and temperature (Hoegh-Guldberg 1999) and seasonally (Brown et al. 1999; Fitt et al. 2000; Chapter 6) and these factors have to be controlled for when using colony brightness as an indicator of changing water quality. Although measurements of colony brightness can be done with colour charts, it would be prudent to standardise measurements among observers to reduce potential sampling errors, i.e. only measuring colour on the top/centre of colonies to reduce effects of spatial heterogeneity of the distribution of photosynthetic pigments (Ralph et al. 2005).

8.1.3 Skeletal and tissue growth of massive *Porites*

The surface rugosity decreased while the thickness of the tissue layer of massive *Porites* increased along the environmental gradient as nutrient and sediment levels decreased from nearshore to outer islands in the Whitsunday Islands. Under controlled experimental conditions, however, the tissue thickness of massive *Porites* increased when exposed to elevated nutrients in the form of suspended particulate matter in the laboratory (Chapter 4). The contrasting patterns between field and laboratory studies may be explained by contrasting responses to different components of water quality, i.e. sedimentation and turbidity. The increase in tissue thickness along the gradient from nearshore to outer islands was consistent with a response to elevated levels of sedimentation (Barnes and Lough 1999). However, the increase in tissue thickness noted in the laboratory experiments may have been due to increased particle feeding in the suspended particulate matter treatments (Anthony 1999; Anthony and Fabricius 2000). Nevertheless, the experiments demonstrated that tissue thickness is sensitive to changes in water quality despite differences in the direction of change of the response that depend on the nature of the stressor. Thus, results of the field and manipulative studies (Chapter 4) as well as existing data (Barnes and Lough 1992) show that skeletal and tissue growth characteristics of massive *Porites* should also be considered for a monitoring toolbox.

Measuring changes in skeletal and tissue growth is considered a high priority indictor for use in water quality monitoring programmes (Table 8.1). Skeletal and tissue growth characteristics of *Porites* are sensitive to changes in water quality, with tissue thickness increasing with exposure to nutrients and particulate organic matter (Barnes and Lough 1992) and declining with increasing exposure to sedimentation (Barnes and Lough 1999). Changes in skeletal and tissue growth can occur with a rapid response time of days to weeks following a change in water quality (Chapter 5). Such responses have been reported primarily for water quality as well as increases in seawater temperatures (e.g. Suzuki et al. 2003) indicating they have medium specificity as indicators. Sampling of tissue thickness and surface rugosity are low-cost, low-technology tools that are highly applicable by a range of personnel. Notwithstanding this, the thickness of the tissue layer can vary within a colony (Barnes and Lough 1992), so sampling must be standardised and replicates should be collected from the upper surfaces of colonies. Moreover, the sampling is intrusive so procedures that mitigate the effects of sampling on the source colony, e.g. plugging core-hole to facilitate regrowth of tissue, need to be considered.

8.1.4 Density of macro-bioeroders in living *Porites*

The 50-fold decrease in density of macro-bioeroders in living colonies of massive *Porites* at a deep depth (~6 m) along an environmental gradient from nearshore to outer islands in the Whitsunday Islands was indicative of increased particle loads on nearshore reefs (Chapter 5). Previous studies have suggested using macro-bioeroder densities and species composition as a potential indicator of changes in water quality on coral reefs (Rose and Risk 1985; Holmes et al. 2000; Hutchings and Peyrot-Clausade 2002). In Chapter 6, the density of macro-bioeroders was consistently greater at a coastal location than two mid-shelf reference locations but there was no significant response in bioeroder density to an acute change in water quality (i.e. a major flood event). This indicates that estimates of macro-bioeroder density have a slow response time to changes in water quality and suggests it would be an appropriate indicator of the chronic effects of water quality on coastal coral reefs.

Measuring changes in the density of bioeroders is considered a high priority indictor for use in water quality monitoring programmes (Table 8.1). Densities of macro-bioeroders have a high specificity to spatial differences in water quality and are thus an appropriate indicator of the chronic effects of water quality on coastal coral reefs (Chapter 6). Assessments of the abundance of bioeroders can be done with low-cost and low-technology equipment such as quadrats and transects making it a highly applicable tool. Currently, estimates of bioerosion are not a component of monitoring programmes on the GBR. The results of Holmes et al. (2000) have considerable merit and need to be examined for applicability on the GBR.

8.1.5 Maximum depth of coral reef development

The 5-fold increase of maximal depth of reef building corals along the environmental gradient from nearshore to outer islands in the Whitsunday Islands suggested that the lower edge of coral distribution may be determined by light availability despite the availability of suitable settlement substrata at deeper depths (Chapter 2). This finding was consistent with Yentsch et al. (2002) who showed the optical properties of the water column exert important controls on the extent and distribution of reef building corals and supports other studies that have shown strong correlations between the maximum depth of coral reef development and gradients in water quality in the central region of the GBR (Kleypas 1996; van Woesik et al. 1999).

Measuring changes in the maximum depth distribution of coral reef development is considered a high priority indictor for use in water quality monitoring programmes (Table 8.1). When evaluated with the assessment framework, this measure was considered to be of high specificity, economic and a practical indicator that provides a time-integrated estimate of changes in environmental conditions on coastal coral reefs. However, the response time of changes in the maximal depth distribution of reef building corals is unknown and requires further investigation. Assessments of the maximum depth of coral reef development can be done with low-cost and low-technology equipment making it a highly applicable tool. Some level of observer training will be required to identify and quantify the transition zone from zooxanthellate hard corals to azooxanthellate octocorals and sponges. This technique is best done using diver surveys and consideration should be given to a sampling protocol that incorporates replicate estimates from independent observers at the same site to account for potential observer bias. Changes in the lower depth distribution in corals may, therefore, be used as an indicator for changes in water quality, similar to the use of lower distribution limits of seagrasses as an indicator of estuarine health (e.g. Abal and Dennison 1996; Dennison and Abal 1999).

8.2 Conclusions

The research presented in this thesis has resulted in the recommendation of a suite of coral response measures to indicate changes in environmental conditions when considered as a change in water quality. Each of the measures proposed, however, has a different sensitivity and specificity to changes in environmental conditions, thus combinations of these measures, i.e. a composite indicator system, is recommended for use in assessing the condition of coastal coral reefs of the GBR. For example, a conceptual model demonstrates that among the water quality specific indicators, few were found to be specific for nutrients, sediments or turbidity (Fig. 8.1). Increases in the photo-physiological parameter E_k, below which corals are light limited, are known for *Symbiodinium* (Anthony and Hoegh-Guldberg 2003b; Chapter 3), whereas exposure to sedimentation may lead to reductions in maximum quantum yield (F_v/F_m) (Philipp and Fabricius

2003; Weber et al. 2006). In contrast, exposure to elevated levels of nutrients, sediments and turbidity may lead to reduced juvenile densities, and changes in the community structure through the loss of susceptible species, resulting in decreased species richness and shifts to communities dominated by resilient coral species and macroalgae (van Woesik et al. 1999; Fabricius et al. 2005; DeVantier et al. 2006). Thus, changes in coral juvenile density, coral community structure and indicator organisms other than corals could potentially act as 'universal' indicators to changes in any of the key components of water quality (Fig. 8.1).

Photo-physiological measures of *Symbiodinium* of ***P. damicornis*** showed significant relationships to an environmental gradient in the Whitsunday Islands. Maximum quantum yield (F_v/F_m) decreases following exposure to sedimentation (Philipp and Fabricius 2003) and low irradiance (Anthony and Hoegh-Guldberg 2003b). PAR-absorptivity and quantitative parameters of rapid light curves including apparent photosynthetic rate, minimum saturating irradiance and light utilisation coefficient correlated strongly with water quality and/or light limitation (Hoegh-Guldberg and Smith 1989; Anthony and Hoegh-Guldberg 2003b; Uthicke 2006; Chapter 3). Importantly, photo-physiological stress to changes in water quality occurs on time-scales of minutes to days (Philipp and Fabricius 2003; Negri et al. 2005; Weber et al. 2006) and on this basis, it is likely to be the most appropriate 'early warning' indicator capable of quantifying a response to changes in water quality. Many of the colony parameters of ***P. damicornis*** and massive *Porites* also related significantly to an environmental gradient in the Whitsunday Islands. Manipulative experiments confirmed that colony brightness and tissue thickness of massive *Porites* respond to changes in water quality (Chapter 5). However, a 2.5-fold decrease in symbiont density of ***P. damicornis*** during the wet compared with the dry season, which in turn influenced colony brightness, was related strongly to seasonal changes in sea surface temperature (SST). Thus, effects of seasonal variation of a range of environmental parameters need to be considered if physiological measures such as colony brightness are used in water quality monitoring programmes (Chapter 6). The maximal depth of coral reef development can serve as a quite specific indicator of longer-term (chronic) exposure to water quality conditions on coral reefs provided the coral reef is not limited by settlement substrata (Titlyanov and Latypov 1991; van Woesik et al. 1999; Chapter 2). Similarly, densities of macro-bioeroders measured in living massive *Porites* are known to proliferate at locations where particulate organic matter are not limiting (Sammarco and Risk 1990; Hutchings and Peyrot-Clausade 2002). The latter two measures are likely to be the most specific indicators for chronic changes in water quality conditions. Thus, differences in the sensitivity and specificity (Fig. 8.1) of the indicators demonstrates that a composite indicator system using multiple coral indicators should be developed for assessments of coastal reefs on the GBR.

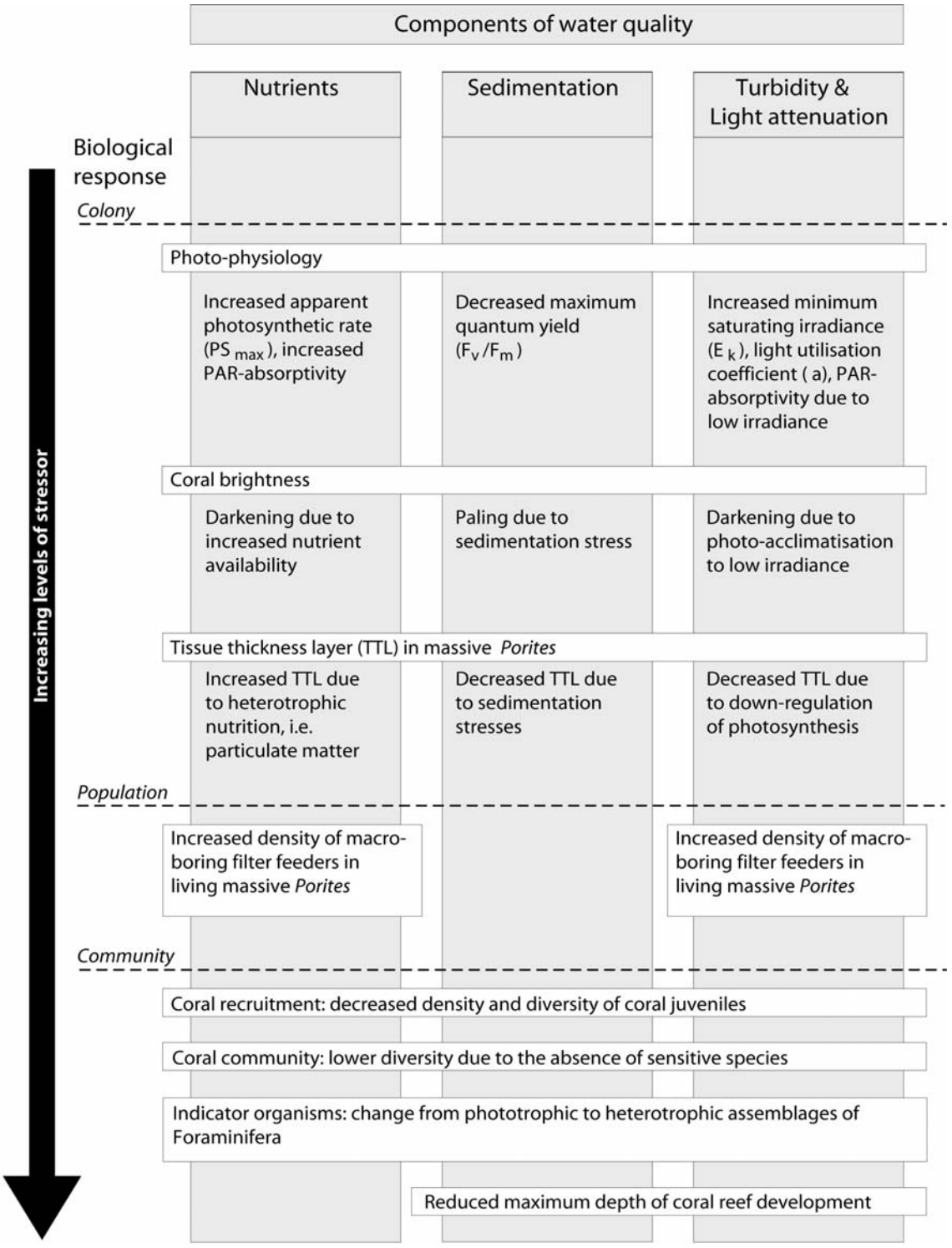

Fig. 8.1. Conceptual model of coral measures to indicate increasing exposure to the key components of water quality. Grey boxes indicate differences in response of the indicator depending on the type of stressor.

This thesis has demonstrated that it is improbable a single indicator exists that could sufficiently describe the condition of a coral reef given the wide variety of natural and anthropogenic influences that act on such complex ecosystems. Within this context, it is important to note that the selection of coral indicators will also vary depending on the specific objectives of different monitoring programmes. For example, the management goals related to a dredging operation that require information on biological responses to mitigate short-term effects on coral communities would be best served with sublethal indicators that have fast response times, e.g. symbiont photo-physiology or colony brightness. In the case of such acute disturbances, the exceedance of some pre-determined photo-physiological or color brightness threshold may trigger a management response that could be used to limit further adverse consequences to a coral community. In contrast, management goals investigating the biological consequences of improved land-use practices, and hence reduced terrestrial runoff, which may occur over time-scales of years, would be better served with indicators with slower response times that are used in conjunction with sublethal indicators to provide an early indication of ecological change. Thus, a composite of the most suitable indicators (e.g. Risk et al. 2001) incorporating responses from different ecological levels of organisation (i.e. colony to communities) has greater potential for success in assessment of the condition of coastal coral reefs. Such an approach has proved successful in evaluations of ecosystem health in estuarine and freshwater ecology, and the lessons learned there in the development of condition indices and predictive models show great potential for use on coastal coral reefs.

Temporal and spatial variation in the growth parameters skeletal density, linear extension and calcification rate in massive *Porites* from two regions of the GBR were examined over a 16 year study period. The temporal declines in the growth parameters were not explained by known regional differences in water quality (Fabricius et al. 2005). Mean annual SST increased by ~0.38°C in the two regions over the study period but calcification rates in massive *Porites* declined by ~21%, which contrasts with previous studies on the environmental controls on the growth parameters in massive *Porites* (Lough and Barnes 2000) and is unprecedented in recent centuries (Lough and Barnes 1997). Changes in the growth parameters were linear over time, while SST had no effect on skeletal density, but a modal effect on annual extension and calcification with maxima at ~26.7°C. Although the findings were consistent with studies of the synergistic effect of elevated seawater temperatures and CO_2 partial pressure (pCO_2) on coral calcification (Reynaud et al. 2003), data on seawater chemistry of the GBR are required to better understand the links between environmental change and effects on coral growth.

8.3 Future research

The focus of this thesis has been on identification and selection of coral indicators to changes in water quality. The challenge ahead will be to improve the understanding of patterns of variation and defining thresholds for the suite of indicators identified here. For example, further work is required to provide estimates of seasonal and temporal variability in symbiont photo-physiology on coastal coral reefs of the GBR. Few studies have examined the influence of nutrients on maximum quantum yield (F_v/F_m) and controlled dose-response experiments are required to validate results of the field correlations.

The maximal depth distribution of coral reef development has potential as a useful measure for monitoring the condition of coastal coral reefs on the GBR (Chapter 2). Comparisons of photo-physiological parameters of *Symbiodinium* found that corals occurring at deep depths on nearshore reefs of the Whitsunday Islands were limited by light availability (Chapter 3). Thus, measurements of the optical properties of the water column quantified by Secchi depth or light attenuation coefficients (Yentsch et al. 2002), combined with monitoring the depth of reef-building corals, should provide time-integrated information on strategies to improve water quality on the GBR. Further work is required to examine the relationship between water quality and the lower depth distribution of reef building corals in other regions of the GBR.

Currently, threshold levels of turbidity that result in stress responses for coastal corals are not well understood. Future research should focus on understanding the physiological, ecological and community responses to differing loads and duration of exposure to turbidity. A key review of the effects of sedimentation on coral reefs suggests background levels are characteristically <10 mg cm^{-2} d^{-1}, levels of 10 to 50 mg cm^{-2} d^{-1} have moderate to severe effects on corals, while severe to catastrophic effects may result from rates of >50 mg cm^{-2} d^{-1} (Rogers 1990). In Chapter 6, it was suggested that levels of turbidity >3 NTU at a shallow depth (~3.5 m) on a coastal reef can lead to conditions known to be light limiting, and hence sublethal photo-physiological stress, for *Symbiodinium* hosted by *P. damicornis*. At levels of turbidity of 4.5 NTU, approximately 6 – 8% of surface irradiance penetrates through the water column to the shallow benthic assemblage, which was determined as the critical level of irradiance required for coral reef development in the Whitsunday Islands. Further, there was complete extinction of benthic irradiance at this depth when turbidity exceeded 15 NTU. While previous studies have quantified the periodicity of turbidity events on coastal coral reefs (Anthony et al. 2004), determined the contribution of turbidity to variation in benthic irradiance (Anthony et al. 2004) and characterised the spatio-temporal variability of turbidity (Orpin et al. 2004), the study in Chapter 6 is the first to quantify a level of turbidity beyond which may represent photo-physiological stress to corals. Combining information from the photo-physiological study in Chapter 3 with data on levels of

irradiance required for reef building corals in Chapter 2, thresholds of turbidity are proposed whereby levels >3 NTU represent sublethal photo-physiological stress and >5 NTU for severe stress effects on *P. damicornis* at shallow depths (~3.5 m) on coastal reefs. It should be noted that these values will vary for corals acclimated to low irradiances at deeper depths. For example, an increase to 1.5 NTU may produce comparable light-limiting conditions for a coral at 7 m as does an increase to 3 NTU at 3.5 m. Further work is required to understand the physiological responses of other coral species to changes in turbidity.

Combining even the best case scenario of projected climate change of the IPCC (2007) (temperature increase of ~1.8°C; CO_2 increase to 600 ppm by 2100) with known environmental controls on coral growth (Hoegh-Guldberg 1999; Kleypas et al. 1999; Lough and Barnes 2000; Hoegh-Guldberg 2005) provides a disturbing outlook for coral reefs. Increasing concentrations of atmospheric CO_2 result in changes in seawater chemistry and the acidification of surface ocean waters (Kleypas et al. 1999; Caldeira and Wickett 2003). Recent predictions suggested that carbonate concentrations in tropical surface waters have already declined compared with pre-industrial levels (Orr et al. 2005). Several studies have argued that changes in SST and seawater chemistry have already had adverse effects on coral calcification (Kleypas et al. 1999; Hoegh-Guldberg 2005), but until now, data from long-term studies in the field have been lacking. The findings of Chapter 7 are both pivotal and concerning. The decline in coral calcification of ~21% over the past 16 years coincided with an increase of ~0.38°C in SST on the GBR. A decline of this nature with rising SST is unprecedented in recent centuries based on analysis of growth records from long cores of massive *Porites* (Lough and Barnes 1997). Whilst this may be the first evidence of the synergistic effects of rising SST and CO_2 partial pressure (pCO_2) on corals of the GBR, manipulative experiments are required to determine the relative contribution of these factors to declines in coral calcification. The focus should be on studies that investigate the responses, adaptation and consequences of corals and coral reefs exposed to changing environmental conditions including water quality, SST and seawater chemistry. The key question will be whether corals can respond and adapt at a rate comparable to the rate of environmental change forecast during this century.

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